Avian Responses to Predator Communities in Fragmented, Urbanizing Landscapes

DISSERTATION

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By

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Abstract

Behavioral responses to predators during the breeding season can critically affect the nest success of songbirds. However, the ability of birds to modify behavior based upon perceived and actual predation risk at multiple spatial scales (e.g. local (within-site), site, and landscape) and in novel (e.g., urban) environments remains poorly understood. In this dissertation, I explored how information about predation risk influenced the nest-site selection and nestling provisioning behavior of two species of songbirds – northern cardinals (*Cardinalis cardinalis*) and Acadian flycatchers (*Empidonax virescens*), which are two relatively common forest songbirds of eastern North America with contrasting responses to urbanization. I studied the use of information regarding predation risk and behavioral responses of birds during the 2006-2010 breeding seasons at riparian forest sites within the urbanizing landscapes of central Ohio. Specifically, I investigated the following questions: 1) how do cardinals and flycatchers choose nest locations based on information about local-scale nest predator activity patterns, 2) do cardinals and flycatchers incorporate private (i.e. detectable information only known to the individual) and public (i.e. detectable information known to all individuals) information about predation risk in nest-site selection, and 3) are provisioning rates to nestlings adjusted relative to public information about site-level predation risk?

To assess the relationship between selection of nest locations and information regarding local-scale nest predator activity, I used cardinal and flycatcher nest location data collected from sites during the 2008-2010 breeding seasons. I created utilization distributions from mapped predator locations at each site and overlaid them with nest locations to determine the corresponding probability of predator activity. Initially, I predicted that nest survival would be negatively related to the level of predator activity in an area. Consequently, birds would avoid locating nests in areas of high nest predator use, particularly if the animal was a dominant nest predator. My results suggest that both species avoided nesting in areas of high nest predator activity, which was consistent with the finding that nest survival declined as predator activity increased at local spatial scales. These findings provide evidence that both cardinals and flycatchers use public information of nest predator activity at local spatial scales.

Because birds are not limited to public information about predators, I also studied the use of private information reflecting prior experience of individuals with predators (i.e., fate of previous nest attempts). I predicted that birds would use private information regarding previous nest fates in addition to public information about site level predation risk. From 2006-2010, I evaluated the changes in nest-site characteristics between successive nest attempts within each breeding season for both species. Cardinals appeared to use both public and private information when selecting nest sites, and seemed to rely heavily on actual predation risk, but the flycatcher used neither. The contrasting responses of the two species suggest differences in behavioral plasticity that may be related to their sensitivity to urban areas.

To evaluate how songbirds used site-level public information about predation risk in caring for young, I observed how cardinals provisioned nestlings at nests during the breeding seasons of 2008-2010. By using video cameras to document parental feeding rates, predator surveys to estimate perceived risk, and nest survival rates to calculate actual risk, I found no evidence that cardinals used information about either type of risk to make decisions about provisioning. Furthermore, provisioning rates were not related to nest fate. If provisioning rates do not influence predation, then cardinals may not need to adjust the frequency with which they feed young in response to predation risk.

In conclusion, the ways that birds used information about predation risk varied with species, type of behavior, and the scale of information. Cardinals incorporated local scale information about predator activity, previous nest fate, and at times, actual predation risk at the site scale, to modify nest-site selection. They demonstrated sensitivity to information at multiple scales and an apparent ability to adjust nesting behaviors in ways that may allow them to thrive in urban areas. On the other hand, flycatchers used only local-scale predator activity information in selecting nest-sites, were less responsive to site-scale information, but likely recognized and responded to predator information or other cues of habitat quality at the landscape level when making breeding decisions. Both songbird species exhibited more cautious breeding behaviors when faced with certain types of predation risk, but seemed sensitive to the scale of predator information in choosing to do so. Thus, differences in use of information about predation risk may reflect constraints on the relative behavioral flexibility of cardinals and flycatchers. Not only does this study reveal ways in which behavioral plasticity can vary between songbirds with different affinities for urbanizing landscapes, but also illuminates the importance of studying various scales and types of information in evaluating songbird responses to predators.

Dedication

To my family,

And of course, the birds

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Publications

Rodewald, A. D. and **L. J. Kearns**. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. Condor 113:899-906.

McShea, W. J., C. M. Stewart, **L. J. Kearns**, and S. Bates. 2011. Road bias for deer density estimates at two national parks in Maryland. Wildlife Society Bulletin 35:177-184.

Rodewald, A. D., **L. J. Kearns**, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecological Applications 21: 936-943.

McShea, W.J., C. M. Stewart, **L. J. Kearns**, S.Liccioli, and D. Kocka. 2008. Factors affecting autumn deer-vehicle collisions in a rural Virginia county. Human-Wildlife Conflicts 2:110-121.

Kearns, L. J., E.D. Silverman, and K.R. Hall. 2006. Black-throated Blue Warbler (*Dendroica caerulescens*) and Veery (*Catharus fuscescens*) abundance in relation to understory composition in northern Michigan forests. Wilson Journal of Ornithology 118:461-470.

Van Alstyne,K.L, J.J. McCarthy III, C.L. Hustead, and **L. J. Kearns**. 1999. Phlorotannin allocation among tissues of Northeastern Pacific kelps and rockweeds. Journal of Phycology 35:483-492.

Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1: Introduction

Predator-prey dynamics are a critical part of ecosystem function through both lethal and non-lethal effects. Mortality due to predation was once thought to be the simple explanation for many well-known predator-prey cycles, but recent studies indicate that behavioral responses of prey to predation risk may better explain these patterns (Peckarsky et al. 2008). The effects of predation risk, known as non-lethal effects (Lima 1998, Schmitz et al. 2004, Preisser et al. 2005, Cresswell 2008), can profoundly impact populations, trophic dynamics, and other elements of ecosystems (Brown et al. 1999, Terborgh 2001, Ripple and Beschta 2003, 2004, Brown and Kotler 2007, Preisser and Bolnick 2008, Schmitz 2008). Some specific outcomes of non-lethal effects include the alteration of the rates of prey dispersal or movements across a landscape (Laundre et al. 2001, Zollner and Lima 2005), changes in the size of flocks/groups and the competitive interactions within those groups (Bednekoff and Lima 2004), and modifications in the physiology of organisms such that the amount or type of sleep that an animal experiences is different (e.g. Rattenborg et al. 1999). Therefore, understanding non-lethal effects of predation can reveal important dynamics among species and populations inhabiting all types of ecosystems.

Predation risk can be particularly important for songbirds making breeding decisions, since predation is the leading cause of mortality for eggs and nestlings

(Ricklefs 1969, Martin 1993). As such, information about predation risk is expected to influence choice of breeding habitats and territories. For example, territory selection may be influenced by predation risk at local scales (i.e., within a site, as with a nest patch) even more strongly than other information about landscape-level habitat quality (Chalfoun and Martin 2007). Predation can also influence nest-site selection (e.g. Martin and Ghalambor 1999, Fontaine and Martin 2006b). For example, birds may alter their selection of nest-site characteristics known to affect nest survival rates and productivity (e.g. Martin and Roper 1988, Hazler et al. 2006, Johnson 1997) in response to the level of predation risk (Knight and Fitzner 1985, Forstmeier and Weiss 2004, Eggers et al. 2006, Peluc et al. 2008). In addition, birds may abandon nests if they sense that the risk is too high (e.g. Berger-Tal et al. 2010). Fear of predators can also affect parental care behaviors during incubation and nestling phases, such as the amount of time the adult(s) incubate the nest (e.g. Fedy and Martin 2009), the rate at which the male will feed an incubating female (Martin and Ghalambor 1999, Ghalambor and Martin 2000, Ghalambor and Martin 2002, Fontaine and Martin 2006b), and nest defense (Caro 2005, Fedy and Martin 2009). Skutch (1949) hypothesized that birds would reduce nest provisioning rates in the face of greater danger, and indeed, birds do modify nest visitation rates in response to predator presence (Caro 2005, Eggers et al. 2005, Peluc et al. 2008, Lima 2009, Thomson et al. 2010). When Fontaine and Martin (2006a) experimentally decreased the number of predators (e.g. red squirrels (*Tamiasciurus hudsonicus*), Stellar's jays (*Cyanocitta stelleri*), and gray-collared chipmunks (*Tamias* *cinereicollis*)) in their study area, birds provisioned nests at higher rates, as well as had larger egg sizes and clutch masses than when predators were more abundant.

With the numerous changes to ecosystems and communities influenced by anthropogenic changes, however, it is not well known how songbirds may adjust behavioral responses to predators. Because both the distribution and abundance of birds and their predators typically change with urbanization (Bessinger and Osborne 1982, Blair 1996, Sorace 2002, Sinclair et al. 2005, Randa and Yunger 2006, Rodewald and Bakermans 2006, Sorace and Gustin 2009, Rodewald et al. 2011), changes in the interactions between songbirds and their nest predators seem likely as well. For predators, greater food availability in urban areas can lead to prey-switching, alterations in activity patterns, or changes in foraging strategies that ultimately may affect encounter rates with songbird nests (Prange et al. 2004, Ditchkoff et al. 2006, Stracey 2011). For songbirds, increases in anthropogenic food sources, noise pollution, and human activity can alter a wide suite of behaviors such as vigilance, foraging, flocking, singing, and aggression (e.g. Valcarcel and Fernandez-Juricic 2009, Halfwerk et al. 2011, Saggese et al. 2011, Scales et al. 2011), which in turn may influence reactions to predators and perceived risk. Collectively, these studies are beginning to reveal behavioral patterns of songbirds in urban environments, but more research is needed to better elucidate how urbanization affects predator-songbird dynamics and modifies the role of non-lethal effects in ecosystems.

In assessing songbird responses to risk in urban environments, the first step is to evaluate the types of information (i.e., facts received by an individual to improve fitness) about predators. Biological information is composed of two main types of information – genetic and non-genetic. The non-genetic information, also known as "detectable information", is able to be directly sensed by an individual from the environment, and is easily measured in a field setting. Information ecologists define two types of "detectable information", where "public information" includes information in the environment such as cues and signals that are available to all individuals, and "private information" is only known to an individual by its own experiences (Wagner and Danchin 2010). Types of public information used by songbird prey to assess risk include the abundance, activity, and behavior of predators. Songbirds can detect this information through visual, olfactory, or auditory cues (Caro 2005). For example, songbirds can visually distinguish individual predators (Ghalambor and Martin 2002), or exhibit increased vigilance when exposed to olfactory cues from the feces of mammalian predators (Roth et al. 2008a), or become silent when they hear the alarm calls of conspecifics (Bednekoff and Lima 2005 (juncos, *Junco hyemalis*), Roth et al. 2008b (finches, *Carpodacus mexicanus*)). Private information, including memory, is also used by prey to assess risk and respond. For example, the strength of a memory about a predator depends on the level of negativity of any previous experience, and this in turn influences the response of an individual when it encounters that same predator again (Ferrari et al. 2010). Understanding the types of information used by songbirds to make decisions related to breeding will help elucidate any changes to predator-prey dynamics found in urban ecosystems.

The main objective of my research was to determine how songbirds incorporated different types of detectable information about predation risk into breeding season behaviors. In addition, I evaluated the effectiveness of those responses to nest fate and nest success, and how those responses might change over a rural-urban gradient or for birds with different adaptabilities to urbanization. I examined both public and private detectable information about predation risk and how two breeding songbirds, the northern cardinal (*Cardinalis cardinalis*), common to urban areas, and the Acadian flycatcher (*Empidonax virescens*), less frequent in urban areas, used this information when choosing nest-sites and provisioning young. In chapter 2, I evaluated the use of local-scale public information of nest predator movements by cardinals and flycatchers in selecting nest locations within riparian forests in urbanizing landscapes. In chapter 3, I studied how predator information might drive decisions about nest placement, focusing specifically on how nest characteristics changed between successive nest attempts of individual breeding pairs. Finally, in chapter 4, I compared how actual and perceived predation risk informed cardinal decisions about nestling provisioning (i.e., feeding). In addition, I tested how provisioning rates might affect nest fates, as visitation rates to the nest may influence the likelihood of nest predation. These studies contribute to our growing understanding of how songbirds respond to predation risk, which types of information are most likely to be used, and how the relationships between predation risk and breeding behavior may change in urban environments or among species with different distribution patterns in more developed habitats. Overall, this will contribute to knowledge of non-lethal effects and predator-prey dynamics in urbanizing landscapes.

Chapter 2: Does Nest Predator Activity Predict Location and Survival of Nests in Urbanizing Landscapes?

Abstract

Choice of nest location is one strategy that songbirds can use to avoid nest predation, and may be informed by local-scale nest predator activity patterns. I investigated the distribution and daily survival rates of nests of northern cardinals (*Cardinalis cardinalis*) and Acadian flycatchers (*Empidonax virescens*) in 13 riparian forests in central Ohio, 2008-2010. Because diurnal predators cause >70% of the songbird nest depredations in the study system, I mapped the diurnal locations of nest predators within a 2-ha grid at each site and created utilization distributions of both mammalian and avian predators, and specifically brown-headed cowbirds (*Molothrus ater*) and blue jays (*Cyanocitta cristata*). For each cardinal (N = 334) and flycatcher (N = 60) nest location, I determined the corresponding probability of use by mammalian and avian nest predators for that site and year. Both predator activity and time of season predicted cardinal nest survival, which most strongly decreased with increasing avian predator activity ($R^2 = 0.179$). Nevertheless, cardinals most strongly avoided nesting in areas used by mammalian predators and blue jays, the latter of which is also not a common nest predator. Predator activity also predicted daily survival rates of flycatcher nests, which were less likely to survive in areas frequented by avian predators. Consistent with this, flycatchers built nests in areas with lower predator activity and tended to avoid areas with high activity of cowbirds, a dominant nest predator and brood parasite. The concordance of data on nest placement, predator activity, and nest survival suggests that flycatchers, and to some degree, cardinals use local-scale information on predator activity in nest site selection.

Keywords: songbird, predator, nest survival, nest location, urbanization, utilization distribution

Introduction

Although birds are thought to assess predation risk when deciding where to place nests or locate breeding territories (Eggers et al. 2006, Morosinotto et al. 2010, Chalfoun and Martin 2010a, Parejo and Aviles 2011), the types of information used to evaluate predation risk remain poorly understood. Both private information, based on an individual's own experience, and public information, which is available to all individuals, can influence prey behaviors (Lind and Cresswell 2005, Wagner and Danchin 2010). Perceived and actual predation risk, both of which are types of public information, can affect anti-predator responses in prey (Forstmeier and Weiss 2004, Ghalambor and Martin 2000, Ghalambor and Martin 2002, Eggers et al. 2006, Fontaine and Martin 2006b, Peluc et al. 2008, Emmering and Schmidt 2011). When making breeding decisions, songbirds also respond to other indicators of risk such as alarm calls of other species, scent trails of predators, and nest predation rates (Bednekoff and Lima 2005, Roth et al. 2008a, Schmidt et al. 2008, Schmidt and Whelan 2010). Predator activity and movement patterns may be a better predictor of the risk to nests than some of these other information types (e.g. Lima 2002, Marzluff et al. 2007, Schmidt and Schauber 2007), but this has yet been shown to be common across avifauna.

Spatial scale is also an important aspect of how prey receive and interpret information about predators because both predators and prey can operate across a range of scales (Fauchald et al. 2000, Chalfoun et al. 2002, Lloyd et al. 2005, Schmidt et al. 2010). While individuals use information from multiple spatial scales to select habitat or to place nests (Luck 2002, Part et al. 2011), recent evidence suggests that prey are both better informed and more responsive to predator activity at the nest-patch and nest substrate levels (e.g. Lima 2002, Chalfoun and Martin 2007, Marzluff et al. 2007, Schmidt and Schauber 2007).

In urbanizing areas, changes in avian communities, predator communities, and vegetation structure also occur at multiple spatial scales (e.g. Chace and Walsh 2006). Hence, urban systems provide an excellent opportunity to examine potential use of predator information at various spatial scales and the consequences to songbird nest survival. Among species that commonly depredate songbird nests, including raptors, corvids, mammalian mesopredators, rodents, and snakes (Stake et al. 2004, Weidinger 2009, Benson et al. 2010, Rodewald and Kearns 2011, Cox et al. 2012), many are positively associated with urbanization (e.g. Prange et al. 2003, Prange and Gehrt 2004, Chace and Walsh 2006, Sorace and Gustin 2009, Stout and Rosenfield 2010). Such burgeoning densities of generalist predators are often attributed to the widespread availability of anthropogenic food sources such as trash and bird feeders (Prange et al. 2004, Chace and Walsh 2006, Shochat et al. 2006). Although recent work suggests that abundant predators in urban systems do not necessarily impose higher rates of predation on breeding birds at the site- or patch-scale (Rodewald et al. 2011), there remains the possibility that birds may respond strongly to the presence and/or activity of predators at these scales. Indeed, non-lethal effects from predator presence are known to have powerful influences on the behavior of prey (e.g. Ripple and Beschta 2004, Salo et al. 2008) and could contribute to declines in certain sensitive birds.

Predator communities in urban areas can be more diverse or change with respect to dominant predators compared to rural areas (Sorace and Gustin 2009, Rodewald and Kearns 2011). Therefore, testing how the identity of specific predators might inform prey behavior is also important for understanding responses to predation risk. Indeed, some studies have shown that breeding birds will respond to specific predators (Ghalambor and Martin 2000, Ghalambor and Martin 2002, Schmidt and Whelan 2005, Schmidt et al. 2006). In an urban area with a diverse community of predators, however, elucidating if songbirds respond to specific predators can help determine whether management strategies should be targeted at individuals or at groups of species. If not cueing into specific predators, songbird prey may be more likely to discriminate response behaviors based on hunting strategies of predators, such as avian predators with visual search strategies or mammalian predators with olfactory search strategies (but see Lima and Dill 1990, Lima and Bednekoff 1999, Ghalambor and Martin 2002).

In this study, I examined how local scale (i.e., within-site) patterns of predator presence and activity predicted nest-site selection and daily survival rates of two common songbird species with different affinities for urban environments, the northern cardinal (*Cardinalis cardinalis*) as an urban adapter, and the Acadian flycatcher (*Empidonax virescens*) as an urban avoider. I predicted that songbirds would build their nests in areas with a lower, and presumably safer, level of diurnal predator activity, and that daily survival rates of nests built in areas of lower predator activity would be higher. Although relative abundance of nest predators is known to be greater in urban than rural landscapes in my study system (Rodewald et al. 2011), both nest survival and post-fledging rates of cardinals and flycatchers are comparable across the urban to rural gradient (Ausprey and Rodewald 2011, A. Rodewald unpublished data). Songbirds, however, may perceive elevated predation risk due to the greater nest predator activity in urban areas, and consequently choose to nest in areas with lower predator activity. Although nests of both species are depredated by a wide variety of nest predators, diurnal predators are responsible for over 70% of nest failures (Rodewald and Kearns 2011). Given the high diversity of nest predators in this environment, I would expect less avoidance of specific predators than diurnal predators in general, unless specific predators were responsible for a larger percentage of nest depredations.

Methods

Study Area

From April – August 2008-2010, cardinals and flycatchers were studied at 13 riparian forest sites varying in widths between 104-277 m and distributed throughout Columbus, Ohio, USA, and vicinity. Forest sites were surrounded by a gradient of urban development, which was characterized by an urban index based on the amount of forest, agriculture, paved areas and numbers of buildings (Rodewald and Shustack 2008a). Common overstory trees in the study sites included sycamore (*Platanus occidentalis* L.), cottonwood (*Populus deltoides* Bartram ex Marsh.), silver maple (*Acer saccharinum* L.), sugar maple (*Acer saccharum* Marsh.), black maple (*Acer nigrum* Michx. f.), Ohio buckeye (*Aesculus glabra* Willd.), honeylocust (*Gleditsia triacanthos* L.), American elm

(*Ulmus americana* L.), black walnut (*Juglans nigra* L.), and ash (*Fraxinus* spp.). The understory was primarily composed of native species such as boxelder (*Acer negundo* L.), pawpaw (*Asimina triloba* (L.) dunal), sugar (*A. saccharum* Marsh.) and black maple (*A. nigrum* Michx. f.) saplings, spicebush (*Lindera benzoin* (L.) Blume), and exotic shrub species, including the Amur honeysuckle (*Lonicera mackii* (Rupr.) Herder) and multiflora rose (*Rosa multiflora* Thunb.). Avian community structure was strongly associated with the amount of urbanization in the surrounding landscape matrix (Rodewald and Bakermans 2006). Common avian nest predators at the sites included blue jays (*Cyanocitta cristata*), American crows (*Corvus brachyrhynchos*), barred owls (*Strix varia*), red-shouldered hawks (*Buteo lineatus*), red-tailed hawks (*Buteo jamaicensis*), broad-winged hawks (*Buteo platypterus*), Cooper's hawks (*Accipiter cooperii*), common grackles (*Quiscalus quiscala*), and brown-headed cowbirds (*Molothrus ater*). Common mammalian species at the sites included northern raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), red foxes (*Vulpes vulpes*), eastern chipmunks (*Tamias striatus*), eastern gray (*Sciurus carolinensis*), fox (*Sciurus niger*), and American red squirrels (*Tamiasciurus hudsonicus*), domestic dogs (*Canis familiaris*), and domestic cats (*Felis catus*).

My study focused on cardinals and flycatchers, not only because of their different responses to urban conditions, but because they are multi-brooded species and their nests are relatively easy to find. In my study system, cardinals breed from April through September and flycatchers from May through August. Both species build nests at a variety of heights (cardinals, 0.5 – 18 m, flycatchers, 2 – 15m) in nest plants including

Amur honeysuckle, multiflora rose, boxelder, and maple saplings. Cardinals complete the nesting cycle from clutch completion to fledging in about 22 days, and flycatchers complete the cycle in about 28 days. Both cardinals and flycatchers usually renest quickly after a nest failure, but if the nest fledges young, the time to renest can vary from immediately to a few weeks later.

Field Methods

I searched for and monitored cardinal nests every 2-4 days at each site. I determined if a nest had successfully produced young by looking for signs of fledglings (e.g. feces under nests, adults chipping, adults carrying food, or begging calls near nest area) around the expected fledge date. If there were no signs of success, I monitored the nest area for up to three more visits to determine if any fledges could be found. Once nests failed or fledged, I searched for any renests. I marked the locations of each nest using a GPS unit (Garmin GPS 12 or DeLorme Earthmate PN-40), typically within an error margin of 5-10m.

To assess activity patterns of nest predators, trained observers mapped locations of predators within a 2 ha grid at each site whenever searching for and monitoring nests (usually three times a week) from April through August between 6am and 2pm. I refer to this technique as the ‘incidental mapping’ technique. Trained observers also conducted spot maps ten times from early May through early July to survey the breeding bird community, but also recorded any mammalian species seen during that time. For each spot map, I mapped species observed by sight and sound for a period of 45 minutes to an hour as I traversed the grid via 50 m markers. All observers wore camouflaged clothing and walked quietly and slowly throughout the study site to minimize effects on wildlife movements.

Data Analysis

At the end of each field season, I downloaded the GPS points of nests and transformed projections as necessary to the North American Datum 1983, Universal Transverse Mercator Zone 17 North. From the gridded maps used to record predator locations during incidental mapping and spot mapping, I digitized predator locations using ArcMap 9.3 at a ratio of 1:1000. I pooled predator detections into diurnal avian (blue jays, crows, grackles, and cowbirds) and diurnal mammalian (chipmunks and squirrels) predators, which depredate approximately 44% and 10% of forest songbird nests in my study system, respectively (Rodewald and Kearns 2011). I excluded diurnal predators such as raptors (16% of predations) because their territories are usually much larger than 2 ha and therefore not observed frequently enough to document activity patterns. I also excluded gray catbirds (*Dumetella carolinensis*) and house wrens (*Troglodytes aedon*), which account for 6% of diurnal nest predations, but may depredate nests for reasons other than predation (e.g. competition). Due to a lack of a priori knowledge of the temporal scales over which birds perceive and respond to predation risk (Lima and Bednekoff 1999), I pooled predator detections across the season. I generated kernel density estimates of predator activity using the least squares cross validation in the kernel function in the Animal Movement extension in ArcView 3.2. If sites had < 10 observations for each predator group, I omitted them from the analysis. I transformed the kernels into probability density functions and then utilization distributions (Worton 1989, Marzluff et al. 2007). I overlaid nest locations on the probability density functions to assign relative values of predator activity at each nest for each predator group at each site (Geospatial Modeling Environment; Beyer 2011). I used the same procedure to quantify activity patterns of brown-headed cowbirds, the most dominant nest predator in my system (18% of nests), and blue jays, a less dominant nest predator (5% of nests) (Rodewald and Kearns 2011).

At least 30-50 points are recommended to create utilization distributions (Seaman et al. 1999). For this reason, I combined observations from incidental maps as well as the spot maps to maximize sampling points. To verify that incidental and spot maps of predators were comparable, I intersected the incidental and spot map probability density functions for each site and predator type, and then calculated the volume of intersection of the probability density functions (after Marzluff et al. 2007). The volume of intersection was approximately 80% for 2010 data, indicating that the two methods of data collection produced comparable results.

To determine if cardinals and flycatchers were avoiding areas of high predator activity, I first verified that the distribution of the values of predator activity around the nests were independent of the distribution of the probability density functions themselves. To do this, I compared the frequency distributions of the predator activity around the nests with the probability density functions of avian predator activity and mammalian predator activity using a G-test. I then used pooled t-tests to compare the probability values of the different types of predator activity around cardinal and flycatcher nests to determine which predators were more strongly avoided. I used the same procedure to compare how predator activity around nests differed between cardinals and flycatchers. Small sample sizes and non-normal distribution of data necessitated use of a Wilcoxon-Mann-Whitney U test for cowbird and blue jay predator activity for the flycatcher.

Using the logistic exposure method for calculating daily survival rates of nests (Shaffer 2004; PROC GENMOD, SAS 2011, Ver. 9.2), I developed a set of 18 models representing alternative hypotheses to explain nest survival. Though my primary interest was in understanding the relationship between nest survival and predator activity (birds and mammals), I had to account for other factors known to affect nest survival, including seasonal changes in nest survival (i.e., nest initiation date; Rodewald et al. 2010) and the amount of urbanization in the surrounding landscape (Table 2.1).

Results

Nest Location

The frequency distribution of cardinal nests differed significantly from the frequency distributions of the combined probability density functions for both avian and mammalian predators from all sites and years ($G_{avian} = 347.35$, $p < 0.001$, Figure 2.1; $G_{mammalian} = 252.43$, $p < 0.001$, Figure 2.2). Cardinals built nests in areas that were within the lower 50% quartile of predator activity (Figure 2.3). Overall, nests were located in areas with less mammalian activity than avian predator activity ($t_{1,333} = -4.26$, $p < 0.001$). Interestingly, cardinals more strongly avoided high use areas of blue jays than brown-headed cowbirds, even though the cowbird is a more dominant nest predator ($t_{1,438} = -2.04$, $p = 0.04$).

The frequency distribution of flycatcher nests was similar to the frequency distribution of the combined probability density functions from all sites and years for avian predators, but was significantly different for mammalian predators ($G_{avian} = 116.07$, $p = 0.10$, Figure 2.1; $G_{mammalian} = 144.16$, $p = 0.002$, Figure 2.2). Acadian flycatchers also built nests in areas within the lower 50% quartile of predator activity (Figure 2.3), although they did not apparently differentiate between mammalian and avian predators ($t_{1, 120} = 0.25$, $p = 0.80$). Flycatchers avoided areas of cowbird activity more than blue jay activity ($U_s = 401.5$, $p = 0.07$).

Cardinals and flycatchers exhibited different patterns relative to nest location. Flycatchers and cardinals built nests in areas with very similar probabilities of mammalian predator use ($t_{1,377} = -0.68$, $p = 0.226$, Figure 2.3), but flycatchers chose nest-sites at locations lower in avian nest predator activity than cardinals ($t_{1,386} = -4.38$, $p < 0.0001$, Figure 2.3). Flycatchers and cardinals built nests in areas surrounded by nearly equivalent probabilities of blue jay activity ($t_{1, 251} = 1.43$, $p = 0.155$, Figure 2.3), but flycatchers more strongly avoided areas of cowbird activity than cardinals ($t_{1, 230} = 3.62$, $p < 0.001$, Figure 2.3).

Daily survival rates of nests

The model that best explained variation in daily survival rates of cardinal nests included the variables of nest initiation date (Julian), avian predator activity, mammalian predator activity, and the interaction of avian and mammalian predator activity (β_{julian} = 0.018 ± 0.002 SE, β_{avian} = 0.676 ± 0.469 SE, $\beta_{mammalian}$ = 1.481 ± 0.535 SE, $\beta_{avian*mamm}$ = -2.642 ± 0.996 SE, β_0 = -0.489 ± 0.371 SE, ω_i = 0.375, *n* = 317, Table 2.2, Figure 2.4 and 2.5). With the exception of avian predator activity, 95% confidence intervals of parameter estimates did not include 0. Nest survival was explained by the interaction of avian and mammalian predator activity, such that survival decreased the most in locations of both high avian and mammalian predator activity. Nest survival also increased with time of season. A second model including the same parameters above with the addition of the urban index was also plausible ($\Delta AIC_c \leq 2$), however, the 95% confidence interval of the urban parameter estimate included 0 (β_{urban} = 0.159 ± 0.093, β_{julian} = 0.018 ± 0.002 SE, β_{avian} = 0.711 ± 0.472 SE, $\beta_{mammalian}$ = 1.478 ± 0.534 SE, $\beta_{avian*mamm}$ = -2.675 ± 0.996 SE, β_0 = -0.610 ± 0.379 SE, ω_i = 0.300, *n* = 317, Table 2.2, Figure 2.4 and 2.5).

The top model explaining nest survival of flycatchers included the variables of avian and mammalian activity and their interaction ($\beta_{mammalian}$ = -3.720 ± 2.041 SE, β_{avian} = -6.056 ± 2.319 SE, $\beta_{mamm*avian}$ = 13.959 ± 5.797 SE, β_0 = 4.765 ± 0.787 SE, ω_i = 0.353, *n* = 53, Table 2.3, Figure 2.6 and 2.7), with only the confidence interval for mammalian activity including 0. Survival of flycatcher nests decreased with higher avian predator activity, particularly when mammalian predator activity was low. Otherwise, there were no clear patterns in daily survival rate and predator activity. Two other models were ranked within a $\Delta AIC_c \leq 2$ and therefore equally plausible for explaining nest survival. One model included nest initiation date (Julian) in addition to the independent variables of the above model (β_{julian} = 0.012 ± 0.011 SE, $\beta_{mammalian}$ = -3.632 ± 1.99 SE, β_{avian} = -

5.789 ± 2.330 SE, $\beta_{mamm*avian} = 13.495 \pm 5.661$ SE, $\beta_0 = 2.647 \pm 1.985$ SE, $\omega_i = 0.165$, n = 53, Table 2.3), and the other included the urban index in addition to the independent variables of the top model ($\beta_{urban} = 0.164 \pm 0.234$, $\beta_{mammalian} = -4.079 \pm 2.164$ SE, $\beta_{avian} = -6.064 \pm 2.373$ SE, $\beta_{mamm*avian} = 14.336 \pm 5.945$ SE, $\beta_0 = 4.896 \pm 0.835$ SE, $\omega_i = 0.107$, n = 53, Table 2.3). However, each of the 95% confidence intervals of these additional parameters included 0.

Discussion

My findings provide evidence that variation in predator activity at local scales can influence nest-site selection and nest survival of songbirds. Both cardinal and flycatcher appeared to use predator information at local scales when selecting locations for nests. Flycatchers, in particular, are known to strongly select habitat at landscape scales (Bakermans and Rodewald 2006, Rodewald and Shustack 2008b), but patterns of predator avoidance from my study corroborate other findings where local cues about predation risk were important for songbird nest-site selection (Lima 2002, Chalfoun and Martin 2007, Marzluff et al. 2007, Schmidt and Schauber 2007).

Results from my study also suggest that use of predator information may be adaptive, as nest survival for both species generally declined with increasing predator activity at local spatial scales. However, the relationship between nest survival and predator activity may depend upon which predators are dominant. Nest survival rates were more closely linked with avian predator activity than mammalian predator activity, which seems intuitive since diurnal avian predators depredate nearly half of the nests in the system (Rodewald and Kearns 2011). Interestingly, survival of flycatcher nests decreased most when avian predator activity was high, but mammalian predator activity was low. Mammalian predators in this study included mainly chipmunks and squirrels, which make up only 10% of nest failures by predators (Rodewald and Kearns 2011). I offer three possible explanations for this pattern. First, habitat within areas that receive less use by mammals may differ in ways that increase exposure to visually-oriented avian predators. Second, squirrels and chipmunks may confer some kind of protection if their high abundances induce prey switching (Holling 1965) such that predators focus less on flycatcher nests. Third, because other species, including birds, are known to react to alarm calls of other species, high numbers of the frequently vocalizing chipmunks may alert flycatchers to the presence of shared predators (Seppanen 2007, Schmidt et al. 2008, Ito and Mori 2010, Magrath and Bennett 2012), which in turn may lead to increased nest survival.

Despite a diverse predator community, responses of both cardinals and flycatchers differed among species of predators, suggesting some ability of these songbirds to identify predators and respond accordingly. Cardinals more strongly avoided mammalian than avian predators, and blue jays than cowbirds, although both diurnal mammals and blue jays are less dominant nest predators in this system (10% and 5% respectively (Rodewald and Kearns 2011)). Flycatchers more strongly avoided brown-headed cowbirds than any other predator, possibly because cowbirds are an important nest predator in my system (Rodewald and Kearns 2011) and heavily parasitize flycatcher nests (Bakermans and Rodewald 2006, Rodewald and Shustack 2008b, Rodewald 2009). In addition, host species that arrive after cowbird settlement at the breeding sites (i.e. Neotropical migrants such as the flycatcher) are more likely than resident species, such as the cardinal, to avoid areas with evidence of cowbirds (Forsman and Martin 2009).

Overall, this study highlights the importance of predator activity at local scales as a source of public information for songbirds selecting nest-sites. Moreover, use of predator information seemed to be consistent across landscapes, though my small sample sizes for rural flycatchers may have limited my ability to detect differences. Although many studies have demonstrated that vegetation structure and composition are important attributes selected by nesting birds, my findings suggest that information about predators is also used to guide nest-site selection. Future research into specific predator –songbird interactions, particularly with diurnal mammalian and nocturnal predators, and how they affect nest-site choices will clarify the use of predator information by songbirds.

References

Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat-selection across a rural-to-urban landscape gradient. Auk 128:293-302.

Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (Empidonax virescens) in central Ohio. Auk 123:368-382.

Bednekoff, P. A., and S. L. Lima. 2005. Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? Animal Behaviour 69:1165-1171.

Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225-234.

Beyer, H. 2011. Geospatial Modeling Environment. URL http://www.spatialecology.com/gme

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Chalfoun, A. D., and T. E. Martin. 2010. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163:885-892.

Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson. 2002. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858-867.

Cox, W. A., F. R. Thompson, III, and J. Faaborg. 2012. Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. Auk 129:147-155.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings of the Royal Society B 273:701-706.

Emmering, Q. C., and K. A. Schmidt. 2011. Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. Journal of Animal Ecology 80:1305-1312.

Fauchald, P., K. E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology 81:773-783.

Fontaine, J. J., and T. E. Martin. 2006b. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428-434.

Forsman, J. T., and T. E. Martin. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. Oikos 118:464-470.

Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behavioral Ecology 13:101-108.

Holling, C.S. 1965. The functional response of predators to prey and its role in mimcry and population regulation. Memoirs of the Entomological Society of Canada 45.

Ito, R., and A. Mori. 2010. Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard Oplurus cuvieri cuvieri (Reptilia: Iguania). Proceedings of the Royal Society B-Biological Sciences 277:1275-1280.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70-75.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation- a review and prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:619-640.

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945-956.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504-1514.

Luck, G. W. 2002. The habitat requirements of the rufous treecreeper (Climacteris rufa). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105:383-394.

Magrath, R. D., and T. H. Bennett. 2012. A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proceedings of the Royal Society B-Biological Sciences 279:902-909.

Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried, S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516-534.

Morosinotto, C., R. L. Thomson, and E. Korpimaki. 2010. Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. Journal of Animal Ecology 79:327-333.

Parejo, D., and J. M. Aviles. 2011. Predation risk determines breeding territory choice in a Mediterranean cavity-nesting bird community. Oecologia 165:185-191.

Part, T., D. Arlt, B. Doligez, M. Low, and A. Qvarnstrom. 2011. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. Journal of Animal Ecology 80:1227-1235.

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Prange, S., and S. D. Gehrt. 2004. Changes in mesopredator-community structure in response to urbanization. Canadian Journal of Zoology-Revue Canadienne De Zoologie 82:1804-1817.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324-333.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. Journal of Mammalogy 85:483-490.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience 54:755-766.

Rodewald, A. D. 2009. Urban-associated habitat alteration promotes brood parasitism of Acadian Flycatchers. Journal of Field Ornithology 80:234-241.

Rodewald, A. D., and L. J. Kearns. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. Condor 113:899-906.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecological Applications 21:936-943.

Rodewald, A. D., and D. P. Shustack. 2008a. Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? Ecology 89:515-521.

Rodewald, A. D., and D. P. Shustack. 2008b. Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77:83-91.

Rodewald, A.D., Shustack, D.P., and L. E. Hitchcock. 2010. Exotic shrubs as ephemeral ecological traps for nestling birds. Biological Invasions 12:33-39.

Roth, T. C., J. G. Cox, and S. L. Lima. 2008a. Can foraging birds assess predation risk by scent? Animal Behaviour 76:2021-2027.

Salo, P., M. Nordstrom, R. L. Thomson, and E. Korpimaki. 2008. Risk induced by a native top predator reduces alien mink movements. Journal of Animal Ecology 77:1092-1098.

Schmidt, K. A., S. R. X. Dall, and J. A. van Gils. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos 119:304-316.

Schmidt, K. A., E. Lee, R. S. Ostfeld, and K. Sieving. 2008. Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. Behavioral Ecology 19:759-763.

Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. Oecologia 148:22-29.

Schmidt, K. A., and E. M. Schauber. 2007. Behavioral indicators of predator space use: Studying species interactions through the behavior of predators. Israel Journal of Ecology & Evolution 53:389-406.

Schmidt, K. A., and C. J. Whelan. 2005. Quantifying male Wood Thrush nest-attendance and its relationship to nest success. Condor 107:138-144.

Schmidt, K. A., and C. J. Whelan. 2010. Nesting in an uncertain world: information and sampling the future. Oikos 119:245-253.

Seaman, D. E., J.J. Millspaugh, B.J. Kernohan, G. C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Seppanen, J. T., J. T. Forsman, M. Monkkonen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622-1633.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186-191.

Sorace, A., and M. Gustin. 2009. Distribution of generalist and specialist predators along urban gradients. Landscape and Urban Planning 90:111-118.

Stake, M. M., J. Faaborg, and F. R. Thompson. 2004. Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337-344.

Stout, W. E., and R. N. Rosenfield. 2010. Colonization, growth, and density of a pioneer Cooper's hawk population in a large metropolitan environment. Journal of Raptor Research 44:255-267.

Wagner, R. H., and E. Danchin. 2010. A taxonomy of biological information. Oikos 119:203-209.

Weidinger, K. 2009. Nest predators of woodland open-nesting songbirds in central Europe. Ibis 151:352-360.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Table 2.1 Independent variables used in alternative hypotheses for explanation of patterns in the dependent variable, daily survival rates of northern cardinal (*Cardinalis cardinalis*) and Acadian flycatcher (*Empidonax virescens*) nests, Franklin and Delaware Counties, Ohio, USA, 2008-2010

Hypotheses	**Independent Variables**
Daily nest survival will increase with time of season	Julian
Daily nest survival will be affected by urbanization	Urban
Daily survival rates of nests built in areas of lower predator activity would be higher	Avian predator activity (avpred) Mammalian predator activity (mpred) Avian predator activity * Mammalian predator activity

Table 2.2 Candidate model set explaining daily survival rates of northern cardinal (*Cardinalis cardinalis*) nests in riparian forests in Franklin and Delaware Counties, Ohio, USA, 2008-2010, (*n* = 317)

Model	K	AIC_c	ΔAIC_c	ω_i
Julian, mpred, avpred, avpred*mpred	5	1682.3	0	0.385
Julian, urban, avpred, mpred, avpred*mpred	6	1682.8	0.5	0.300
Julian	2	1686.0	3.7	0.061
Julian, avpred	3	1686.3	4.0	0.052
Julian, urban	3	1686.3	4.0	0.052
Julian urban avpred	4	1686.8	4.5	0.041
Julian, avpred, mpred	4	1687.2	4.9	0.033
Julian mpred	3	1687.6	5.3	0.027
Julian, avpred, mpred, urban	5	1687.8	5.5	0.025
Julian, urban, mpred	4	1687.8	5.5	0.025
Null	1	1763.3	81.0	0.000
Urban	2	1763.3	81.0	0.000
Urban mpred	3	1763.5	81.2	0.000
Avpred mpred avpred*mpred	4	1764.2	81.9	0.000
Avpred	2	1764.3	82.0	0.000
Urban avpred	3	1764.5	82.2	0.000
Urban avpred mpred avpred*mpred	5	1764.7	82.4	0.000
Mpred	2	1765.0	82.7	0.000
Avpred mpred	3	1765.6	83.3	0.000
Urban avpred mpred	4	1765.9	83.6	0.000

Table 2.3 Candidate model set explaining daily survival rates of Acadian flycatcher (*Empidonax virescens*) nests in riparian forests in Franklin and Delaware Counties, Ohio, USA, 2008-2010, (*n*=53)

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**ω_i**
Avpred, mpred, avpred*mpred	4	277.79	0	0.231
Julian, avpred, mpred avpred*mpred	5	278.46	0.67	0.165
Urban, avpred, mpred avpred*mpred	5	279.33	1.54	0.107
Julian, urban, avpred, mpred, avpred*mpred	6	280.07	2.28	0.074
Null	1	280.19	2.40	0.070
Julian	2	280.35	2.56	0.064
Urban	2	281.25	3.46	0.041
Julian, urban	2	281.56	3.77	0.035
Mpred	2	281.59	3.80	0.035
Julian, mpred	3	281.75	3.96	0.032
Avpred	3	281.98	4.19	0.028
Julian, avpred	3	282.32	4.53	0.024
Mpred, avpred	3	282.81	5.02	0.019
Urban, mpred	3	282.89	5.10	0.018
Urban, avpred	3	283.15	5.36	0.016
Julian, urban, mpred	4	283.21	5.42	0.015
Julian, mpred, avpred	4	283.34	5.55	0.014
Julian, urban, avpred	4	283.58	5.79	0.013
Urban, avpred, mpred	4	284.40	6.61	0.008
Julian, urban, avpred, mpred	5	284.99	7.20	0.006

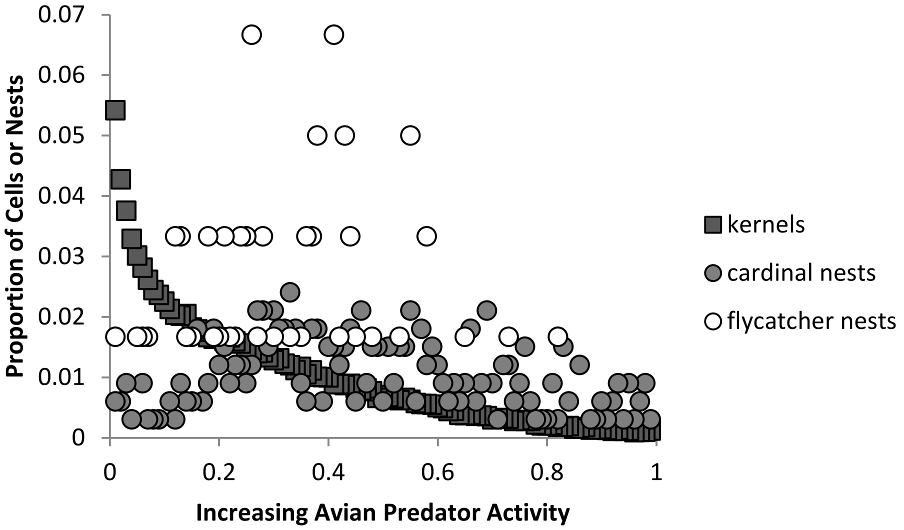

Figure 2.1 Comparisons of the frequency distributions of northern cardinal (*Cardinalis cardinalis*) and Acadian flycatcher (*Empidonax virescens*) nest locations and the utilization distributions (kernels) for avian predators in riparian forests in Franklin and Delaware Counties, Ohio, USA, 2008-2010

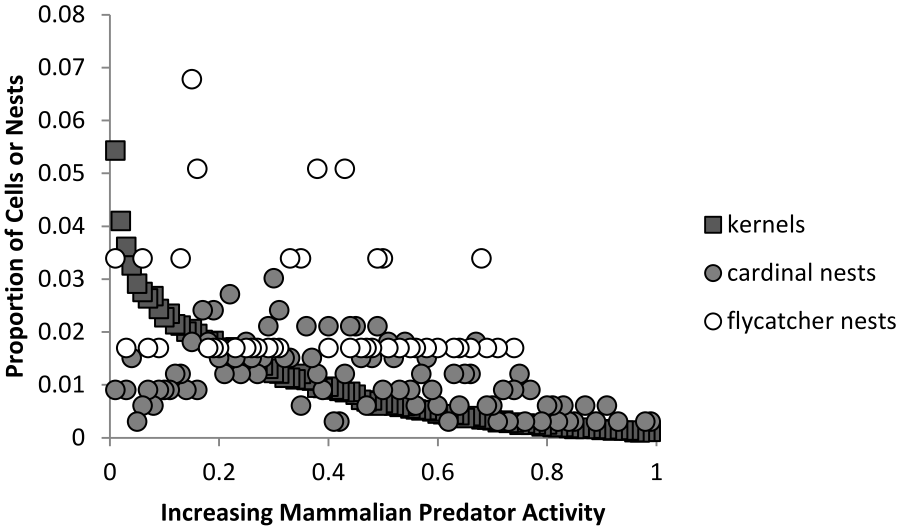

Figure 2.2 Comparisons of the frequency distributions of northern cardinal (*Cardinalis cardinalis)* and Acadian flycatcher (*Empidonax virescens*) nest locations and the utilization distributions (kernels) for mammalian predators in riparian forests in Franklin and Delaware Counties, Ohio, USA, 2008-2010

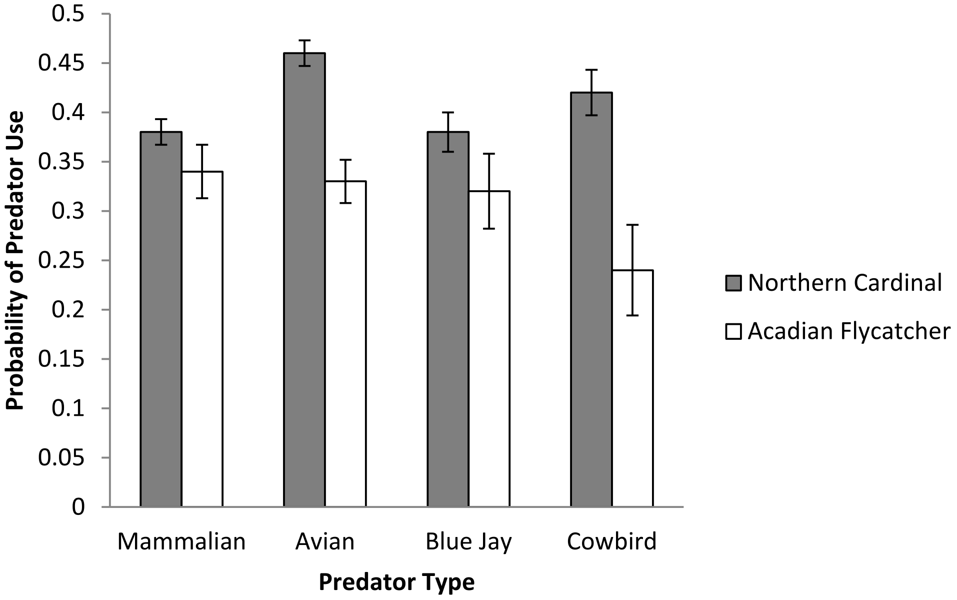

Figure 2.3. Nest locations of northern cardinal (*Cardinalis cardinalis*) and Acadian flycatcher (*Empidonax virescens*) nests with respect to probability of predator activity around the nest-site, Franklin and Delaware Counties, Ohio, 2008-2010. Sample sizes are as follows: Cardinal – mammalian: *n* = 317, avian: *n* = 334, blue jay (*Cyanocitta cristata*): *n* = 167, brown-headed cowbird (*Molothrus ater*): *n* = 145; Flycatcher - mammalian: *n* = 62, avian: *n* = 60, blue jay: *n* = 21, cowbird: *n* = 24. Error bars represent standard error.

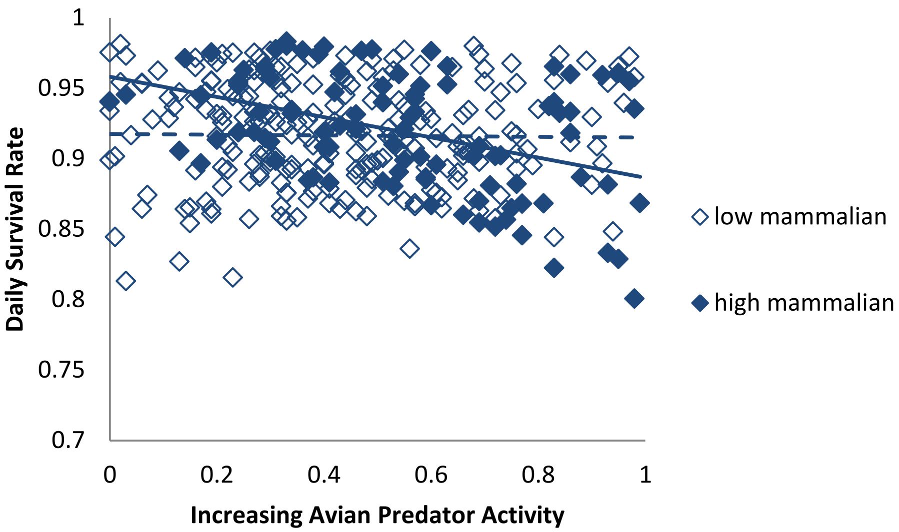

Figure 2.4 Daily survival rates of northern cardinal (*Cardinalis cardinalis*) nests in relation to probability of predator activity in central Ohio, 2008-2010, (*n* = 317): increasing avian predator activity when mammalian predator activity is low (0-0.5, trend line (dashed): y = -0.003x + 0.918, R^2 = 0.0003) and high (0.51-1, trend line (solid): y = -0.072x + 0.958, R^2 = 0.179)

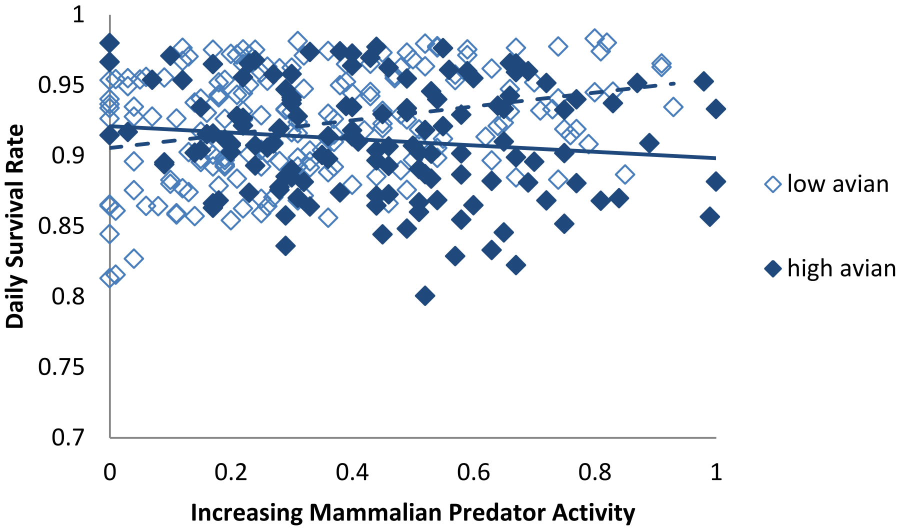

Figure 2.5 Daily survival rates of northern cardinal (*Cardinalis cardinalis*) nests in relation to probability of predator activity in central Ohio, 2008-2010, (n = 317): increasing mammalian predator activity when avian predator activity is low (0 - 0.5, trend line (dashed): y = 0.049x + 0.906, R^2 = 0.089) and high (0.51-1, trend line (solid): y = -0.0226x + 0.9208, R^2 = 0.017)

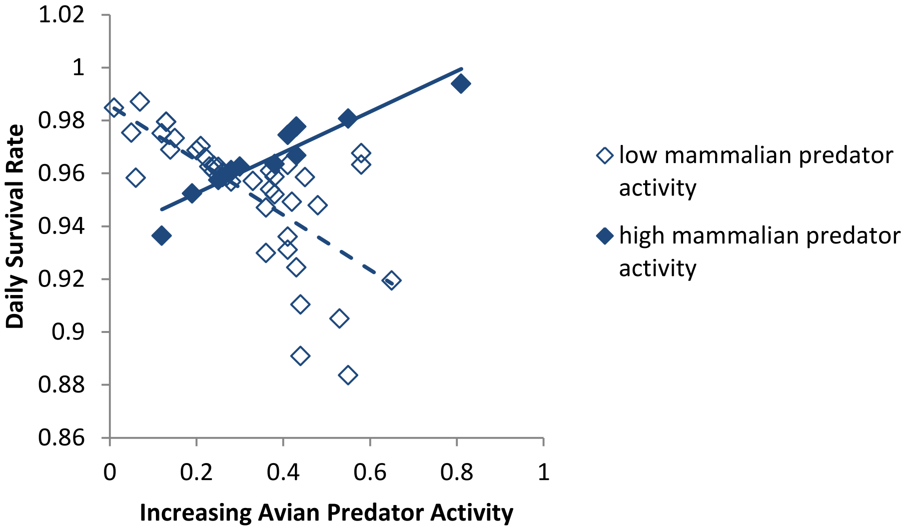

Figure 2.6 Daily survival rates of Acadian flycatcher (*Empidonax virescens*) nests in relation to probability of predator activity in central Ohio, 2008-2010, (*n* = 53): increasing avian predator activity when mammalian predator activity is low (0-0.5, trend line (dashed): y = -0.104x + 0.986, R^2 = 0.474) and high (0.51-1, trend line (solid): y = -0.077x + 0.937, R^2 = 0.894)

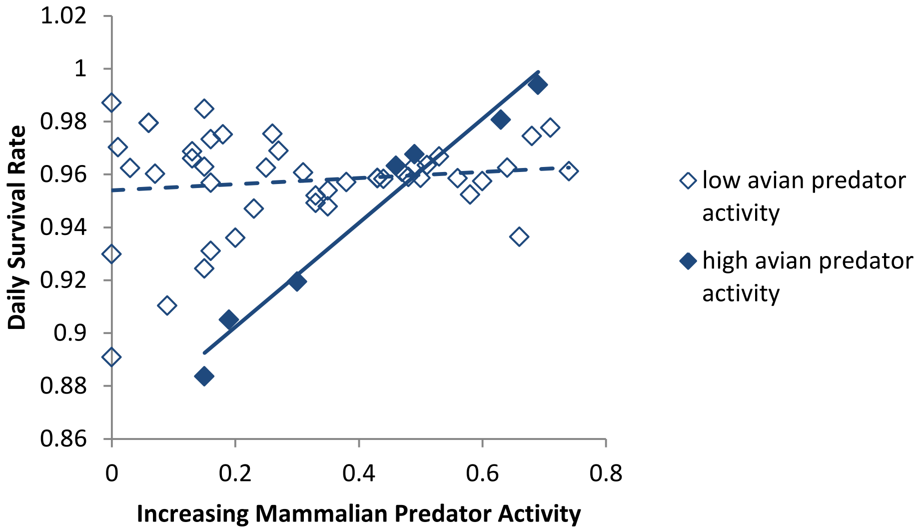

Figure 2.7 Daily survival rates of Acadian flycatcher (*Empidonax virescens*) nests in relation to probability of predator activity in central Ohio, 2008-2010, (*n* = 53): increasing mammalian predator activity when avian predator activity is low (0-0.5, trend line (dashed): y = 0.012 + 0.954, R^2 = 0.019) and high (0.51-1, trend line (solid): y = 0.197x + 0.863, R^2 = 0.967)

Chapter 3: Within-season use of public and private information on predation risk in nest-site selection

Abstract

Nest-site selection can be an important preemptive defense strategy for songbirds to reduce the risk of predation and is likely most effective when it incorporates both public and private information about predation. I examined the degree to which two songbirds, the Northern Cardinal (*Cardinalis cardinalis*, $n = 160$ pairs) and the Acadian Flycatcher (*Empidonax virescens*, $n = 70$ pairs), changed nest-site attributes (e.g., nest height, nest concealment, and vegetation density surrounding the nests) between subsequent within-season nesting attempts from 2006-2010 in Ohio. Specifically, I asked if birds adjusted nest-sites based upon information such as prior experience with nest predation, perceived predation risk (relative detections of predators), and actual predation risk (daily mortality rates of nests). Only cardinals, not flycatchers, showed evidence of using of private and public information in changing nest-site attributes. There were greater changes in nest height when previous nests failed, and greater changes in nest concealment at riskier sites compared to those with low daily predation rates. These findings suggest that species differ in behavioral plasticity and use of information in ways that can both reflect and predict their ability to adapt to novel conditions.

Keywords nest-site selection, songbird, predation, information, Northern Cardinal, Acadian Flycatcher

Introduction

Because the primary cause of nest failure in songbirds is predation (Ricklefs 1969, Martin 1993a), birds are expected to make a variety of behavioral decisions that reduce the risk of nest predation. Nest-site selection can be an important preemptive defense strategy against predation, as nest characteristics can influence the likelihood of depredation (Martin and Roper 1988, Howlett and Stutchbury 1997, Johnson 1997, Hazler et al. 2006, Colombelli-Negrel and Kleindorfer 2009). As such, birds should use multiple sources of information about predation when selecting nest-sites. Private information, which is known to the individual only (e.g., their own nesting history), and public information, which is knowable to all (e.g., abundance of predators at a site; Wagner and Danchin 2010), can be incorporated into the decision-making process for selecting safe nest sites (e.g., Doligez et al. 2002).

Several studies have examined how birds will alter characteristics of nesting sites based on their previous experience (i.e., private information) with nest predation, both within season (Greig-Smith 1982, Howlett and Stutchbury 1997, Lima 2009, Chalfoun and Martin 2010a) and between seasons (Hoover 2003, Schmidt 2004) and relative to tradeoffs with future reproductive success (Schmidt and Whelan 2010). The situation in which birds continue to use similar nest-sites after nest success but select different nest-site characteristics after failure is known as a win-stay, lose-switch strategy (see Schmidt 2001). In contrast, choosing nest-sites irrespective of nest fate is known as a stay-stay strategy (e.g., Schmidt 2001, Chalfoun and Martin 2010a). In the case of the win-stay, lose-switch strategy, birds likely modify nesting decisions based on a variety of information sources about predation in addition to prior experience, such as perceived and actual predation risk. Birds can also respond to this information across broad spatial (e.g., immediate nest area, territory, site; Chalfoun and Martin 2007) and temporal scales (within vs. between season; Hoover 2003).

Many studies document that birds modify nest-site characteristics or choose nesting habitat based on perceived predation risk, even in the absence of actual depredation (Knight and Fitzner 1985, Martin and Roper 1988, Schmidt and Whelan 1998, Forstmeier and Weiss 2004, Eggers et al. 2006, Fontaine and Martin 2006a, Marzluff et al. 2007, Peluc et al. 2008). A few studies have examined songbird responses to predation rates or risk between nesting seasons in terms of site or territory fidelity (e.g., Hoover 2003, Schmidt and Whelan 2010, Chen et al. 2011), but almost none have examined responses within the same breeding season (Schmidt and Whelan 2010). In addition, few have simultaneously examined within-season responses and the degree to which songbirds use multiple public and private cues about predation risk (e.g., Chalfoun and Martin 2010b).

Individual experiences should be among the most helpful sources of information when breeding environments are unpredictable (see Schmidt et al. 2010). Ecosystems with diverse nest predator communities represent one such type of unpredictable environment. The ability of a breeding bird to select a safe nest site should be greatest when the breeding habitat has predictable patterns of depredation and/or simple predator communities. Several studies have shown that songbirds will alter their nest-site placement predictably in response to densities or activity patterns of specific predators, such as chipmunks, mice, cowbirds, and owls (Forstmeier and Weiss 2004, Schmidt et al. 2006, Forsman and Martin 2009, Morosinotto et al. 2010). In systems with diverse suites of predators, however, the lack of predictability may make it more difficult for prey species to adjust behavior in a way that reduces risk (Lima 2009, Martin and Briskie 2009). The absence of a "safe" nest site is particularly likely when the site is used by a variety of predator types that employ divergent search strategies, to the point where any given nest characteristic may reduce risk to one predator while increasing vulnerability to another (e.g., Remeš 2005, Colombelli-Negrel and Kleindorfer 2009; but see Chalfoun and Martin 2010a). Thus, when faced with diverse predator communities, the best strategy may simply be to renest many times over the season (Filliater et al. 1994, Davis 2005).

Given the paucity of studies examining interactions among information sources in environments with less predictable predator-prey interactions, I evaluated the relative importance of and potential interactions among different private and public information sources in such a system. Based on previous efforts to video-document nest predators of understory-nesting birds, my study system is the most diverse nest predator community thus far described in North America (Rodewald and Kearns 2011). Moreover, in my system, no single predator dominates, which means that birds face real threats from many species. In addition, long-term study of the system allowed me to focus on a variety of predator information types including prior individual experience, perceived risk (activity of predators at the breeding site), and actual risk of nest predation (indicated by daily nest survival rate at sites).

I considered nesting decisions of two breeding songbird species, the Northern Cardinal (*Cardinalis cardinalis*) and the Acadian Flycatcher (*Empidonax virescens*). Both species will readily renest within a breeding season and can produce double broods, or more in the case of cardinals. In my study area, both species are common breeders and build open-cup nests in shrubs and trees, although the architecture and vertical position of nests differ. Migratory strategy and sensitivity to anthropogenic disturbance also are dissimilar, with the cardinal, a resident, reaching its highest densities in urban environments and the flycatcher, a Neotropical migrant, negatively associating with urbanization (Rodewald and Bakermans 2006, Rodewald and Shustack 2008a, b). I suspected that differences in behavioral plasticity might underlie the patterns of sensitivity.

I focused on three nest-site variables known to influence nest-site selection and/or nest survival of these and similar species of songbirds: nest height (Wilson and Cooper 1998, Smith-Castro and Rodewald 2010a,b, AD Rodewald unpublished data), nest concealment (i.e. the foliage or cover immediately surrounding the nest, Kelly 1993, Chapa-Vargas and Robinson 2006, Lima 2009), and vegetation density within the nest patch (Bakermans and Rodewald 2006, Leston and Rodewald 2006). Given the high diversity of the predator community, these three variables represent characteristics that may provide protection to the nests from the major groups of predators (nest height – mesopredators/olfactory predators, nest concealment – avian predators, vegetation density – both). Thus, I predicted that private and public information would contribute to nesting decisions such that in cases where previous nests failed and on sites with high risk of nest predation, birds should make the largest changes in the height, concealment, and surrounding vegetation density of subsequent nests, presumably making nests safer.

Methods

Study Area

I studied Northern Cardinals and Acadian Flycatchers and their predators from April-August 2006-2010 at 14 riparian forests (104-277 m wide) located along rivers (between 39° 50’39” - 40° 21’14” N latitude, 82° 52’ 734” – 83° 14’ 752” longitude) in Franklin and Delaware Counties, Ohio, USA. All forest sites occurred in human-dominated, highly fragmented landscapes characterized as a gradient ranging from urban/suburban (i.e., dominated by residential and commercial areas) to rural (i.e., dominated by agriculture and pasture; Rodewald and Shustack 2008a). Overstory and subcanopy layers of forests were dominated by native trees including cottonwood (*Populus deltoides* Bartram ex Marsh.), sycamore (*Plantanus occidentalis* L.), silver maple (*Acer saccharinum* L.), black maple (*Acer nigrum* Michx. f.), sugar maple (*Acer saccharum* Marsh.), black walnut (*Juglans nigra* L.), American elm (*Ulmus americana* L.), and ash (*Fraxinus* spp.). The understory tree and shrub layers were dominated by the non-native shrubs, Amur honeysuckle (*Lonicera maackii* (Rupr) Herder) and multiflora rose (*Rosa multiflora* Thunb.), and native species such as spicebush (*Lindera benzoin* (L.) Blume), American bladdernut (*Staphylea trifolia* L.), boxelder (*Acer negundo* L.), and pawpaw (*Asimina triloba* (L.)).

In previous work within the study area, 22 species depredated nests of understory birds (Rodewald and Kearns 2011, *n* = 99). Northern Raccoon (*Procyon lotor*) and Brown-headed Cowbird (*Molothrus ater*) were responsible for 29% of recorded depredation events, and other common nest predators included Cooper's Hawk (*Accipter cooperii*), Barred Owl (*Strix varia*), Red-shouldered Hawk (*Buteo lineatus),* Red-tailed Hawk (*Buteo jamaicensis*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), Common Grackle (*Quiscalus quiscala*), Virginia Opossum (*Didelphis virgianus*), Eastern Chipmunk (*Tamias striatus*), squirrels (*Sciurus* spp.), and domestic cats (*Felis catus*). Gray Catbirds (*Dumetella carolinensis*) and House Wrens (*Troglodytes aedon*) also punctured or removed eggs from Northern Cardinal nests. In my study system, snakes appear to be relatively infrequent nest predators, as they were identified in only 3 of 99 depredation events (Rodewald and Kearns 2011).

Field Methods

In central Ohio, cardinals nest from April to September and will renest after both failed and successful nests, with some pairs renesting up to seven times per season. Cardinals build nests in a variety of woody plants and at heights ranging from 0.5 m to 20 m above the ground (L. Kearns pers. obs.). Flycatchers breed from late May to August, typically renesting after both failed and successful attempts. They build nests in woody shrubs and saplings, typically at the end of branches, and at heights ranging from 1.5 m to 15 m above the ground.

Within the first couple months of each breeding season at my study sites, adult cardinals and flycatchers were captured using mist-nets and banded each with a unique color combination composed of a stainless steel (cardinal) or aluminum (flycatcher) US Geological Survey band and three plastic color bands. Occasionally, adults were banded later in the season, but due to relatively high site fidelity of both species, returning banded individuals were monitored over several years. Over the five years of the study, approximately 500 adult cardinals, half of which were female, and approximately 90 flycatchers, one-quarter of which were female, were banded. In addition, many of the birds banded in years previous to 2006 were still breeding at the time of my study.

Sites were visited 2-3 times weekly to search for nests for each mated pair. Once nesting attempts were found, each was monitored every 2-4 days until nests failed or fledged young. A nest was considered successful if fledglings were sighted with the parents, or if nest activity stopped near the estimated fledge date and other indicators were present, such as fecal droppings in and around the nest, or parental behaviors (carrying food, defensive chipping) indicating that fledglings were nearby. A nest was considered as failed when no sign of eggs, nestlings, or fledglings were found during the 2-3 subsequent visits to the nest after activity had ceased. For nests that were too high to directly view, fate was determined by observing the nest for up to one hour and up to a minimum of three visits after no activity was observed at the nest.

As soon as possible after nest completion (typically 1-20 days), vegetation characteristics were sampled at nest sites. Nest height was measured from the ground. To measure nest concealment, the nest was sighted through an ocular tube while standing 1m from the nest within its horizontal plane in each of the four cardinal directions, and the amount of the nest covered by vegetation immediately surrounding the nest was assessed to the nearest 5%. For nests too high to reach, concealment was estimated visually from the best possible angle. These values were averaged into a single nest concealment measure. To gain a measurement of the vegetation structure within the nest patch, vegetation density was measured at 5 points spaced every 2 m along a line radiating in each cardinal direction from the nest (20 points total), within an 11.3-m radius circle. At each point, the number of times any part of a woody plant touched a PVC-pole between the heights of 0.5 m to 3 m was counted. The vegetation hits from all four cardinal directions were summed to quantify vegetation density.

The predator community at each site was assessed from 2007-2010 by conducting line-transect surveys. In order to maximize the amount of a site covered by the surveys, a 250 m line was placed near the center of a 2-ha rectangular grid established at each forest site. In the case of a few oddly shaped sites, the line was divided into sections that maximized site coverage and summed to 250 m. From April to August, each transect was surveyed by a trained observer over a period of approximately 20 min twice weekly at different times between 6am and 2pm. To minimize observer influences on detections, observers wore camouflaged clothing, walked slowly, and remained as quiet as possible. All potential avian, mammalian, and snake predators, detected by sight or sound, were mapped, recorded, and the perpendicular distance of each from the line transect was determined using an optical range finder.

Avian species detected during the surveys and used to determine the relative detections of predators included American Crow, Brown-headed Cowbird, Barred Owl, Blue Jay, Common Grackle, Cooper's Hawk, Great-horned Owl (*Bubo virginals*), Gray Catbird, House Wren, Red-bellied Woodpecker (*Melanerpes carolinus*), Red-shouldered Hawk, Red-tailed Hawk, and Sharp-shinned Hawk (*Accipter striatus*). I also surveyed for domestic cats, Northern Raccoons, Eastern Chipmunks, and squirrels, including Fox Squirrels (*Sciurus niger*), Eastern Gray Squirrels (*Sciurus carolinensis*), American Red Squirrels (*Tamiasciurus hudsonicus*), and Southern Flying Squirrels (*Glaucomys volans*). With a few exceptions, I detected these species at all sites. I pooled across species of raptors and squirrels, because raptors are difficult to detect, and squirrels are often hard to identify to species. I excluded snakes from the index since they were so infrequently observed and not a major nest predator. Additional species surveyed but not documented as nest predators in my system are known predators of songbird nests in other studies (Great-horned Owl, Houston et al. 1998; Red-bellied Woodpecker, Shackelford et al. 2000, Hazler et al. 2004; Sharp-shinned Hawk, Bildstein and Meyer 2000).

Data Analysis

To calculate the extent to which a breeding pair changed nest placement between renests within a given season, I first determined pairings of consecutively-built nests for banded males/females. Rather than restrict the analysis to only the initial attempt of the season, I used any pair of nests throughout the season that were in chronological order (e.g., second and third attempt, third and fourth attempt). As I lacked sufficient data on cardinals or flycatchers at some sites, I used cardinal nests from thirteen and flycatcher nests from twelve of the fourteen sites in the analyses. To account for possible seasonal effects, I included a variable to represent the time of season (see below). I calculated changes in nest height, nest concealment, and vegetation density between nesting attempts as the difference between each of those variables from the initial and subsequent nest attempt (e.g., difference in nest height between first and second nests for a given bird). To eliminate concerns about possible correlations of the vegetation variables with the season, I explored the relationships between these variables using Pearson's correlation coefficient.

Predictor variables included (1) previous nest fate of the individual bird (hereafter termed, "prior experience"), (2) relative detections of nest predators (hereafter termed "perceived risk"), and (3) actual risk of nest predation for that species and site (hereafter termed "actual risk"). For prior experience, I scored each nest attempt as 0 if the initial or previous nest had failed, or 1 if the previous nest had fledged at least 1 young (whether host or cowbird). To calculate "perceived risk", I averaged the number of detections of potential predators per survey visit over all survey visits for each year (2007 – 2010) at each site. Because I was interested in the effect of an overall level of site risk on responses, I calculated a single mean activity level for all predator species combined. I pooled predator observations across each season due to limited sample sizes and our lack of a priori knowledge of the temporal scales over which birds perceive and respond to predation risk (Lima and Bednekoff 1999). In 2006, I did not conduct predator surveys, but since yearly predator detections were highly correlated with the average detections over 2007-2010 (2007 – $r = 0.482$, $P = 0.043$; 2008 – $r = 0.672$, $P = 0.002$; 2009 - $r = 0.737$, $P < 0.001$; 2010 – $r = 0.716$, $P < 0.001$), I used the 2007-2010 average to represent perceived risk at the sites in that year. I derived actual risk from estimates of nest daily survival rate, since nest predation is the most frequent cause of nest failure for both study species (approximately 90% of nest failures, Rodewald et al. 2011). Using nest monitoring data from 2006-2010, I determined daily survival rates (DSR) of nests for each site, year, and species (cardinals, $n = 1585$; flycatchers, $n = 212$) using the logistic exposure model (Shaffer 2004) and PROC GENMOD in SAS (Ver. 9.2, SAS Institute 2011). I then calculated daily risk of predation as 1-DSR, which represents the final value for actual risk at each site and for each species. To represent time of season, I used the estimated Julian date of the first egg laid (hereafter termed "Julian date").

To evaluate the relationships between predictor variables (prior experience, perceived risk, actual risk, Julian date) and changes in nest characteristics (nest height change, nest concealment change, and vegetation density change), I used mixed effects models with maximum likelihood estimation in SAS (PROC MIXED, Ver. 9.2, SAS Institute 2008) with site and year included as random effect variables. I considered model sets containing both additive and interactive effects of the predictor variables. For each nest characteristic, I constructed separate model sets. Using Akaike's Information Criterion corrected for small sample sizes (AIC_c), I ranked the individual mixed effects models (Burnham and Anderson 2002). I considered models within 2 units of the top model (Δ $AIC_c < 2$) to be equally plausible in explaining the response variable. The only response variable with a non-normal distribution was cardinal nest height, which I transformed with the base 10 logarithm.

Results

Vegetation

For cardinals, there was a strong increase in nest height as the season progressed ($r = 0.43$, $P < 0.001$, $n = 314$). However, there were no significant relationships between nest concealment and vegetation density with change in season ($r = 0.09$, $P = 0.10$, $n = 306$; $r = 0.02$, $P = 0.67$, $n = 313$ respectively). For flycatchers, there were marginally significant relationships between season and nest height ($r = 0.17$, $P = 0.06$, $n = 130$), nest concealment($r = 0.17$, $P = 0.05$, $n = 130$), and vegetation density ($r = 0.17$, $P = 0.06$, $n = 130$).

Northern Cardinals

At the thirteen sites used in the analysis for cardinals, perceived risk among sites and years ranged from 2.5 – 15.7 nest predators detected per survey hour. Daily risk of predation for cardinals ranged from 0.01 – 0.22 across sites and years.

Change in nest height was best explained by prior experience and Julian date ($\beta_{prevfate}= -0.16 \pm 0.077$ SE, $\beta_{julian}= 0.002 \pm 0.001$ SE, $\beta_0= 1.32 \pm 0.215$ SE, $n = 160$, Table 3.1). Whereas cardinals tended to renest at increasing heights as the season progressed, cardinals whose previous nests failed renested at greater heights (Figure 3.1). All other models within the top set (i.e., $\Delta AIC_c \leq 2$) included prior experience as an explanatory variable (Table 3.1).

Change in nest concealment was best explained by two models. The best-ranked model included prior experience, actual risk, and Julian date ($\beta_{prevfate}$= -7.78 ± 4.833 SE, $\beta_{predationrisk}$= 250.27 ± 95.993 SE, β_{julian}= 0.14 ± 0.078 SE, β_0= -32.849 ± 15.408 SE, n = 152, Table 3.2), and this was followed by the full model ($\beta_{prevfate}$= -7.90 ± 4.799 SE, $\beta_{predationrisk}$= 253.26 ± 95.325 SE, $\beta_{predindex}$ = -1.46 ± 0.982, β_{julian}= 0.13 ± 0.077 SE, β_0= -22.42 ± 16.831 SE, n = 152, Table 3.2). Actual risk was the only regression parameter in each of these models that did not include 0 within the 95% confidence intervals. The greatest increases in concealment between initial and subsequent nests were found at sites with comparatively low predation risk, in cases where the previous nest had failed, and as the season progressed (Figure 3.2 and 3.3).

Changes in vegetation density of the nest patch between subsequent nest attempts were best explained by actual risk and Julian date. ($\beta_{predrisk}$ = -348.25 ± 163.91, β_{julian}= -0.09 ± 0.130, β_0= 36.93 ± 25.086 SE, n = 160, Table 3.3). If sites were riskier, changes in vegetation density between paired attempts were lower yet also decreased as the season progressed (Figure 3.4). Alternatively, the model containing actual risk, prior experience, and Julian date was ranked equally, but the 95% confidence intervals of all regression parameters included 0, indicating weak evidence of a relationship.

Acadian Flycatchers

At the twelve sites with flycatchers, perceived risk by site and year ranged from 1.1 – 15.7 predators detected per survey hour. Daily risk of predation for flycatchers ranged from 0 – 0.50.

For all nest-site placement metrics, changes between initial and renest locations were best explained by Julian date, though 95% confidence intervals of parameter estimates included 0. Over the season, I found decreasing changes in both nest height (β_{julian}= -0.01 ±0.028 SE, β_0= 1.98 ± 4.979 SE, *n* = 70, Table 4) and nest concealment (β_{julian}= -0.17 ± 0.235 SE, β_0= 39.97 ± 42.768 SE, *n* = 66, Table 5). In contrast, change in vegetation density tended to increase as the season progressed (β_{julian}= 0.13 ± 0.295 SE, β_0= -21.65 ± 53.40 SE, *n* = 67, Table 6).

Discussion

Information can reduce uncertainty and improve an individual’s ability to respond effectively to situations (Schmidt et al. 2010), yet the two songbird species differed widely in their apparent use of information in choosing nest-sites. Cardinals, but not flycatchers, adjusted nest placement based on public and private information about nest predation and nest predators. Specifically, cardinals made greater changes in the height of subsequent nests when previous nests had failed, suggesting that their previous experience influenced nest-site decisions. Whereas others have reported that nest height of cardinals increases with time of season (Filliater et al. 1994, Rodewald et al. 2010), my results provide evidence that changes in nest height are not simply a function of seasonal changes in vegetation but may also be explained by prior experience. Indeed, greater nest height does provide protection against some predators, such as climbing mammals (Soderstrom et al. 1998), and higher nests are known to have greater survival rates in my system (e.g. Smith-Castro and Rodewald 2010a,b) and elsewhere (e.g., Schmidt and Whelan 1999 (woodlands), Burhans et al. 2002 (old fields).

Not only did prior experience seem to be an important source of information, but I also found evidence that cardinals used public information about actual risk of predation, as daily nest survival rates strongly predicted changes in nest concealment and vegetation density. Increase in the change of nest concealment of subsequent cardinal nests was most pronounced at the riskiest sites when previous nests had failed, but actually decreased over the season when the previous nest had been successful. Greater nest concealment has been documented as an important factor for songbird nest success in some studies (Burhans and Thompson 1998, Hoover and Brittingham 1998, Rangen et al. 1999), but increasing nest cover may not protect nests from all kinds of predators (e.g. Remeš 2005), which may explain the decrease in nest concealment change over the season. Curiously, when sites were riskier, cardinals placed nests in areas with less dense vegetation. Many sites in my system have dense patches of the invasive Amur honeysuckle shrub, which can reduce breeding success (Borgmann and Rodewald 2004, Rodewald et al. 2010). Nests built in dense honeysuckle may be more susceptible to predation for two possible reasons. First, dense vegetation may hide predators, making it easier for them to ambush prey. Second, cardinals build a high proportion of their nests in honeysuckle, particularly early in the season (Rodewald et al. 2010), and the resulting homogeneity of nest locations can improve the ability of predators to find nests (e.g.

Martin 1993b). Therefore, selecting for lower vegetation density may be advantageous if it means that cardinals are avoiding the riskier honeysuckle locations. Additionally, and as observed previously in my system, the different patterns in changes in nest concealment and vegetation density reflect that cardinals' choices of placement within the nest substrate plant can remain independent of the nest patch vegetation characteristics (AD Rodewald, unpublished data).

Based on these results, cardinals appear to be adjusting nest-site selection in ways that promote success, and to some extent, are adopting a "win-stay, lose-switch" strategy (Nowak and Sigmund 1993, Schmidt 2001, Chalfoun and Martin 2010a). My findings contrast other studies that have suggested that nest-site characteristics of cardinals do not confer greater nest success (e.g. Filliater et al. 1994). Filliater et al. surmised that the best strategy for cardinals breeding in areas with diverse and unpredictable predator communities was to renest multiple times. Even though renesting alone can improve reproductive success, cardinals in my system also seemed to incorporate information about predation into changing vegetation characteristics of their renests. Despite some changes in nest characteristics due to seasonal effects, changes in nest attributes were also notably different in response to information about previous nest fates and riskiness of the sites. Unlike other studies of cardinal nest-site selection (e.g. Filliater et al. 1994), I incorporated nests over multiple years and multiple forest sites within a variety of landscapes, increasing my ability to detect patterns in nest-site selection and the use of information.

Unlike cardinals, Acadian flycatchers did not seem to change nest placement in response to information, which may be the consequence of the different life history strategies (Nocera et al. 2006, Schmidt et al. 2010). For example, flycatchers are migratory, specialized in their habitat requirements (i.e., mature, mesic forests; Whitehead and Taylor 2002), and reluctant to occupy urban environments (Bakermans and Rodewald 2006, Rodewald and Shustack 2008b). Other songbird species that share similar traits with the flycatcher also exhibit lowered behavioral plasticity, usually represented as a smaller relative brain size, and have difficulty adapting to novel environments (Via and Lande 1985, Sol et al. 2005, Moller 2010, Maklakov 2011). Another possibility is that flycatcher nests, which are often located >1m from tree trunks and on relatively thin branches, might be less accessible to predators, such as mesopredators, that have more predictable hunting patterns. As a result, flycatchers may have less to gain by changing the vegetation characteristics of their nests if they are more likely to be attacked by predators with a greater diversity of hunting strategies (e.g. avian predators).

Neither cardinals nor flycatchers modified nest-site selection in response to predator abundance or activity levels as a source of information. Numbers or activity levels of predators can be useful predictors of risk in rural landscapes or less human-dominated systems (Zanette and Jenkins 2000, Weidinger 2002, Rodewald et al. 2011), and some avian species are known to use cues about predator density in nest or territory selection (Forstmeier and Weiss 2004, Fontaine and Martin 2006a, Marzluff et al. 2007). However, in urban areas where predator populations are likely food subsidized (e.g., raccoons and anthropogenic foods like garbage, bird seed, and pet food) and rely less on natural prey, high densities of predators may poorly reflect risk (Rodewald et al. 2011). Likewise, species that are important nest predators from rural areas can switch prey and/or food preferences in urban areas such that they seldom depredate nests (Chiron and Julliard 2007, Weidinger 2009, Stracey 2011). Another possible explanation is that despite being active diurnally, the birds may be responding to nocturnal activity of predators. In this system, raccoons, opossums, and owls are important nest predators (Rodewald and Kearns 2011), and I occasionally detected them during daylight hours, but was unable to survey them at night. Finally, I was unable to measure all possible behavioral responses to predators, such as reducing activity at the nest during incubation or nest provisioning, which songbirds might otherwise exhibit in response to predator abundance or activity (e.g. Chalfoun and Martin 2010b).

My findings have several important caveats. First, flycatchers might use and process information about predators and predation at spatial scales different than those I measured. For example, Chalfoun and Martin (2007) found that the scale of breeding habitat selection of Brewer's Sparrows (*Spizella breweri*) was mediated by foraging resources at larger scales and predation risk at smaller scales (territory and nest patch). Whereas the private and public information I examined included both nest-patch (prior experience) and site scales (perceived and actual predation risk), responses were exclusively measured in terms of nest placement. Birds may use information to guide nest-site selection at much larger scales, and previous work from my system shows that flycatchers select habitats more strongly at the landscape scale than the territory scale

(Bakermans and Rodewald 2006, Rodewald and Shustack 2008b). Likewise, female flycatchers sometimes leave sites after an initial nest failure (Shustack and Rodewald 2010). Another caveat is that birds can show a variety of responses to information, of which altering nest site selection is only one. For example, evidence suggests that songbirds will alter other nest characteristics, such as the distances between subsequent nests, in order to ensure reproductive success (Howlett and Stutchbury 1997, Chalfoun and Martin 2010a). Predator information also may provoke changes in clutch sizes of subsequent nests, increased defense of nests, or decreased parental care activity at nests (Lima 2009). I also recognize that my inference is limited to three sources of information (i.e., previous experience, predator activity or abundance, and risk of predation at a site), and others have demonstrated that conspecifics are an alternative source of information (Doligez et al. 2002, Parejo et al. 2007, Betts et al. 2008). Finally, the smaller sample size of flycatchers may have made detection of changes in nest-sites more difficult.

In sum, cardinals and flycatchers responded differently to private and public information about predation within the same season and seem to respond to different spatial scales. In addition, as anthropogenic influences alter ecosystems and information sources, behavioral responses may no longer provide the same fitness benefits. Future studies of how fitness of songbird species are influenced by behavioral responses to predators in novel environments will be needed with increasing anthropogenic changes to habitats.

References

Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax virescens*) in central Ohio. Auk 123:368-382.

Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proceedings of the Royal Society B-Biological Sciences 275:2257-2263.

Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipter striatus*). The Birds of North America, No. 482. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Borgmann, K. L. and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14: 1757-1765.

Burhans, D. E., D. Dearborn, F. R. Thompson, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66:240-249.

Burhans, D. E., and F. R. Thompson. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. Condor 100:663-672.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Spring-Verlag, New York, New York, USA.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Chalfoun, A. D., and T. E. Martin. 2010a. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163:885-892.

Chalfoun, A. D., and T. E. Martin. 2010b. Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. Condor 112:701-710.

Chapa-Vargas, L., and S. K. Robinson. 2006. Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: local fragmentation vs. vegetation structure. Landscape Ecology 21:525-537.

Chen, J. N., N. F. Liu, C. Yan, and B. An. 2011. Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. Journal of Ornithology 152:603-608.

Chiron, F., and R. Julliard. 2007. Responses of songbirds to magpie reduction in an urban habitat. Journal of Wildlife Management 71:2624-2631.

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

Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107:605-616.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings of the Royal Society B-Biological Sciences 273:701-706.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on northern-cardinal nests– does choice of nest site matter. Condor 96:761-768.

Fontaine, J. J., and T. E. Martin. 2006a. Habitat selection responses of parents to offspring predation risk: An experimental test. American Naturalist 168:811-818.

Forsman, J. T., and T. E. Martin. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. Oikos 118:464-470.

Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Greig-Smith, P. W. 1982. Dispersal between nest-sites by stonechats *Saxicola torquata* in relation to previous breeding success. Ornis Scandinavica 13:232-238.

Hazler, K. R., A. J. Amacher, R. A. Lancia, and J. A. Gerwin. 2006. Factors influencing Acadian flycatcher nesting success in an intensively managed forest landscape. Journal of Wildlife Management 70:532-538.

Hazler, K. R., D. E. W. Drumtra, M. R. Marshall, R. J. Cooper, and P. B. Hamel. 2004. Common, but commonly overlooked: Red-bellied woodpeckers as songbird nest predators. Southeastern Naturalist 3:467-474.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84:416-430.

Hoover, J. P., and M. C. Brittingham. 1998. Nest-site selection and nesting success of Wood Thrushes. Wilson Bulletin 110:375-383.

Houston CS, Smith DG, Rohner C. 1998. Great-horned Owl (*Bubo virginianus*). The Birds of North America, No. 372. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Howlett, J. S., and B. J. M. Stutchbury. 1997. Within-season dispersal, nest-site modification, and predation in renesting hooded warblers. Wilson Bulletin 109:643-649.

Johnson, M. S. 1997. The effect of age on nest concealment and its complimentary effect on production of Wood Thrush. Wilson Bulletin 109:68-73.

Kelly JP. 1993. The effect of nest predation on habitat selection by dusky flycatchers in limber pine-juniper woodland. Condor 95:83-93.

Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. Journal of Field Ornithology 56:153-157

Leston LF, Rodewald AD. 2006. Are urban forests ecological traps for understory birds? An examination using northern cardinals. Biol Cons 131: 566-574.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649-659.

Maklakov, A., I. Simone, A. Gonzalez-Voyer, J. Ronn and N. Kolm. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. Biology Letters 7:730-732.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types – revising the dogmas. American Naturalist 141:897-913.

Martin, T.E. 1993b. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-532.

Martin, T. E., and J. V. Briskie. 2009. Predation on Dependent Offspring A Review of the Consequences for Mean Expression and Phenotypic Plasticity in Avian Life History Traits. Year in Evolutionary Biology 2009 1168:201-217.

Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51-57.

Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried,S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516-534.

Moller, A. P. 2010. Interspecific variation in fear responses predicts urbanization in birds. Behavioral Ecology 21:365-371.

Morosinotto, C., R. L. Thomson, and E. Korpimaki. 2010. Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. Journal of Animal Ecology 79:327-333.

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B-Biological Sciences 273:349-355.

Nowak, M., and K. Sigmund. 1993. A strategy of win stay, lose shift that outperforms tit-for-tat in the prisoners-dilemma game. Nature 364:56-58.

Parejo, D., J. White, J. Clobert, A. Dreiss, and E. Danchin. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. Ecology 88:2373-2382.

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Rangen, S. A., R. G. Clark, and K. A. Hobson. 1999. Influence of nest-site vegetation and predator community on the success of artificial songbird nests. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1676-1681.

Remes, V. 2005. Birds and rodents destroy different nests: a study of Blackcap *Sylvia atricapilla* using the removal of nest concealment. Ibis 147:213-216.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology:1-48.

Rodewald, A. D., and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? Biological Conservation 128:193-200.

Rodewald, A. D., and L. J. Kearns. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. Condor 113:899-906.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecological Applications 21:936-943.

Rodewald, A. D., and D. P. Shustack. 2008a. Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? Ecology 89:515-521.

Rodewald, A. D., and D. P. Shustack. 2008b. Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77:83-91.

Rodewald, A. D., D. P. Shustack, and L. E. Hitchcock. 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. Biological Invasions 12:33-39.

SAS Institute. 2008. SAS 9.2. SAS Institute, Cary, NC, USA.

Schmidt, K. A. 2001. Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. Evolutionary Ecology Research 3:633-648.

Schmidt, K. A. 2004b. Site fidelity in temporally correlated environments enhances population persistence. Ecology Letters 7:176-184.

Schmidt, K. A., S. R. X. Dall, and J. A. van Gils. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos 119:304-316.

Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. Oecologia 148:22-29.

Schmidt, K. A., and C. J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: Experimental and observational evidence. American Naturalist 152:393-402.

Schmidt, K.A. and C.J. Whelan. 1999. Effects of exotic Lonicera and Rhamnus on songbird nest predation. Conservation Biology 13:1502-1506.

Schmidt, K. A., and C. J. Whelan. 2010. Nesting in an uncertain world: information and sampling the future. Oikos 119:245-253.

Shackelford C.E., R.E. Brown, and R.N. Connor. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). The Birds of North America, No. 500. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Shustack, D. P., and A. D. Rodewald. 2010. Attenuated nesting season of the Acadian flycatcher (*Empidonax virescens*) in urban forests. Auk 127:421-429.

Smith-Castro J.R., and A.D. Rodewald. 2010a. Behavioral responses of nesting birds to human disturbance along recreational trails. Journal of Field Ornithology 81:130-138

Smith-Castro J.R. and A.D. Rodewald. 2010b. Effects of recreational trails on northern cardinals (Cardinalis cardinalis) in forested urban parks. Nat Areas Journal 30:328-337.

Soderstrom, B, T. Part, and J. Ryden. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia 117: 108-118.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102:5460-5465.

Stracey, C. M. 2011. Resolving the urban nest predator paradox: The role of alternative foods for nest predators. Biological Conservation 144:1545-1552.

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505-522.

Wagner, R. H., and E. Danchin. 2010. A taxonomy of biological information. Oikos 119:203-209.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424-437.

Weidinger, K. 2009. Nest predators of woodland open-nesting songbirds in central Europe. Ibis 151:352-360.

Whitehead D.R., and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). The Birds of North America, No. 614. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Wilson, R. R., and R. J. Cooper. 1998a. Acadian Flycatcher nest placement: Does placement influence reproductive success? Condor 100:673-679.

Zanette, L. Y. and B. Jenkins. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117:445-454

Table 3.1 Candidate models to explain changes in nest height of northern cardinal (*Cardinalis cardinalis*) nests between consecutive nesting attempts in response to predation pressure and seasonality in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (n = 160). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC$_c$**	**ΔAIC$_c$**	ω_i	**k**
prevfate	195.90	0	0.285	3
prevfate,arisk,prevfate*arisk	196.20	0.3	0.245	7
prevfate arisk	197.70	1.8	0.116	5
prevfate prisk	197.90	2.0	0.105	5
null	198.10	2.2	0.095	2
prevfate, prisk, prevfate*prisk	199.50	3.6	0.047	4
prevfate prisk arisk	199.80	3.9	0.041	7
arisk	200.20	4.3	0.033	3
prisk	200.20	4.3	0.033	6

Table 3.2 Candidate models to explain changes in nest concealment of northern cardinal (*Cardinalis cardinalis*) nests between consecutive nesting attempts in response to predation pressure and seasonality in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (n = 152). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC_c**	**ΔAIC_c**	**ω_i**	**k**
prevfate arisk	1435.4	0	0.271	5
prevfate prisk arisk	1435.4	0	0.271	6
arisk	1435.9	0.5	0.211	3
prevfate,arisk,prevfate*arisk	1436.2	0.8	0.182	7
prisk	1440.8	5.4	0.018	3
null	1440.9	5.5	0.017	2
prevfate prisk	1441.6	6.2	0.012	5
prevfate	1441.7	6.3	0.012	4
prevfate,prisk,prevfate*prisk	1443.5	8.1	0.005	7

Table 3.3 Candidate models to explain changes in vegetation density surrounding northern cardinal (*Cardinalis cardinalis*) nests within an 11.3 m radius between consecutive nesting attempts in response to predation pressure and seasonality in Franklin and Delaware Counties, Ohio, USA, 2006-2010 (n = 160). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC$_c$**	**ΔAIC$_c$**	**ω_i**	**k**
arisk	1692.2	0	0.269	3
prevfate arisk	1692.2	0	0.269	5
prevfate	1693.3	1.1	0.155	4
prevfate prisk arisk	1694.3	2.1	0.094	6
prevfate,arisk,prevfate*arisk	1694.4	2.2	0.089	7
prevfate prisk	1695.3	3.1	0.057	5
null	1696.5	4.3	0.031	2
prevfate,prisk,prevfate*prisk	1697.0	4.8	0.024	7
prisk	1698.6	6.4	0.011	3

Table 3.4 Candidate models to explain changes in nest height of Acadian flycatcher (*Empidonax virescens*) nests between consecutive nesting attempts in response to predation pressure and seasonality in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (*n* = 70). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC_c**	**ΔAIC_c**	**ω_i**	**k**
null	369.1	0	0.332	2
arisk	370.6	1.5	0.157	3
prevfate	370.7	1.6	0.149	4
prisk	370.9	1.8	0.135	3
prevfate arisk	372.1	3	0.074	5
prevfate prisk	372.4	3.3	0.064	5
prevfate,prisk,pfate*prisk	373.5	4.4	0.037	7
prevfate, prisk, arisk	374.0	4.9	0.029	6
prevfate,arisk,pfate*arisk	374.3	5.2	0.025	7

Table 3.5 Candidate models to explain changes in nest concealment of Acadian flycatcher (*Empidonax virescens*) nests between consecutive nesting attempts in response to predation pressure and seasonality in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (n = 66). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC$_c$**	**ΔAIC$_c$**	ω_i	**k**
null	627.1	0	0.371	2
prisk	628.7	1.6	0.167	3
prevfate	628.8	1.7	0.159	4
arisk	629.1	2.0	0.137	3
prevfate prisk	630.7	3.6	0.061	5
prevfate arisk	631.0	3.9	0.053	5
prevfate prisk arisk	633.1	6.0	0.018	6
prevfate,prisk,prevfate*prisk	633.1	6.0	0.018	7
prevfate,arisk,prevfate*arisk	633.4	6.3	0.018	7

Table 3.6 Candidate models to explain changes in vegetation density surrounding Acadian flycatcher (*Empidonax virescens*) nests within an 11.3 m radius between consecutive nesting attempts in response to predation pressure and seasonality in Franklin/Delaware Counties, Ohio, USA, 2006-2010, (n = 67). Prior experience = prevfate, perceived risk = prisk, actual risk = arisk.

Model	**AIC$_c$**	**ΔAIC$_c$**	ω_i	**k**
null	666.1	0	0.433	2
prevfate	668.2	2.1	0.152	4
prisk	668.4	2.3	0.137	3
prevfate,arisk,prevfate*arisk	668.9	2.8	0.107	7
prevfate arisk	670.3	4.2	0.053	5
arisk	670.5	4.4	0.048	3
prevfate prisk	670.5	4.4	0.048	5
prevfate,prisk,prevfate*prisk	672.5	6.4	0.018	7
prevfate, prisk, arisk	675.3	9.2	0.004	6

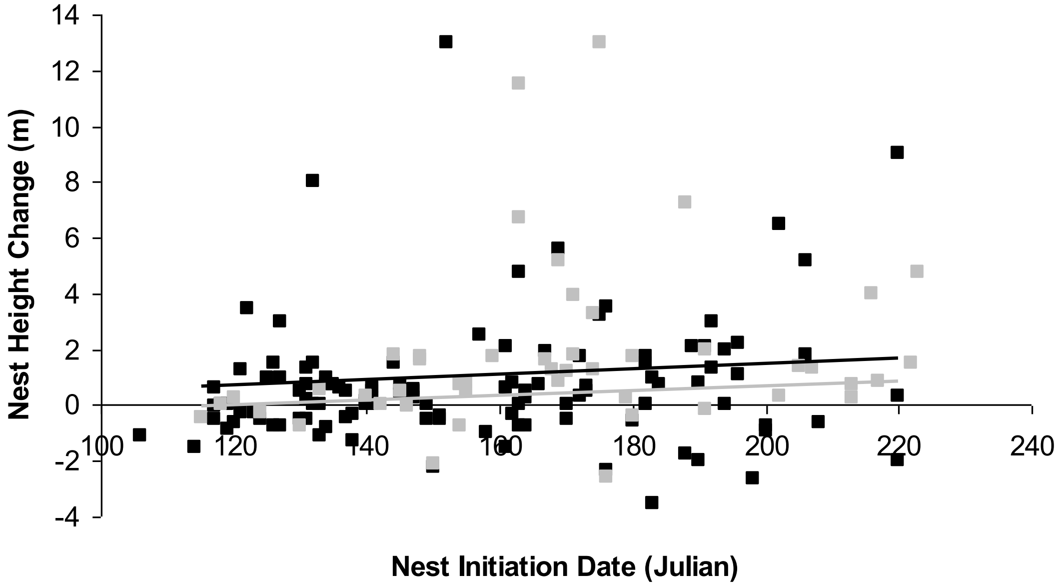

Figure 3.1 Changes in nest height between consecutive nesting attempts of northern cardinals (*Cardinalis cardinalis*) in response to previous nest fate and time of season (Julian date) in Franklin and Delaware Counties, Ohio, USA , 2006-2010, (*n* = 160, black squares = actual changes in nest height following a failed nest, and gray squares = actual changes in nest height following a successful nest). Predicted values were generated using equation of top model including previous fate and Julian date (115-220). (β_{prevfate}= -0.16 ± 0.077 SE, β_{julian}= 0.002 ±0.001 SE, β_0= 1.32 ± 0.215 SE, *n* = 160; black line = predicted change in nest height following a failed nest, y = 0.0098x - 0.4678, R^2 = 0.9992; gray line = predicted change in nest height following a successful nest, y = 0.0083x - 0.994, R^2 = 0.9992)

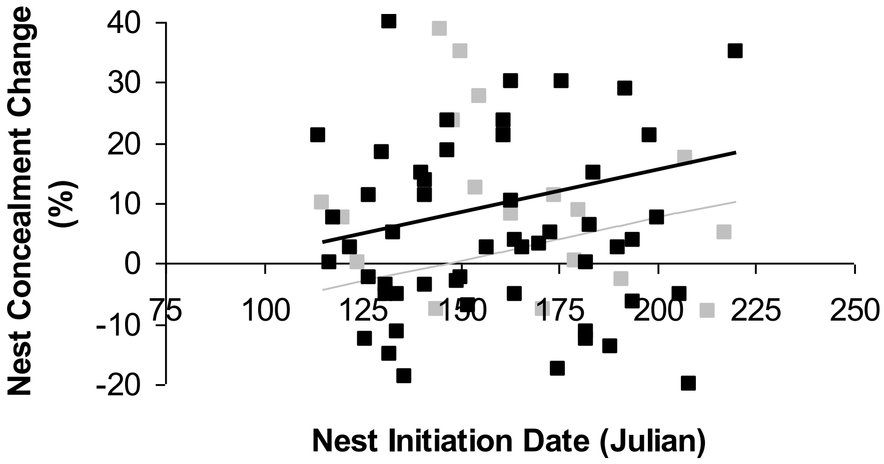

Figure 3.2 Changes in nest concealment between consecutive nesting attempts of northern cardinals (*Cardinalis cardinalis*) at high risk sites (0.05-0.10) in response to previous nest fate, actual predation risk, and time of season (Julian date) in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (*n* = 152, black squares = actual changes in nest concealment following a failed nest, and gray squares = actual changes in nest concealment following a successful nest). Predicted values were generated using the simpler top model with previous fate, actual predation risk, and Julian date (β_{prevfate}= -7.78 ± 4.833 SE, $\beta_{\text{predationrisk}}$= 250.27 ± 95.993 SE, β_{julian}= 0.14 ± 0.078 SE, β_0= -32.849 ± 15.408 SE, risk = 0.08, Julian date = 115-220, *n* = 152, black lines = predicted change in nest concealment following a failed nest, y = 0.0098x - 0.4678, R^2 = 0.9992; light gray lines = predicted change in nest concealment following a successful nest, y = 0.0098x - 0.4678, R^2 = 0.9992)

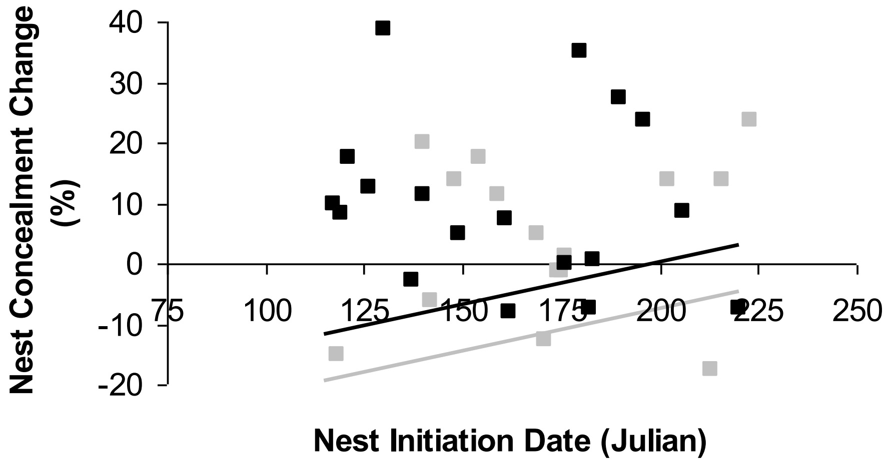

Figure 3.3 Changes in nest concealment between consecutive nesting attempts of northern cardinals (*Cardinalis cardinalis*) at low risk sites (0-0.05), in response to previous nest fate, actual predation risk, and time of season (Julian date) in Franklin and Delaware Counties, Ohio, USA , 2006-2010, (*n* = 152, black squares = actual changes in nest concealment following a failed nest, and gray squares = actual changes in nest concealment following a successful nest). Predicted values were generated using the simpler top model with previous fate, actual predation risk, and Julian date ($\beta_{prevfate}$= -7.78 ± 4.833 SE, $\beta_{predationrisk}$= 250.27 ± 95.993 SE, β_{julian}= 0.14 ± 0.078 SE, β_0= -32.849 ± 15.408 SE, risk = 0.02, Julian date = 115-220, *n* = 152, black lines = predicted change in nest concealment following a failed nest, y = 0.0098x - 0.4678, R^2 = 0.9992; light gray lines = predicted change in nest concealment following a successful nest, y = 0.0098x - 0.4678, R^2 = 0.9992)

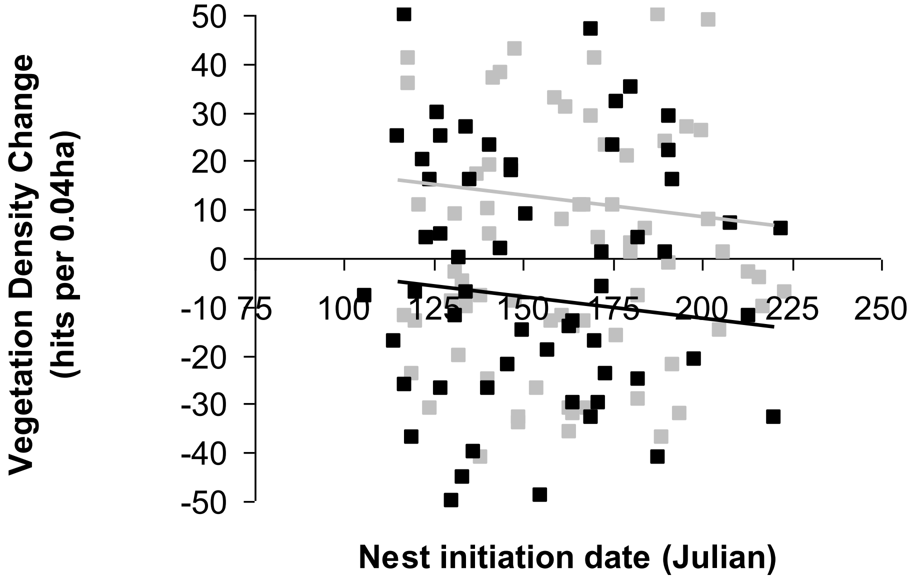

Figure 3.4 Changes in vegetation density surrounding the nest within an 11.3 m radius between consecutive nesting attempts of Northern Cardinals (*Cardinalis cardinalis*) in response to actual predation risk and time of season (Julian date 115-220) in Franklin and Delaware Counties, Ohio, USA, 2006-2010, (n = 160, black squares = actual changes in vegetation density in areas of high predation risk, and gray squares = actual changes in vegetation density in areas of low predation risk). Predicted values were generated using the top model of actual predation risk and Julian date ($\beta_{predrisk} = -348.25 \pm 163.91$, $\beta_{julian} = -0.09 \pm 0.130$, $\beta_0 = 36.93 \pm 25.086$ SE, n = 160, black line = predicted changes in vegetation density at high risk sites, $y = -0.09x + 5.5875$, $R^2 = 0.441$; gray line = predicted changes in vegetation density at low risk sites, $y = -0.09x + 26.483$, $R^2 = 0.441$)

Chapter 4: Unruffled in the face of danger: Parental care decisions of a common songbird do not reflect predation risk

Abstract

Predation risk can inform decisions about parental care, such as how frequently songbird parents provision young at the nest, but types of information used to make these decisions remain unclear. Because visits to nests can facilitate detection by predators, I predicted that birds would use public information regarding predation risk to make decisions about the frequency with which they provisioned nestlings. Moreover, as numbers or activity of nest predators can increase with urbanization and not necessarily be accompanied by increasing rates of nest predation, I predicted that birds nesting in urban landscapes would provision nestlings at similar rates as in rural landscapes. Using video obtained from continuous running, digital video cameras, I monitored provisioning rates of northern cardinals (*Cardinalis cardinalis*) at days 5, 6, or 7 of the nestling stage during the breeding seasons of 2008-2010 at forests within urbanizing landscapes of Ohio. Contrary to my expectations, provisioning rates were not related to public information reflecting either perceived (i.e., activity level of predators) or actual predation risk (i.e., average daily mortality rate of nests at the site), nor to vegetation. Rather, provisioning rates were best explained by and increased with brood size and to a lesser extent, the amount of urbanization. The fact that I found no evidence that provisioning behavior influenced nest fate suggests that other factors more strongly affect likelihood of nest predation. Thus, the degree to which decisions about provisioning are related to predation risk versus other ecological factors, such as food resources, may reflect the likelihood of other pressures that constrain reproductive success.

Keywords: urbanization, nestling, provisioning rate, parental care, predation risk, public information

Introduction

In ecosystems where predation risk is high and constant, breeding birds should reduce visits to nests to minimize detectability of the nest to predators (Skutch 1949). Indeed, empirical studies simulating risk with predator models or playbacks of predator calls confirm that parents and non-breeding helpers reduce both mate and nestling provisioning rates in risky environments, choosing instead to bring larger food portions in fewer visits (e.g. Ghalambor and Martin 2000, 2001, 2002, Eggers et al. 2005, Feretti et al. 2005, Fontaine and Martin 2006a, Martin et al. 2011). Less understood, however, are the types of information that birds use to assess predation risk and guide decisions about parental care of breeding birds (Lima 2009).

Public and private information are types of "detectable information", i.e. information in the environment that an organism senses and that provides individual awareness about predation risk (Wagner and Danchin 2010). Examples of public and private information that can be important when parents are caring for their young include actual and perceived predation risk (public) and previous nest fate (private) (Fontaine and Martin 2006, Chalfoun and Martin 2010b, Thomson et al. 2010). Information on actual predation risk can be acquired from mortality rates of neighborhood nests (Doligez et al. 2002, Fontaine and Martin 2006a), and information on perceived predation risk can be acquired from observations of predator numbers, activity rates, or vocalizations within a given area (Schmidt and Whelan 2005, Fontaine and Martin 2006a, Marzluff et al. 2007, Emmering and Schmidt 2011).

If decisions about provisioning reflect information about predation risk, then one might expect birds to adjust parental behavior in highly-altered and human-dominated systems, where predator-prey dynamics may be profoundly changed. The sheer diversity of potential predators in urban systems (Rodewald and Kearns 2011) provides a unique opportunity to investigate use of contrasting information sources about risk. For example, numbers of generalist predators tend to increase with urban development (Sorace 2002, Sorace and Gustin 2009, Rodewald et al. 2011), though actual predation rates may or may not be associated with urbanization (Gering and Blair 1999, Jokimaki and Huhta 2000, Thorington and Bowman 2003, Reale and Blair 2005, Rodewald et al. 2011). Furthermore, there is contrasting evidence on how birds may perceive and respond to risk in urban environments. In some studies, birds act as if they perceive higher predation risk in urban areas, such that individuals wait longer to resume feeding after being surprised by a predator, flock more readily, and startle from much further distances (Valcarcel and Fernandez-Juricic 2009, Seress et al. 2011). In contrasting studies, individuals in urban areas tolerate feeding at farther distances from cover or protection and startle from predators at closer proximity (Moller 2008, Tsurim et al. 2008), suggesting a perception of lower risk. In addition, few studies have examined how modifications in songbird behaviors, particularly provisioning rates, relate to perceived versus actual risk, and in areas with diverse predator communities (Martin and Briskie 2009), as found in cities.

While decisions about feeding may be related to predation risk (Martin et al. 2000, Massaro et al. 2008), provisioning rates also may be influenced by other individual or environmental factors, such as changes in food abundance or type (Wright et al. 1998, Mennechez and Clergeau 2006, Isaksson and Anderson 2007, Low et al. 2012). In addition, factors such as nest-site, brood, parental, or temporal characteristics can also influence provisioning rates (Linville et al. 1998, Martin et al. 2000, Schwagmeyer and Mock 2003, Leech 2006, Reed et al. 2007). Vegetation characteristics of the nests can influence the rate of nest predation (Martin et al. 2000, Weidinger 2002), thus vegetation structures and cover have the potential to provide extra protection such that birds might maintain or increase nest visitation rates. For example, decreases in vegetation cover near the nest explained reduced provisioning rates in jays and warblers when perceived predation risk was high (Eggers et al. 2008, Peluc et al. 2008). However, dense vegetation may also potentially increase predation risk by providing cover for predators. Thus, accounting for individual factors such as parental and brood characteristics and environmental factors such as food availability and vegetation surrounding the nest area are important for drawing conclusions about the impact of predation risk on provisioning rates.

To assess the influence of public information on parental behaviors and the consequent effects on predation, I examined how provisioning rates of songbird parents depended on perceived and actual predation risk, nest-site characteristics, and urbanization. I also analyzed the relationship between provisioning rate and nest fate. My study species was the northern cardinal (*Cardinalis cardinalis*), which is a common songbird species throughout eastern North America that responds positively to urban conditions. In central Ohio riparian forests, urbanization is associated with two key ecological changes that may affect nest provisioning behavior. First, numbers of predators tend to increase with urbanization, but do not predict rates of nest predation at sites (Rodewald et al. 2011). The disconnect between predator numbers and predation rates makes it possible to discriminate use of information related to predator numbers (i.e., perceived risk) from that related to actual risk of predation. Second, understory vegetation density increases with urbanization, largely due to invasion by the exotic Amur honeysuckle (*Lonicera maackii*) (Borgmann and Rodewald 2005), which might affect the frequency of nest visitations by concealing movements of parents. I hypothesized that provisioning rates would decline with both higher perceived and actual predation risk but would increase with greater nest concealment, and that nests with lower provisioning rates would be more likely to succeed. With respect to urbanization, even though predator numbers increase with urbanization (Rodewald et al. 2011), the increased amount of vegetation found in urban areas (Borgmann and Rodewald 2005) may compensate for any need to reduce provisioning rates, which in turn suggests that provisioning frequencies would remain the same over the urban-rural gradient. In addition, the consistency in nest predation rates across the urban-rural gradient (Rodewald et al. 2011) suggests that provisioning rates would remain the same as in rural areas.

Methods

Study Site and Study Species

I studied northern cardinals in ten riparian forest sites in central Ohio within a 40-km (25 mi) radius of the city of Columbus, in both Franklin and Delaware counties. Sites were located in areas surrounded by variable amounts of urban development. To represent the amount of urbanization surrounding each site, an urban index was created based on the number of buildings and amount of pavement, forest cover, and agriculture found within a 1-km radius of the center of each study site (Rodewald and Shustack 2008a). The forest sites included common overstory trees such as cottonwood (*Populus deltoides* Bartram ex Marsh.), sycamore (*Platanus occidentalis* L.), ash (*Fraxinus spp.),* and maple (*Acer spp.*). Shrubs and small trees such as the exotic Amur honeysuckle (*Lonicera mackii* (Rupr.) Herder), multiflora rose (*Rosa multiflora* Thunb.), buckeye (*Aesculus glabra* Willd.), box elder (*Acer negundo* L.), pawpaw (*Asimina triloba* L.), and spicebush (*Lindera benzoin* (L.) Blume) dominated the understory. The community of nest predators at sites was diverse (Rodewald and Kearns 2011). Avian nest predators present at the sites included brown-headed cowbirds (*Molothrus ater*), blue jays (*Cyanocitta cristata*), common grackles (*Quiscalus quiscala*), American crows (*Corvus brachyrhynchos*), Cooper's hawks (*Accipiter cooperii*), red-shouldered hawks (*Buteo lineatus*), red-tailed hawks (*Buteo jamaicensis*), broad-winged hawks (*Buteo platypterus*), and barred owls (*Strix varia*). Mammalian nest predators present were northern raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), gray squirrels (*Sciurus carolinensis*), red squirrels (*Tamiasciurus hudsonicus*), southern flying squirrels

(*Glaucomys volans*), chipmunks (*Tamias striatus*), and feral/domesticated cats (*Felis catus*) and dogs (*Canis familiaris*).

Northern cardinals are common breeding birds in riparian forests, and nest repeatedly throughout a 5-6 month long breeding season. Both parents provision young, and although male cardinals typically provision more than females, rates of provisioning are highly correlated between mates (Filliater and Breitwisch 1997, Linville et al. 1998). Others have reported that provisioning rates do not vary with the time of day (Filliater-Lee 1992), but do increase with number of nestlings (Filliater and Breitwisch 1997) and for males in better body condition (Jawor and Breitwisch 2004).

Field Data Collection

Cardinals were captured, banded, and measured at sites from 2008-2010. Each cardinal received three plastic and one unique steel US Geological Survey band so that I could identify individual birds and their nests. From April through August, sites were visited three times per week to locate and monitor nests of banded individuals. I determined nest fate by looking for evidence of failure or success at the estimated dates of fledging. Nests that finished prior to the estimated fledge date and had no evidence of young were considered to have failed. Successful nests were those that finished on or after the estimated fledge date, and for which I found fledglings or signs of fledging, such as fecal material around the nest or parents carrying food or defensively chipping nearby. The nest area and territory was visited at least two more times within one week in order to confirm failure or success.

Potential nest predators were surveyed twice per week at different times between 6am and 2pm at each site. The perpendicular distance to any avian or mammalian nest predators observed by sight or sound within 100 m of a 250-m transect was recorded. Each survey took approximately 20 minutes. Observers were trained to identify predators by sight and sound, wore camouflaged –colored clothing, and walked slowly and quietly to minimize effects on predator detectability.

As soon as possible after a nest fledged or failed, I measured nest vegetation characteristics. Using an ocular tube and standing 1m from the nest, I estimated the percent nest cover above, below, and at the sides of the nest in all four cardinal directions. I then averaged these cover estimations to represent overall nest cover for each nest. To estimate the vegetation density within the nest area, I counted the number of times vegetation touched a vertical pole at sampling points every 2m along four 11.3 m radii at each cardinal direction. For each sampling point (20 total per nest), I counted the number of times vegetation touched the pole between 0.5-3m in height, and summed these for each nest.

I observed nest provisioning using battery-powered video cameras; one type was produced by Fuhrman Diversified, but the other type we built ourselves using a model developed by Cox et al. (2012). I deployed 16 cameras per season to observe nests opportunistically, such as when a female had completed laying the eggs in a nest, when nests were in areas that supported and/or concealed the camera equipment, and in such a way to make a relatively equal number of observations at each site throughout the breeding system. The systems recorded digital video continuously, enabling us to monitor parental behaviors at the nest by watching the video at a later date.

Provisioning Observations

Because females often continue brooding the first few days after hatching, we observed cardinal provisioning at nests that survived to at least day 5 of the nestling stage. Starting at this stage also allowed for maximization of sample size, as many nests were depredated at day 5 or later. I watched video of the parents provisioning their young on day 5, 6, or 7, because provisioning rates are similar during this time (Filliater and Breitwisch 1997), and again to maximize sample size. For nests that were active all 3 days of the sampling period, I chose the date of observation based on which days the video monitoring had not been interrupted by a field technician checking the nest and which days had complete and uninterrupted video. If there was a choice between days, I used a random number table to choose the day of observation. Nests contained 1 to 3 nestlings, most of which were cardinal young. A few nests contained cowbird young, but previous work shows that cardinal provisioning rates do not vary by species of nestling (Eckerle and Breitwisch 1997). In my sample, I included 60 video-recorded nests that had survived until at least day 5.

I watched all nests for the 6 hours after sunrise, similar to Martin et al. (2000). I chose to survey over a longer period of time, rather than just an hour, to account for differences in individual preferences in provisioning schedules. Because at times the watch period was truncated due to video failure, changing weather conditions, or nest depredation, I used the average number of visits per hour as my response variable.

To calculate an index of perceived predation risk (hereafter “perceived risk”), I used the predator survey data. For each site and year, I summed all the observations of predators, standardized them by effort, and calculated the number of predators encountered per hour. I used observations of all predators across each entire season, because I wanted to test the response to a generalized level of predation risk and due to the lack of a priori knowledge about how birds perceive and respond to risk over time (Lima and Bednekoff 1999).

I used daily mortality rate (1- daily survival rate) of cardinal nests at each site to represent actual predation risk (hereafter “actual risk”). I calculated daily survival rate of cardinal nests (n = 784) for each site by year using the logistic exposure method (Shaffer 2004, PROC GENMOD with maximum likelihood estimation, SAS ver. 9.2), which uses a generalized linear model that accounts for the period of time between nest checks (exposure days), as well as the age of the nest. The average number of exposure days per nest was 11.91 ± 0.28 SE.

Data Analysis

To determine if predation risk informed cardinal provisioning rates, I first selected a set of potentially important variables that might explain provisioning rates based on the literature. Variables that I considered included perceived risk, actual risk, brood size, the percentage of immediate nest concealment provided by vegetation, the vegetation density within the nest patch, and the urban index of the site. As I limited my observations to the same morning period for all nests and because cardinal provisioning rates are reported to be consistent over the course of a day (Filliater-Lee 1992, Figure 4.1), I did not include time of day in analyses. I also restricted my observations to a brief nestling period (5-7 days) known to have relatively stable rates of provisioning (Filliater and Breitwisch 1997), and, as such, did not include nestling age in the analyses. Even though I recorded both parents visiting all nests, I did not distinguish between sexes when scoring the number of visits to the nests, and thus I excluded the number and sex of parents from the analysis. As territory sizes of cardinals tend to be smaller within urban versus rural forests (Rodewald and Shustack 2008a) and may have a possible effect on provisioning rates, incorporating the urban index into the analysis helped to account for the associated differences in territory size with urbanization.

To compare a set of candidate models with the remaining variables of brood size, the urban index, immediate and patch level nest concealment, actual risk, and perceived risk, I used a mixed effects model (PROC MIXED, SAS ver. 9.2), with site and year as random effects. Because numerous studies show that provisioning behavior is sensitive to brood size (e.g. Filliater and Breitwisch 1997), I included the number of nestlings in all models with the exception of the null. This allowed me to account for the effect of brood size such that I could evaluate other models of interest. I then ranked each model within an information theoretic framework using the Akaike's Information Criterion corrected for small sample sizes (AIC_c, Burnham and Anderson 2002). I used a similar approach to examine how provisioning rate, actual predation risk, and vegetation characteristics might explain nest fate. In this case, I used logistic regression (PROC LOGISTIC, SAS ver. 9.2.) to examine the relationship of these variables to nest fate, and then evaluated each model within the information theoretic framework.

Results

The best model explaining hourly provisioning rate included only the variables of brood size and the urban index ($\beta_{nstlg} = 1.159 \pm 0.229$, $\beta_{urban} = 0.314 \pm 0.172$, $\beta_0 = 1.597 \pm 0.536$, $\omega_i = 0.287$, Table 4.1), and provisioning rate increased with both the number of nestlings and the urban index (Figure 4.2 and 4.3). However, the 95% confidence interval for urbanization included zero, indicating that the effect was very small. The other two models ranked within $\Delta AIC_c \leq 2$ and equally plausible included 1) brood size ($\beta_{nstlg} = 1.129 \pm 0.235$, $\beta_0 = 1.797 \pm 0.539$, $\omega_i = 0.174$, Table 4.1), and 2) brood size and vegetation density ($\beta_{nstlg} = 1.140 \pm 0.233$, $\beta_{vegdens} = -0.005 \pm 0.004$, $\beta_0 = 2.109 \pm 0.601$, $\omega_i = 0.106$, Table 4.1). The 95% confidence interval for vegetation density included zero however, indicating little effect. None of the models with Δ $AIC_c = 2$ included either predation risk variable (Table 4.1).

I found little evidence that provisioning rates, either alone or in combination with information on vegetation and nest predation, explained nest fate, as the null was the best model ($\beta_0 = 1.012 \pm 0.292$, $\omega_i = 0.217$, *n* = 60, Table 4.2). Although nests that failed tended to be at sites with higher levels of actual predation risk (daily predation rates of sites with failed nests: 0.064 ± 0.004 SE, with successful nests: 0.057 ± 0.002 SE), provisioning rates were actually higher for successful nests (failed: 3.91 ± 0.39 SE, successful: 4.38 ± 0.23 SE).

Discussion

Despite the fact that nest predators were more active and/or abundant in urban than rural forests in my system, provisioning rates were not strongly associated with urbanization, nor were they explained by nest-site characteristics or site-level estimates of predation risk. Rather, brood size was the strongest predictor of provisioning rates in my system, and the apparent lack of use of predator information is consistent with the absence of a relationship between nest visits and nest fate. It is not uncommon that brood size explains provisioning rate, as many others have found (Filliater and Breitwisch 1997, Olsen et al. 2008, Chalfoun and Martin 2010b); more mouths to feed prompts more trips to the nest. Although predation is thought to be a major driver of provisioning rates (e.g., Skutch 1949; Martin et al. 2000), availability of food and other resources also may constrain the number of feeding trips, especially in anthropogenic-influenced environments (Shochat 2004, Mennechez and Clergeau 2006, Sauter et al. 2006, Isaksson and Andersson 2007, Ibanez-Alamo and Soler 2011). For example, provisioning rates may be influenced by nutrient content of food (Isaksson and Anderson 2007), or reduced food for young in some areas such as city centers (Mennechez and Cleargeau 2006). However, some combination of predation risk and food in conjunction with other environmental factors likely explains provisioning (e.g. Eggers et al. 2008). In addition, urban environments introduce novel stressors that can increase the frequency of provisioning behaviors, such as noise from roads that induce higher stress levels in songbirds that result in higher provisioning rates (Crino et al. 2011), or stress from human visitation that invokes more cautious visitation (Valcarcel and Fernandez-Juricic 2009). Finally, fledgling production may provide a better metric to evaluate the effects of provisioning on reproductive success (Fontaine et al. 2007). By examining only nest fate, I did not account for the effect of partial nest predation, particularly near the time of fledging, on productivity rates.

Life history theory may provide an alternative explanation for the apparent reduced sensitivity of cardinals to predation risk. Passerines with relatively short life spans and high fecundity have demonstrated a higher tolerance to risk (Ghalambor and Martin 2000). The life span of cardinals typically ranges from 3 to 6 years (Laskey 1944, Halkin and Linville 1999), and they are prolific breeders, renesting up to seven times and capable of producing three or more successful nests within a single breeding season (A. Rodewald, unpublished data). Hence, cardinals may represent shorter-lived species with a greater tolerance to predation risk, which is consistent with their successful colonization of urban areas (Moller 2009).

There are three important caveats to my findings. First, although I found no evidence that cardinals adjusted provisioning behavior based on public information about predators, there remains the possibility that private information (e.g., previous nest fate) was used. For example, Chalfoun and Martin (2010a) found that for Brewer’s sparrows (*Spizella breweri*), private information about risk in the form of previous fate was more important in explaining nest-site selection than public information. In addition, I found that cardinals used information regarding private information in nest-site selection (Kearns Ch.3). Though a limited sample size prevented me from including previous nest fate in the analysis of provisioning rates, I conducted a post-hoc test on a subsample of 40 nests. I found no support, however, for the idea that previous nest fate influenced provisioning behavior. Second, cardinals may have used other types of cues about predators or focused only on specific predator species. For example, some birds may be able to sense the level of danger from the direction of a predator's gaze (e.g. Carter et al. 2008). Moreover, birds may be more sensitive to predator information about only those species that are likely to attack during provisioning, such as raptors. Because the predator community is so diverse in my system with no single species dominating (Rodewald and Kearns 2011), I used surveys for the entire predator community. However, closer examination of responses to specific predators and their behaviors, along with experimental work, would be helpful to ascertain if predator species is important for cardinals in assessing risk. Third, the scale of information at which I assessed predation risk may also differ from the scale at which cardinals assess risk during nest provisioning. Both perceived risk and actual risk were measured at the site level whereas provisioning behavior occurs at the nest or territory site level. Birds can assess information about the predation risk of habitats at multiple scales, but predation risk influencing provisioning rate may be assessed at the territory or nest-site level (Lima 2002, Chalfoun and Martin 2007, Schmidt and Schauber 2007).

In conclusion, provisioning behavior of cardinals appears not to reflect predation risk, both actual and perceived, at the site scale during the nestling stage. The instinct to provision regardless of possible risk may be one of the many behaviors that enable them to flourish, particularly in urban areas. However, the potential importance of food availability in governing feeding rates warrants further study particularly in urban areas. In addition to this, examination of additional cues of predation risk and at finer scales, particularly with experimental work, will further elucidate how adjustments in provisioning rates can act as a defense against nest predation for cardinals and other songbirds.

References

Borgmann, K. L., and A. D. Rodewald. 2005. Forest restoration in urbanizing landscapes: Interactions between land uses and exotic shrubs. Restoration Ecology 13:334-340.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.

Carter, J. N., J. Lyons, H. L. Cole, and A. R. Goldsmith. 2008. Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. Proceedings of the Royal Society B-Biological Sciences 275:1709-1715.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Chalfoun, A. D., and T. E. Martin. 2010a. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163:885-892.

Chalfoun, A. D., and T. E. Martin. 2010b. Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nests. Condor 112:701-710.

Cox, W. A., F. R. Thompson, III, and J. Faaborg. 2012. Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. Auk 129:147-155.

Crino, O. L., B. K. Van Oorschot, E. E. Johnson, J. L. Malisch, and C. W. Breuner. 2011. Proximity to a high traffic road: Glucocorticoid and life history consequences for nestling white-crowned sparrows. General and Comparative Endocrinology 173:323-332.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170.

Eckerle, K. P., and R. Breitwisch. 1997. Reproductive success of the Northern Cardinal, a large host of Brown-headed Cowbirds. Condor 99:169-178.

Eggers, S., M. Griesser, T. Andersson, and J. Ekman. 2005. Nest predation and habitat change interact to influence Siberian jay numbers. Oikos 111:150-158.

Eggers, S., M. Griesser, and J. Ekman. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. Behavioral Ecology 19:1056-1062.

Emmering, Q. C., and K. A. Schmidt. 2011. Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. Journal of Animal Ecology 80:1305-1312.

Ferretti, V., P. E. Llambias, and T. E. Martin. 2005. Life-history variation of a neotropical thrush challenges food limitation theory. Proceedings of the Royal Society B-Biological Sciences 272:769-773.

Filliater, T. S., and R. Breitwisch. 1997. Nestling provisioning by the extremely dichromatic Northern Cardinal. Wilson Bulletin 109:145-153.

Filliater-Lee, T.S. 1992. Parental roles in feeding nestlings, and nest sites and nest success in Northern Cardinals (Cardinalis cardinalis). M.S. thesis, Univ. of Dayton, Dayton, Ohio.

Fontaine, J. J., and T. E. Martin. 2006a. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428-434.

Fontaine, J. J., M. Martel, H. A. Markland, A. A. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116:1887-1894.

Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532-541.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494-497.

Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behavioral Ecology 13:101-108.

Halkin, S. L. and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). The birds of North America online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/440 doi:10.2173/bna.440

Ibanez-Alamo, J. D., and M. Soler. 2010. Does urbanization affect selective pressures and life-history strategies in the common blackbird (Turdus merula L.)? Biological Journal of the Linnean Society 101:759-766.

Isaksson, C., and S. Andersson. 2007. Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. Journal of Avian Biology 38:564-572.

Jawor, J. M., and R. Breitwisch. 2004. Multiple ornaments in male northern cardinals, Cardinalis cardinalis, as indicators of condition. Ethology 110:113-126.

Jokimaki, J., and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838-847.

Laskey, A.R. 1944. A study of the cardinal in Tennessee. Wilson Bulletin 56:27-44.

Leech, D. I., L. V. Rowe, and I. R. Hartley. 2006. Experimental evidence for adjustment of parental investment in relation to brood sex ratio in the blue tit. Animal Behaviour 72:1301-1307.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70-75.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649-659.

Linville, S. U., R. Breitwisch, and A. J. Schilling. 1998. Plumage brightness as an indicator of parental care in northern cardinals. Animal Behaviour 55:119-127.

Low, M., T. Makan, and I. Castro. 2012. Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. Behavioral Ecology 23:25-34.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types – revising the dogmas. American Naturalist 141:897-913.

Martin, T.E. 1993b. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-532.

Martin, T. E., and J. V. Briskie. 2009. Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Year in Evolutionary Biology 2009 1168:201-217.

Martin, T. E., P. Lloyd, C. Bosque, D. C. Barton, A. L. Biancucci, Y. R. Cheng, and R. Ton. 2011. Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. Evolution 65:1607-1622.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London Series B-Biological Sciences 267:2287-2293.

Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried, S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516-534.

Massaro, M., A. Starling-Windhof, J. V. Briskie, and T. E. Martin. 2008. Introduced Mammalian Predators Induce Behavioural Changes in Parental Care in an Endemic New Zealand Bird. Plos One 3.

Mennechez, G., and P. Clergeau. 2006. Effect of urbanisation on habitat generalists: starlings not so flexible? Acta Oecologia 30:182-191.

Moller, A. P. 2008. Flight distance and population trends in European breeding birds. Behavioral Ecology 19:1095-1102.

Moller, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159:849-858.

Olsen, B., J. Felch, R. Greenberg, and J. Walters. 2008. Causes of reduced clutch size in a tidal marsh endemic. Oecologia 158:421-435.

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Reale, J.A. and R. B. Blair. 2005. Nesting success and life-history attributes of bird communities along an urbanization gradient. Urban Habitats 3:1-24.
Available from http://urbanhabitats.org [accessed April 2012].

Reed, L., R. Vallender, and R. Robertson. 2007. Provisioning Rates by Golden-Winged Warblers. Wilson Journal of Ornithology 119:350-355.

Rodewald, A. D., and L. J. Kearns. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. Condor 113:899-906.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecological Applications 21:936-943.

Rodewald, A. D., and D. P. Shustack. 2008a. Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? Ecology 89:515-521.

Sauter, A., R. Bowman, S. J. Schoech, and G. Pasinelli. 2006. Does optimal foraging theory explain why suburban Florida scrub-jays (Aphelocoma caerulescens) feed their young human-provided food? Behavioral Ecology and Sociobiology 60:465-474.

Schmidt, K. A., and E. M. Schauber. 2007. Behavioral indicators of predator space use: Studying species interactions through the behavior of predators. Israel Journal of Ecology & Evolution 53:389-406.

Schmidt, K. A., and C. J. Whelan. 2005. Quantifying male Wood Thrush nest-attendance and its relationship to nest success. Condor 107:138-144.

Schwagmeyer, P., and D. Mock. 2003. How consistently are good parents good parents? Repeatability of parental care in the House Sparrow, Passer domesticus. Ethology 109:303-313.

Seress, G., V. Bokony, J. Heszberger, and A. Liker. 2011. Response to Predation Risk in Urban and Rural House Sparrows. Ethology 117:896-907.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. Oikos 106:622-626.

Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430-55.

Sorace A. 2002. High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fennica 79:60-71.

Sorace, A., and M. Gustin. 2009. Distribution of generalist and specialist predators along urban gradients. Landscape and Urban Planning 90:111-118.

Thomson, R. L., G. Tomas, J. T. Forsman, J. Broggi, and M. Monkkonen. 2010. Predator proximity as a stressor in breeding flycatchers: mass loss, stress protein induction, and elevated provisioning. Ecology 91:1832-1840.

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

Tsurim, I., Z. Abramsky, and B. P. Kotler. 2008. Foraging behavior of urban birds: are human commensals less sensitive to predation risk than their nonurban counterparts? Condor 110:772-776.

Valcarcel, A., and E. Fernandez-Juricic. 2009. Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? Behavioral Ecology and Sociobiology 63:673-685.

Wagner, R. H., and E. Danchin. 2010. A taxonomy of biological information. Oikos 119:203-209.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424-437.

Wright, J., C. Both, P. A. Cotton, and D. Bryant. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology 67:620-634.

Table 4.1 Candidate model set for nest provisioning rate per hour of northern cardinals (*Cardinalis cardinalis*) in response to number of nestlings (nestlings), amount of urbanization, nest concealment immediately surrounding the nest (nestcover), vegetation density within the nest patch, actual predation risk, and perceived predation risk in Franklin and Delaware Counties, Ohio, USA, 2008-2010, (*n* = 60)

Model	**K**	**AIC_c**	**ΔAIC_c**	**ω_i**
Nestlings urban	3	207.7	0.0	0.287
Nestlings	2	208.7	1.0	0.174
Nestlings, vegetation density	3	209.7	2.0	0.106
Nestlings, nest cover	3	209.9	2.2	0.096
Nestlings, actual predation risk	3	210.1	2.4	0.086
Nestlings, urban, nest cover, vegetation density	5	210.5	2.8	0.071
Nestlings, perceived predation risk	3	210.8	3.1	0.061
Nestlings, vegetation density, nest cover	4	211.2	3.5	0.050
Nestlings, urban, actual predation risk, perceived predation risk	5	212.1	4.4	0.032
Nestlings, actual predation risk, perceived predation risk	4	212.5	4.8	0.026
Nestlings, urban, vegetation density, nest cover, actual predation risk, perceived predation risk	7	215.2	7.5	0.007
Nestlings, nest cover, vegetation density, actual predation risk, perceived predation risk	6	215.6	7.9	0.006
Null	1	227.7	20.0	0.000

Table 4.2 Candidate model set examining relationship of actual predation risk, vegetation (vegetation density and nest cover), and northern cardinal (*Cardinalis cardinalis*) visits per nest per hour with dependent variable of nest fate in Franklin and Delaware Counties, Ohio, USA, 2008-2010, (*n* = 60)

Model	**K**	**AIC**	**ΔAIC**	**ω_i**
Null	1	71.59	0	0.138
Actual predation risk	2	72.03	0.44	0.110
Visits/hr	2	72.44	0.85	0.090
Visits/hr, actual predation risk	3	72.58	0.99	0.084
Nest cover	2	72.91	1.32	0.071
Actual predation risk, nest cover	3	73.44	1.85	0.055
Vegetation density	2	73.50	1.91	0.053
Visits/hr, nest cover	3	73.55	1.96	0.052
Visits/hr, actual predation risk, nest cover	4	73.77	2.18	0.046
Actual predation risk, vegetation density	3	73.84	2.25	0.045
Visits/hr, vegetation density	3	74.40	2.81	0.034
Visits/hr, actual predation risk, vegetation density	4	74.46	2.87	0.033
Visits/hr * actual predation risk	4	74.57	2.98	0.031
Visits/hr, nest cover, vegetation density	4	74.81	3.22	0.028
Nest cover, vegetation density	3	74.81	3.22	0.028
Actual predation risk, nest cover	3	74.84	3.25	0.027
Actual predation risk, nest cover, vegetation density	4	75.23	3.64	0.022
Visits/hr*nest cover	4	75.46	3.87	0.020
Visits/hr, actual predation risk, nest cover, vegetation density	5	75.61	4.02	0.018
Visits/hr*vegetation density	4	75.87	4.28	0.016

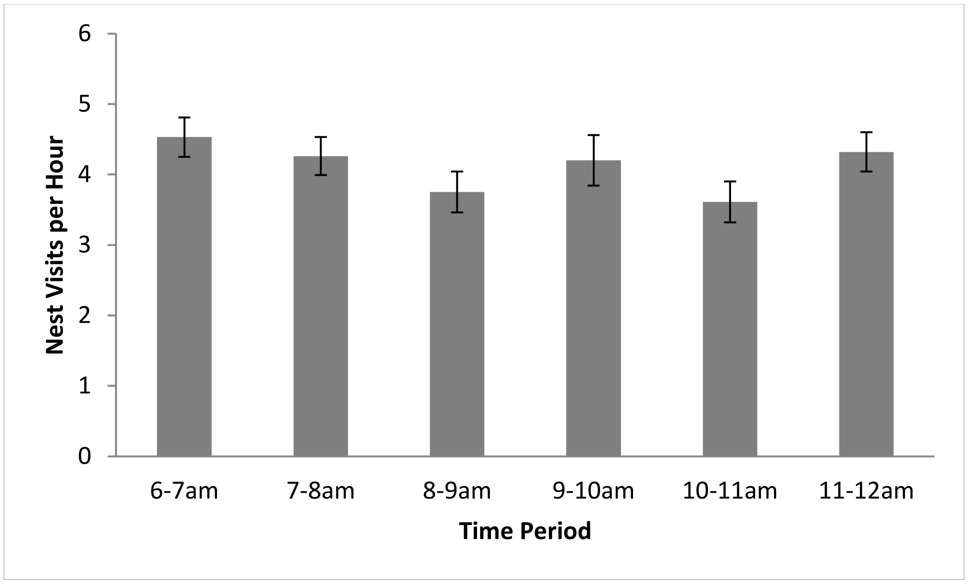

Figure 4.1 Parental provisioning rate per hour of northern cardinal (*Cardinalis cardinalis*) nests from day 5-7 of nestling stage, Franklin and Delaware Counties, Ohio, USA, 2008-2010, (n = 60)

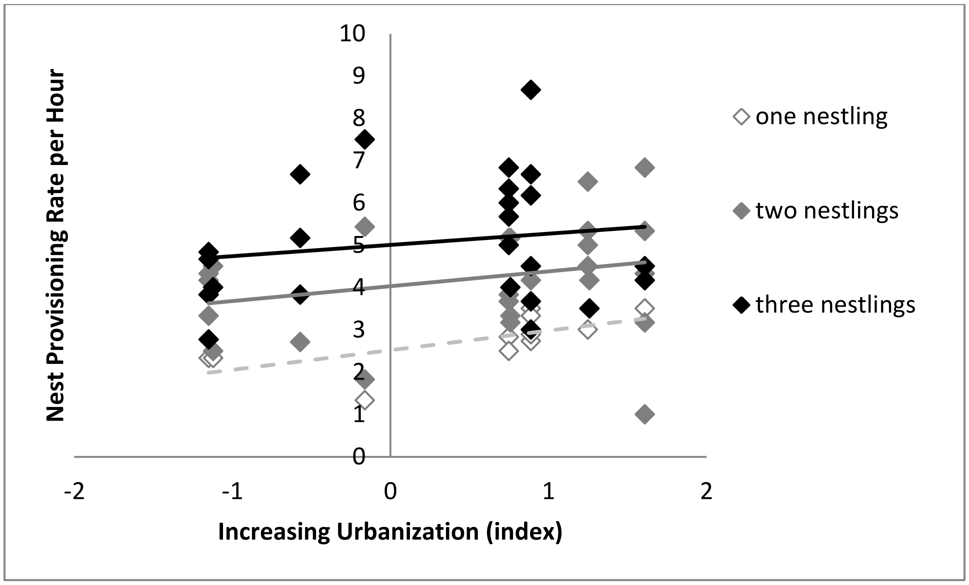

Figure 4.2 Nest provisioning rate per hour of northern cardinals (*Cardinalis cardinalis*) with respect to increasing urbanization and number of nestlings in the nest in Franklin and Delaware Counties, Ohio, USA, 2008-2010, (n = 60).. Trend lines for each nestling count with relation to urbanization: one nestling – $y = 0.464x + 2.520$, $R_2 = 0.449$; two nestlings – $y = 0.350x + 4.031$, $R_2 = 0.072$, three nestlings – $y = 0.267x + 5.006$, $R_2 = 0.028$

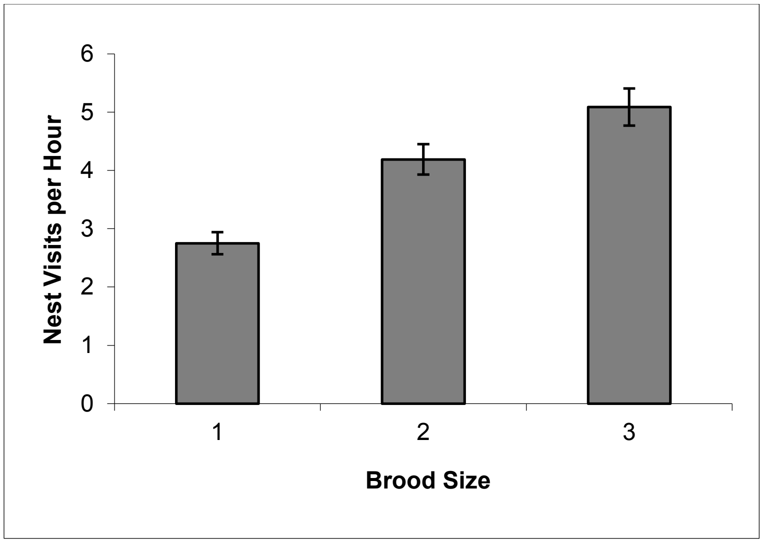

Figure 4.3. Nest provisioning rate per hour of northern cardinals (*Cardinalis cardinalis*) with respect to brood size in Franklin and Delaware Counties, Ohio, USA, 2008-2010. One nestling, *n* = 11; two nestlings, *n* = 27; three nestlings, *n* = 22

Bibliography

Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat-selection across a rural-to-urban landscape gradient. Auk 128:293-302.

Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (Empidonax virescens) in central Ohio. Auk 123:368-382.

Bednekoff, P. A., and S. L. Lima. 2004. Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. Proceedings of the Royal Society of London Series B-Biological Sciences 271:1491-1496.

Bednekoff, P. A., and S. L. Lima. 2005. Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? Animal Behaviour 69:1165-1171.

Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225-234.

Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proceedings of the Royal Society B-Biological Sciences 275:2257-2263.

Bessinger SR and DR Osbourne. 1982. Effects of urbanization on avian community organization. Condor 84:75-83.

Berger-Tal, R., O. Berger-Tal, and K. Munro. 2010. Nest desertion by Grey Fantails during nest building in response to perceived predation risk. Journal of Field Ornithology 81:151-154.

Beyer, H. 2011. Geospatial Modeling Environment. URL http://www.spatialecology.com/gme

Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipter striatus*). The Birds of North America, No. 482. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506-519.

Borgmann, K. L. and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14: 1757-1765.

Borgmann, K. L., and A. D. Rodewald. 2005. Forest restoration in urbanizing landscapes: Interactions between land uses and exotic shrubs. Restoration Ecology 13:334-340.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399.

Brown, J.S. and B. P. Kotler. 2007. Foraging and the ecology of fear. Pp. 437-482 *in* Foraging, eds. D.W. Stephens, J.S. Brown, and R. Ydenberg. The University of Chicago Press, Chicago.

Burhans, D. E., D. Dearborn, F. R. Thompson, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66:240-249.*

Burhans, D. E., and F. R. Thompson. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. Condor 100:663-672.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.

Caro, T. 2005. Antipredator defenses in birds and mammals. The University of Chicago Press, Chicago.

Carter, J., N. J. Lyons, H. L. Cole, and A. R. Goldsmith. 2008. Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. Proceedings of the Royal Society B-Biological Sciences 275:1709-1715.

Chace, JF and JJ Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Chalfoun, A. D., and T. E. Martin. 2010a. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163:885-892.

Chalfoun, A. D., and T. E. Martin. 2010b. Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nests. Condor 112:701-710.

Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson. 2002. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858-867.

Chapa-Vargas, L., and S. K. Robinson. 2006. Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: local fragmentation vs. vegetation structure. Landscape Ecology 21:525-537.

Chen, J. N., N. F. Liu, C. Yan, and B. An. 2011. Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. Journal of Ornithology 152:603-608.

Chiron, F., and R. Julliard. 2007. Responses of songbirds to magpie reduction in an urban habitat. Journal of Wildlife Management 71:2624-2631.

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

Cox, W. A., F. R. Thompson, III, and J. Faaborg. 2012. Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. Auk 129:147-155.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis 150:3-17.

Crino, O. L., B. K. Van Oorschot, E. E. Johnson, J. L. Malisch, and C. W. Breuner. 2011. Proximity to a high traffic road: Glucocorticoid and life history consequences for nestling white-crowned sparrows. General and Comparative Endocrinology 173:323-332.

Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107:605-616.

Ditchkoff, S. S., S. T. Saalfeld, and C. J. Gibson. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Pages 5-12 in Urban Ecosystems, vol. 9.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170.

Eckerle, K. P., and R. Breitwisch. 1997. Reproductive success of the Northern Cardinal, a large host of Brown-headed Cowbirds. Condor 99:169-178.

Eggers, S., M. Griesser, T. Andersson, and J. Ekman. 2005. Nest predation and habitat change interact to influence Siberian jay numbers. Oikos 111:150-158.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings of the Royal Society B 273:701-706.

Eggers, S., M. Griesser, and J. Ekman. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. Behavioral Ecology 19:1056-1062.

Emmering, Q. C., and K. A. Schmidt. 2011. Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. Journal of Animal Ecology 80:1305-1312.

Fauchald, P., K. E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology 81:773-783.

Fedy, B. C., and T. E. Martin. 2009. Male songbirds provide indirect parental care by guarding females during incubation. Behavioral Ecology 20:1034-1038.

Ferrari, M. C. O., G. E. Brown, G. R. Bortolotti, and D. P. Chivers. 2010. Linking predator risk and uncertainty to adaptive forgetting: a theoretical framework and empirical test using tadpoles. Proceedings of the Royal Society B-Biological Sciences 277:2205-2210.

Ferretti, V., P. E. Llambias, and T. E. Martin. 2005. Life-history variation of a neotropical thrush challenges food limitation theory. Proceedings of the Royal Society B-Biological Sciences 272:769-773.

Filliater, T. S., and R. Breitwisch. 1997. Nestling provisioning by the extremely dichromatic Northern Cardinal. Wilson Bulletin 109:145-153.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on northern-cardinal nests– does choice of nest site matter. Condor 96:761-768.

Filliater-Lee, T.S. 1992. Parental roles in feeding nestlings, and nest sites and nest success in Northern Cardinals (Cardinalis cardinalis). M.S. thesis, Univ. of Dayton, Dayton, Ohio.

Fontaine, J. J., M. Martel, H. A. Markland, A. A. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116:1887-1894.

Fontaine, J. J., and T. E. Martin. 2006a. Habitat selection responses of parents to offspring predation risk: An experimental test. American Naturalist 168:811-818.

Fontaine, J. J., and T. E. Martin. 2006b. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428-434.

Forsman, J. T., and T. E. Martin. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. Oikos 118:464-470.

Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Gering JC, and RB Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532-541.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494-497.

Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behavioral Ecology 13:101-108.

Greig-Smith, P. W. 1982. Dispersal between nest-sites by stonechats *Saxicola torquata* in relation to previous breeding success. Ornis Scandinavica 13:232-238.

Halfwerk, W., S. Bot, J. Buikx, M. van der Velde, J. Komdeur, C. ten Cate, and H. Slabbekoorn. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences of the United States of America 108:14549-14554.

Halkin, S. L. and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). The birds of North America online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/440

doi:10.2173/bna.440

Hazler, K. R., A. J. Amacher, R. A. Lancia, and J. A. Gerwin. 2006. Factors influencing Acadian flycatcher nesting success in an intensively managed forest landscape. Journal of Wildlife Management 70:532-538.

Hazler, K. R., D. E. W. Drumtra, M. R. Marshall, R. J. Cooper, and P. B. Hamel. 2004. Common, but commonly overlooked: Red-bellied woodpeckers as songbird nest predators. Southeastern Naturalist 3:467-474.

Holling, C.S. 1965. The functional response of predators to prey and its role in mimcry and population regulation. Memoirs of the Entomological Society of Canada 45.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84:416-430.

Hoover, J. P., and M. C. Brittingham. 1998. Nest-site selection and nesting success of Wood Thrushes. Wilson Bulletin 110:375-383.

Houston, C. S., D. G. Smith, and C. Rohner. 1998. Great-horned Owl (*Bubo virginianus*). The Birds of North America, No. 372. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Howlett, J. S., and B. J. M. Stutchbury. 1997. Within-season dispersal, nest-site modification, and predation in renesting hooded warblers. Wilson Bulletin 109:643-649.

Ibanez-Alamo, J. D., and M. Soler. 2010. Does urbanization affect selective pressures and life-history strategies in the common blackbird (Turdus merula L.)? Biological Journal of the Linnean Society 101:759-766.

Isaksson, C., and S. Andersson. 2007. Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. Journal of Avian Biology 38:564-572.

Ito, R., and A. Mori. 2010. Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard Oplurus cuvieri cuvieri (Reptilia: Iguania). Proceedings of the Royal Society B-Biological Sciences 277:1275-1280.

Jawor, J. M., and R. Breitwisch. 2004. Multiple ornaments in male northern cardinals, Cardinalis cardinalis, as indicators of condition. Ethology 110:113-126.

Johnson, M. S. 1997. The effect of age on nest concealment and its complimentary effect on production of Wood Thrush. Wilson Bulletin 109:68-73.

Jokimaki, J., and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838-847.

Kelly, J.P. 1993. The effect of nest predation on habitat selection by dusky flycatchers in limber pine-juniper woodland. Condor 95:83-93.

Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. Journal of Field Ornithology 56:153-157.

Laskey, A.R. 1944. A study of the cardinal in Tennessee. Wilson Bulletin 56:27-44

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology-Revue Canadienne De Zoologie 79:1401-1409.

Leech, D. I., L. V. Rowe, and I. R. Hartley. 2006. Experimental evidence for adjustment of parental investment in relation to brood sex ratio in the blue tit. Animal Behaviour 72:1301-1307.

Leston L.F., and A.D. Rodewald. 2006. Are urban forests ecological traps for understory birds? An examination using northern cardinals. Biological Conservation 131: 566-574.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions - What are the ecological effects of anti-predator decision-making? Bioscience 48:25-34.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70-75.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation- a review and prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:619-640.

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology 16:945-956.

Linville, S. U., R. Breitwisch, and A. J. Schilling. 1998. Plumage brightness as an indicator of parental care in northern cardinals. Animal Behaviour 55:119-127.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504-1514.

Low, M., T. Makan, and I. Castro. 2012. Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. Behavioral Ecology 23:25-34.

Luck, G. W. 2002. The habitat requirements of the rufous treecreeper (Climacteris rufa). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105:383-394.

Magrath, R. D., and T. H. Bennett. 2012. A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proceedings of the Royal Society B-Biological Sciences 279:902-909.

Maklakov, A., I. Simone, A. Gonzalez-Voyer, J. Ronn and N. Kolm. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. Biology Letters 7:730-732.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types – revising the dogmas. American Naturalist 141:897-913.

Martin, T.E. 1993b. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-532.

Martin, T. E., and J. V. Briskie. 2009. Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. Year in Evolutionary Biology 2009 1168:201-217.

Martin, T. E., and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation. American Naturalist 153:131-139.

Martin, T. E., P. Lloyd, C. Bosque, D. C. Barton, A. L. Biancucci, Y. R. Cheng, and R. Ton. 2011. Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. Evolution 65:1607-1622.

Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51-57.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London Series B-Biological Sciences 267:2287-2293.

Marzluff, J. M., J. C. Withey, K. A. Whittaker, M. D. Oleyar, T. M. Unfried, S. Rullman, and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516-534.

Massaro, M., A. Starling-Windhof, J. V. Briskie, and T. E. Martin. 2008. Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. Plos One 3.

Mennechez, G., and P. Clergeau. 2006. Effect of urbanisation on habitat generalists: starlings not so flexible? Acta Oecologia 30:182-191.

Moller, A. P. 2008. Flight distance and population trends in European breeding birds. Behavioral Ecology 19:1095-1102.

Moller, A. P. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159:849-858.

Moller, A. P. 2010. Interspecific variation in fear responses predicts urbanization in birds. Behavioral Ecology 21:365-371.

Morosinotto, C., R. L. Thomson, and E. Korpimaki. 2010. Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. Journal of Animal Ecology 79:327-333.

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B-Biological Sciences 273:349-355.

Nowak, M., and K. Sigmund. 1993. A strategy of win stay, lose shift that outperforms tit-for-tat in the prisoners-dilemma game. Nature 364:56-58.

Olsen, B., J. Felch, R. Greenberg, and J. Walters. 2008. Causes of reduced clutch size in a tidal marsh endemic. Oecologia 158:421-435.

Parejo, D., and J. M. Aviles. 2011. Predation risk determines breeding territory choice in a Mediterranean cavity-nesting bird community. Oecologia 165:185-191.

Parejo, D., J. White, J. Clobert, A. Dreiss, and E. Danchin. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. Ecology 88:2373-2382.

Part, T., D. Arlt, B. Doligez, M. Low, and A. Qvarnstrom. 2011. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. Journal of Animal Ecology 80:1227-1235.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416-2425.

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Prange, S., and S. D. Gehrt. 2004. Changes in mesopredator-community structure in response to urbanization. Canadian Journal of Zoology-Revue Canadienne De Zoologie 82:1804-1817.

Prange S, SD Gehrt, and EP Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324-333.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. Journal of Mammalogy 85:483-490.

Preisser, E. L., and D. I. Bolnick. 2008. The Many Faces of Fear: Comparing the Pathways and Impacts of Nonconsumptive Predator Effects on Prey Populations. Plos One 3.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban-rural gradient: A landscape-level analysis. Journal of Mammalogy 87:1154-1164.

Rangen, S. A., R. G. Clark, and K. A. Hobson. 1999. Influence of nest-site vegetation and predator community on the success of artificial songbird nests. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1676-1681.

Rastogi, A. D., L. Zanette, and M. Clinchy. 2006. Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, Melospiza melodia. Animal Behaviour 72:933-940.

Rattenborg, N. C., S. L. Lima, and C. J. Amlaner. 1999. Half-awake to the risk of predation. Nature 397:397-398.

Reale, J.A. and R. B. Blair. 2005. Nesting success and life-history attributes of bird communities along an urbanization gradient. Urban Habitats 3:1-24.
Available from http://urbanhabitats.org [accessed April 2012].

Reed, L., R. Vallender, and R. Robertson. 2007. Provisioning Rates by Golden-Winged Warblers. Wilson Journal of Ornithology 119:350-355.

Remeš, V. 2005. Birds and rodents destroy different nests: a study of Blackcap *Sylvia atricapilla* using the removal of nest concealment. Ibis 147:213-216.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology:1-48.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299-313.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience 54:755-766.

Rodewald, A. D. 2009. Urban-associated habitat alteration promotes brood parasitism of Acadian Flycatchers. Journal of Field Ornithology 80:234-241.

Rodewald, A. D., and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? Biological Conservation 128:193-200.

Rodewald, A. D., and L. J. Kearns. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. Condor 113:899-906.

Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecological Applications 21:936-943.

Rodewald, A. D., and D. P. Shustack. 2008a. Consumer resource matching in urbanizing landscapes: Are synanthropic species over-matching? Ecology 89:515-521.

Rodewald, A. D., and D. P. Shustack. 2008b. Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77:83-91.

Rodewald, A.D., Shustack, D.P., and L. E. Hitchcock. 2010. Exotic shrubs as ephemeral ecological traps for nestling birds. Biological Invasions 12:33-39.

Roth, T. C., J. G. Cox, and S. L. Lima. 2008a. Can foraging birds assess predation risk by scent? Animal Behaviour 76:2021-2027.

Roth, T. C., J. G. Cox, and S. L. Lima. 2008b. The use and transfer of information about predation risk in flocks of wintering finches. Ethology 114:1218-1226.

Saggese, K., F. Korner-Nievergelt, T. Slagsvold, and V. Amrhein. 2011. Wild bird feeding delays start of dawn singing in the great tit. Animal Behaviour 81:361-365.

Salo, P., M. Nordstrom, R. L. Thomson, and E. Korpimaki. 2008. Risk induced by a native top predator reduces alien mink movements. Journal of Animal Ecology 77:1092-1098.

SAS Institute. 2008. SAS 9.2. SAS Institute, Cary, NC

Sauter, A., R. Bowman, S. J. Schoech, and G. Pasinelli. 2006. Does optimal foraging theory explain why suburban Florida scrub-jays (Aphelocoma coerulescens) feed their young human-provided food? Behavioral Ecology and Sociobiology 60:465-474.

Scales, J., J. Hyman, and M. Hughes. 2011. Behavioral Syndromes Break Down in Urban Song Sparrow Populations. Ethology 117:887-895.

Schmidt, K. A. 2001. Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. Evolutionary Ecology Research 3:633-648.

Schmidt, K. A. 2004. Site fidelity in temporally correlated environments enhances population persistence. Ecology Letters 7:176-184.

Schmidt, K. A., S. R. X. Dall, and J. A. van Gils. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos 119:304-316.

Schmidt, K. A., E. Lee, R. S. Ostfeld, and K. Sieving. 2008. Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. Behavioral Ecology 19:759-763.

Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. Oecologia 148:22-29.

Schmidt, K. A., S. A. Rush, and R. S. Ostfeld. 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. Journal of Animal Ecology 77:830-837.

Schmidt, K. A., and E. M. Schauber. 2007. Behavioral indicators of predator space use: Studying species interactions through the behavior of predators. Israel Journal of Ecology & Evolution 53:389-406.

Schmidt, K. A., and C. J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: Experimental and observational evidence. American Naturalist 152:393-402.

Schmidt, K.A. and C.J. Whelan. 1999. Effects of exotic Lonicera and Rhamnus on songbird nest predation. Conservation Biology 13:1502-1506.

Schmidt, K. A., and C. J. Whelan. 2005. Quantifying male Wood Thrush nest-attendance and its relationship to nest success. Condor 107:138-144.

Schmidt, K. A., and C. J. Whelan. 2010. Nesting in an uncertain world: information and sampling the future. Oikos 119:245-253.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153-163.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function.

Science 319:952-954.

Schwagmeyer, P., and D. Mock. 2003. How consistently are good parents good parents? Repeatability of parental care in the House Sparrow, Passer domesticus. Ethology 109:303-313.

Seaman, D. E., J.J. Millspaugh, B.J. Kernohan, G. C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Seppanen, J. T., J. T. Forsman, M. Monkkonen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622-1633.

Seress, G., V. Bokony, J. Heszberger, and A. Liker. 2011. Response to Predation Risk in Urban and Rural House Sparrows. Ethology 117:896-907.

Shackelford CE, Brown RE, Connor RN. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). The Birds of North America, No. 500. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. Oikos 106:622-626.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186-191.

Shustack, D. P., and A. D. Rodewald. 2010. Attenuated nesting season of the Acadian flycatcher (*Empidonax virescens*) in urban forests. Auk 127:421-429.

Sinclair KE, Hess GR, Moorman CE, and JH Mason. 2005. Mammalian nest predators respond to greenway width, landscape context and habitat structure. Landscape and Urban Planning 71:277-293.

Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430-55.

Smith-Castro J.R., and A.D. Rodewald. 2010a. Behavioral responses of nesting birds to human disturbance along recreational trails. Journal of Field Ornithology 81:130-138

Smith-Castro J.R. and A.D. Rodewald. 2010b. Effects of recreational trails on northern cardinals (Cardinalis cardinalis) in forested urban parks. Nat Areas Journal 30:328-337.

Soderstrom, B, T. Part, J. Ryden. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia 117: 108-118.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102:5460-5465.

Sorace A. 2002. High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fennica 79:60-71.

Sorace, A., and M. Gustin. 2009. Distribution of generalist and specialist predators along urban gradients. Landscape and Urban Planning 90:111-118.

Stake, M. M., J. Faaborg, and F. R. Thompson. 2004. Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337-344.

Stout, W. E., and R. N. Rosenfield. 2010. Colonization, growth, and density of a pioneer Cooper's hawk population in a large metropolitan environment. Journal of Raptor Research 44:255-267.

Stracey, C. M. 2011. Resolving the urban nest predator paradox: The role of alternative foods for nest predators. Biological Conservation 144:1545-1552.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923-1926.

Thomson, R. L., G. Tomas, J. T. Forsman, J. Broggi, and M. Monkkonen. 2010. Predator proximity as a stressor in breeding flycatchers: mass loss, stress protein induction, and elevated provisioning. Ecology 91:1832-1840.

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

Tsurim, I., Z. Abramsky, and B. P. Kotler. 2008. Foraging behavior of urban birds: are human commensals less sensitive to predation risk than their nonurban counterparts? Condor 110:772-776.

Valcarcel, A., and E. Fernandez-Juricic. 2009. Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? Behavioral Ecology and Sociobiology 63:673-685.

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505-522.

Wagner, R. H., and E. Danchin. 2010. A taxonomy of biological information. Oikos 119:203-209.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424-437.

Weidinger, K. 2009. Nest predators of woodland open-nesting songbirds in central Europe. Ibis 151:352-360.

Whitehead D.R. and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). The Birds of North America, No. 614. In: Poole A, Gill F (eds) The Birds of North America, Philadelphia, PA

Wilson, R. R., and R. J. Cooper. 1998. Acadian Flycatcher nest placement: Does placement influence reproductive success? Condor 100:673-679.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Wright, J., C. Both, P. A. Cotton, and D. Bryant. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology 67:620-634.

Zanette, L. Y. and B. Jenkins. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117:445-454

Zollner, P. A., and S. L. Lima. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219-230.

Appendix A – General Characteristics and Locations of Study Sites

Table A.1 Landscape composition within 1 km radius of 14 riparian forest sites where northern cardinals (*Cardinalis cardinalis*) and Acadian flycatchers (*Empidonax virescens*) were studied in Franklin and Delaware Counties, USA, 2006-2010 (from Rodewald and Shustack 2008a). Urban index represents a principal component explaining approximately 80% of variation in landscape using number of buildings, % agriculture, lawn, pavement, and roads.

Sites	Urban Index	No. buildings	Forest width (m)	Agriculture (% area)	Lawn (% area)	Pavement (% area)	Roads (% area)
Ngalena	-1.27	34	135	0.36	0.05	0.01	0.01
Pubhunt	-1.15	210	194	0.32	0.08	0.01	0.01
Prairie	-1.12	58	148	0.47	0.12	0.03	0.02
Creeks	-0.71	92	133	0.10	0.10	0.04	0.02
Sgalena	-0.57	185	163	0.14	0.30	0.02	0.01
Galena	-0.48	360	277	0.15	0.22	0.04	0.02
Elkrun	-0.16	812	167	0.31	0.27	0.06	0.05
Woodside	0.32	1227	104	0.11	0.40	0.07	0.05
Rushrun	0.75	1611	150	0	0.41	0.09	0.06
Cherry	0.76	997	165	0.02	0.36	0.16	0.07
Kenny	0.89	1733	126	0	0.34	0.17	0.06
Casto	1.25	1776	202	0	0.42	0.20	0.08
Lou	1.26	2272	156	0	0.28	0.23	0.08
Tuttle	1.61	1733	126	0	0.34	0.17	0.06

Table A.2 Geographic coordinates of 14 riparian forest sites for study of northern cardinals (*Cardinalis cardinalis*) and Acadian flycatchers (*Empidonax virescens*) Franklin and Delaware Counties, USA, 2006-2010

Sites (in order from rural to urban)	Urban Index	Latitude	Longitude
Ngalena	-1.27	40º 21' 14" N	82º 55’ 36” W
Pubhunt	-1.15	39º 50' 39" N	83º 12' 08" W
Prairie	-1.12	39º 59' 03" N	83º 14' 56" W
Creeks	-0.71	39º 52' 55" N	82º 54' 32" W
Sgalena	-0.57	40º 14' 08" N	82º 53' 43" W
Galena	-0.48	40º 12' 51" N	82º 52' 50" W
Elkrun	-0.16	39º 53' 48" N	82º 53' 59" W
Woodside	0.32	40º 02' 41" N	82º 52' 49" W
Rushrun	0.75	40º 04' 28" N	83º 01' 53" W
Cherry	0.76	40º 03' 44" N	82º 54' 16" W
Kenny	0.89	40º 03’55” N	83º 01’ 48” W
Casto	1.25	40º 05' 00" N	82º 55' 26" W
Lou	1.26	39º 56' 03" N	83º 00' 14" W
Tuttle	1.61	40º 00’43” N	83º 01’49” W

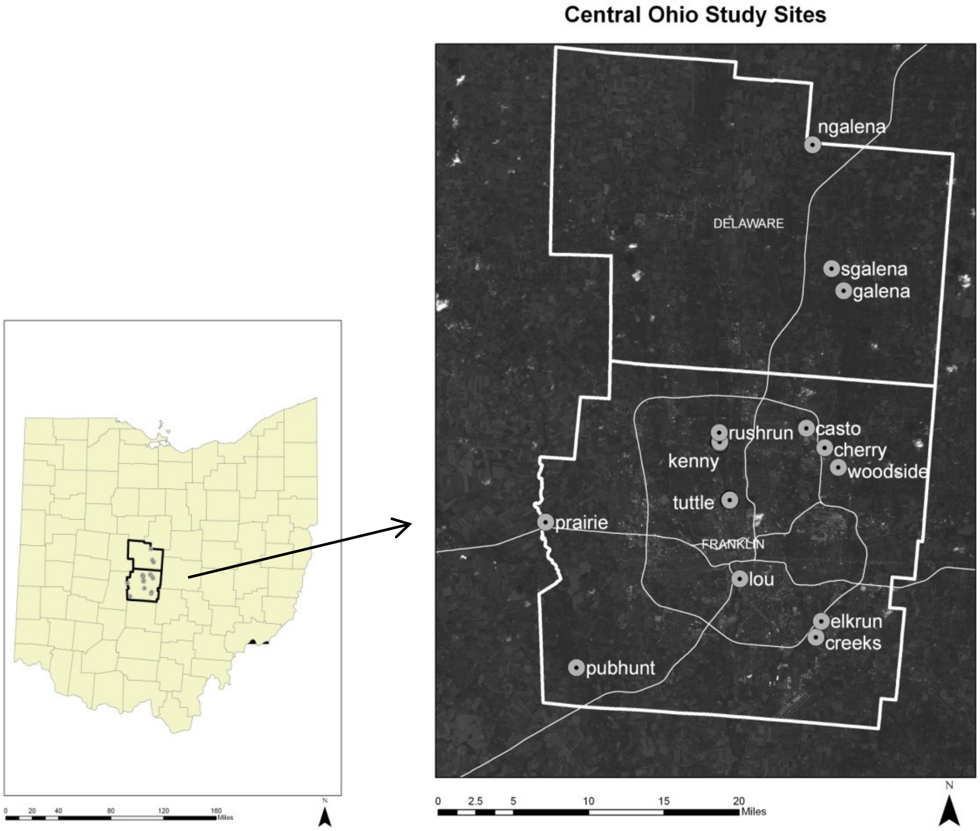

Figure A.1 Locations of 14 riparian forest sites for study of northern cardinals (*Cardinalis cardinalis*) and Acadian flycatchers (*Empidonax virescens*), Franklin and Delaware Counties, Ohio, USA, 2006-2010

Appendix B – Measures of Predation Risk by Site

Table B.1 Relative detections of predators (perceived risk) by site and year for 14 riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2007-2010

Sites (in order from rural to urban)	Urban Index	2007	2008	2009	2010	2007-2010
Ngalena	-1.27	7.72	2.75	-	6.80	5.76
Pubhunt	-1.15	7.74	5.13	6.51	7.18	6.64
Prairie	-1.12	7.32	4.36	9.06	10.76	7.87
Creeks	-0.71	8.57	1.13	1.71	4.21	3.91
Sgalena	-0.57	11.54	4.61	6.28	7.08	7.38
Galena	-0.48	6.61	3.98	5.98	4.83	5.35
Elkrun	-0.16	6.37	2.72	3.36	6.02	4.62
Woodside	0.32	15.58	4.41	5.43	4.90	7.58
Rushrun	0.75	7.99	4.86	7.13	12.69	8.17
Cherry	0.76	15.73	2.54	4.99	3.83	6.77
Kenny	0.89	7.91	5.07	7.99	10.10	7.77
Casto	1.25	9.04	3.45	6.22	3.77	5.62
Lou	1.26	6.21	4.68	5.97	4.24	5.28
Tuttle	1.61	14.60	3.66	5.20	6.09	7.39

Table B.2 Daily survival rates (DSR) of northern cardinal (*Cardinalis cardinalis*) nests (actual predation risk = 1 - DSR) by site and year for 14 riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2006-2010

Sites (in order from rural to urban)	Urban Index	2006	*n*	2007	*n*	2008	*n*	2009	*n*	2010	*n*
Ngalena	-1.27	0.9263	12	0.9386	5	0.9256	4	0.9581	2	0.9805	4
Pubhunt	-1.15	0.9451	11	0.9677	14	0.9490	9	0.9290	14	0.9759	18
Prairie	-1.12	0.9334	13	0.9457	17	0.9264	12	0.9434	17	0.9540	15
Creeks	-0.71	0.9596	7	0.9339	24	0.9705	7	0.9450	13	0.9428	11
Sgalena	-0.57	0.9207	29	0.9285	27	0.9187	23	0.9337	17	0.9160	17
Galena	-0.48	0.9589	13	0.9527	18	0.9407	15	0.9114	18	0.9572	8
Elkrun	-0.16	0.7727	5	0.9530	22	0.9558	15	0.9262	30	0.9232	16
Woodside	0.32	0.9321	9	0.9576	29	0.9424	22	0.8989	30	0.9326	21
Rushrun	0.75	0.9375	25	0.9515	44	0.9349	37	0.9264	44	0.9187	62
Cherry	0.76	0.9136	8	0.9541	21	0.9593	7	0.9086	18	0.9696	13
Kenny	0.89	0.9511	46	0.9480	60	0.9391	50	0.9116	66	0.9225	65
Casto	1.25	0.9332	11	0.9457	26	0.9511	21	0.9516	24	0.9584	13
Lou	1.26	0.9536	49	0.9373	30	0.9541	19	0.9396	27	0.9459	22
Tuttle	1.61	0.9585	43	0.9600	36	0.9592	27	0.9412	26	0.9582	36

Table B.3 Daily survival rates (DSR) of Acadian flycatcher (*Empidonax virescens*) nests (actual predation risk = 1 - DSR) by site and year for 14 riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2006-2010. Sites without data are those sites with no nests.

Sites (in order from rural to urban)	Urban Index	2006	*n*	2007	*n*	2008	*n*	2009	*n*	2010	*n*
Ngalena	-1.27	0.6888	10	0.8045	6	0.7751	5	0.9781	5	0.9612	16
Pubhunt	-1.15	0.8070	7	0.7555	2	0.8157	3	0.9298	7	0.9747	7
Prairie	-1.12	0.8539	3	0.7519	3	0.8989	3	0.9338	2	0.9855	3
Creeks	-0.71	0.7459	5	0.8216	7	0.7418	4	0.9686	9	0.9411	8
Sgalena	-0.57	0.8232	4	0.8070	3	-	0	0.9750	2	-	0
Galena	-0.48	0.6834	10	0.7508	6	0.7472	6	0.9667	7	0.9397	7
Elkrun	-0.16	-	0	0.8489	1	0.9314	2	1.000	1	1.000	2
Woodside	0.32	0.5839	2	0.8143	5	0.7640	4	0.9379	4	0.9307	4
Rushrun	0.75	-	0	0.8928	1	0.7795	2	-	0	-	0
Cherry	0.76	0.9500	2	-	0	0.9524	1	0.5004	2	0.9084	3
Kenny	0.89	-	0	-	0	-	0	-	0	-	0
Casto	1.25	-	0	0.8544	2	0.7803	2	1.0000	2	0.9671	3
Lou	1.26	-	0	-	0	0.8571	1	0.9093	2	0.9810	2
Tuttle	1.61	-	0	-	0	-	0	1.000	1	0.9668	3

Appendix C - Supplement to Chapter 2

Table C.1 Utilization distribution kernel smoothing parameter (i.e., bandwidth, *h*) and sample sizes (*n*) for avian predators by site and year at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2008-2010.

		2008		2009		2010	
Site	Urban	*h*	*n*	*h*	*n*	*h*	*n*
Ngalena	-1.27	.	.	.	.	26.203086	38
Pubhunt	-1.15	20.001216	67	19.874596	132	18.612469	158
Prairie	-1.12	21.489395	35	17.498707	208	15.732621	260
Creeks	-0.71	41.165885	25	29.368982	14	27.476919	34
Sgalena	-0.57	22.890924	88	19.788711	141	22.036881	145
Galena	-0.48	29.834352	15	19.225417	191	20.576937	146
Elkrun	-0.16	30.83024	41	19.84284	74	17.406498	127
Woodside	0.32	26.573936	32	21.632735	76	20.758157	164
RushrunN	0.75	18.301749	71	20.138229	134	18.031625	134
RushrunS	0.75	17.864009	80	22.543866	128	21.922701	113
Cherry	0.76	20.7905	39	20.234588	60	17.002802	142
KennyN	0.89	20.60166	44	19.570721	140	19.642326	92
KennyS	0.89	25.568929	32	19.437338	109	21.201525	127
Casto	1.25	38.403089	13	28.112278	109	28.283953	90
LouN	1.26	25.727758	11	21.56472	20	19.972638	34
LouS	1.26	35.286247	31	27.789332	21	28.078635	34
TuttleN	1.61	20.556166	60	20.250652	22	18.819481	49
TuttleS	1.61	20.79022	39	16.318924	30	20.449493	44

Table C.2 Utilization distribution kernel smoothing parameter (i.e., bandwidth, *h*) and sample sizes for mammalian predators by site and year at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2008-2010.

		2008		2009		2010	
Site	Urban	*h*	*n*	*h*	*n*	*h*	*n*
Ngalena	-1.27	25.444008	19	.	.	24.691608	38
Pubhunt	-1.15	.	.	33.014943	12	23.409977	36
Prairie	-1.12	22.419816	15	17.321891	95	19.352755	77
Creeks	-0.71	35.898096	24	26.0658	24	27.973095	14
Sgalena	-0.57	26.83937	19	35.830598	11	28.344935	33
Galena	-0.48	30.559282	35	24.072425	35	24.446535	53
Elkrun	-0.16	19.710002	43	20.199656	43	21.918026	37
Woodside	0.32	25.918513	25	23.407801	58	19.966093	83
RushrunN	0.75	19.734616	42	21.889438	48	17.352954	107
RushrunS	0.75	27.602347	20	23.990803	34	22.451054	79
Cherry	0.76	25.743099	25	18.516675	76	20.225216	54
KennyN	0.89	19.371948	67	17.181451	84	18.146909	90
KennyS	0.89	18.348749	88	20.023263	98	19.788404	95
Casto	1.25	40.129248	18	25.231476	100	27.776835	77
LouN	1.26	22.68466	46	15.099342	38	.	.
LouS	1.26	.	.	23.144914	62	31.39	49
TuttleN	1.61	20.552582	100	19.175119	23	21.818492	70
TuttleS	1.61	18.849726	70	17.425956	56	18.485183	58

Table C.3 Utilization distribution kernel smoothing parameter (i.e., bandwidth, *h*) and sample sizes for brown-headed cowbirds (*Molothrus ater*) by site and year at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2008-2010.

		2008		2009		2010	
Site	Urban	*h*	*n*	*h*	*n*	*h*	*n*
Ngalena	-1.27	.	.	.	.	26.969751	21
Pubhunt	-1.15	21.32988	41	20.361147	68	19.591693	64
Prairie	-1.12	.	.	21.420724	50	19.843312	55
Creeks	-0.71	.	.	.	.	31.397484	14
Sgalena	-0.57	.	.	22.174133	38	26.825193	30
Galena	-0.48	.	.	22.392655	69	32.065106	22
Elkrun	-0.16	.	.	.	.	19.416814	21
Woodside	0.32	.	.	28.233359	24	22.835176	58
RushrunN	0.75	.	.	.	.	.	.
RushrunS	0.75	20.977271	27	.	.	.	.
Cherry	0.76	.	.	.	.	17.759265	42
KennyN	0.89	.	.	24.031672	31	32.54958	15
KennyS	0.89	.	.	21.576648	38	26.033155	20
Casto	1.25	.	.	.	.	.	.
LouN	1.26	.	.	.	.	.	.
LouS	1.26	.	.	.	.	.	.
TuttleN	1.61	21.181844	32	.	.	.	.
TuttleS	1.61	22.583819	22	.	.	.	.

Table C.4 Utilization distribution kernel smoothing parameter (i.e., bandwidth, *h*) and sample sizes for blue jays (*Cyanocitta cristata*) by site and year at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2008-2010.

		2008		2009		2010	
Site	Urban	*h*	*n*	*h*	*n*	*h*	*n*
Ngalena	-1.27	.	.	.	.	.	.
Pubhunt	-1.15	.	.	25.523436	32	23.406881	37
Prairie	-1.12	23.971395	21	19.892516	87	18.197425	89
Creeks	-0.71	.	.	.	.	.	.
Sgalena	-0.57	24.914893	61	21.980471	62	24.959666	45
Galena	-0.48	.	.	24.461705	56	25.053153	37
Elkrun	-0.16	.	.	22.815797	32	17.640198	55
Woodside	0.32	.	.	24.086603	28	24.446115	35
RushrunN	0.75	20.276675	28	24.674915	29	21.028948	59
RushrunS	0.75	22.259749	35	23.35577	56	24.638251	42
Cherry	0.76	.	.	.	.	25.704421	28
KennyN	0.89	.	.	.	.	22.882915	20
KennyS	0.89	.	.	21.638069	21	24.811976	39
Casto	1.25	.	.	.	.	33.596604	38
LouN	1.26	.	.	.	.	.	.
LouS	1.26	.	.	.	.	.	.
TuttleN	1.61	.	.	.	.	.	.
TuttleS	1.61	.	.	.	.	.	.

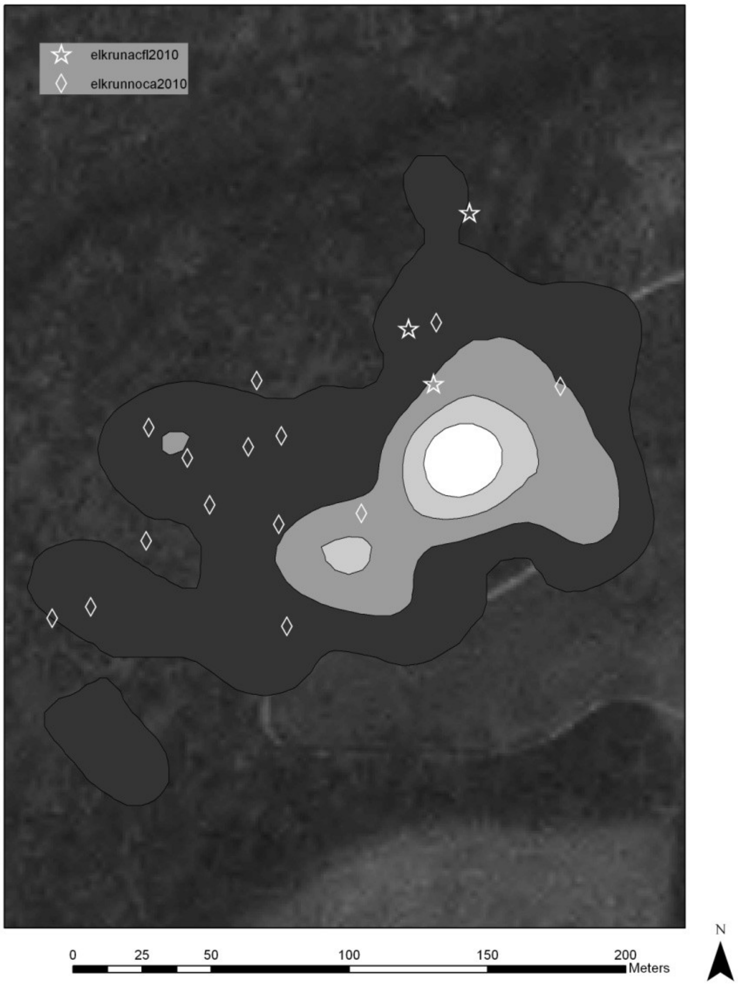

Figure C.1 Example of a site (Elkrun) with utilization distributions of avian predator activity and northern cardinal (*Cardinalis cardinalis,* diamonds) and Acadian flycatcher (*Empidonax virescens,* stars) nests. White represents area of most predator use, near black represents area of least use.

Appendix D – Supplement to Chapter 3

Table D.1 Data for analyses to determine effect of previous nest fate, perceived and actual risk on changes in northern cardinal (*Cardinalis cardinalis*) nest characteristics between successive nest attempts at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2006-2010. Terr ID = Territory ID for pairs used in the analysis, Male ID = male USGS band number, Female ID = female USGS band number, Fate = nest fate (0 = failed, 1 = fledged), Pfate = fate of previous nest, Nh = nest height, Nc = nest concealment, Vd = vegetation density, ΔNh = change in nest height between successive nests, ΔNc = change in nest concealment between successive nests, ΔVd = change in vegetation density between successive nests, Urb = urban index, Predrd = relative detections of predators (perceived predation risk), DSR = daily survival rate of cardinal nests by site and year (1 – DSR = actual predation risk). See Chapter 3 for additional details.

Table D.1 continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
casto1112006	casto	2006	610049	198100140	198100142	0	.	1.5	38	81	.	.	.	1.25	5.62	0.9332
casto1112006	casto	2006	610086	198100140	198100142	1	0	2.0	33	54	0.5	-5	-27	1.25	5.62	0.9332
casto912006	casto	2006	611045	180130586	198100305	1	.	1.5	28	65	.	.	.	1.25	5.62	0.9332
casto912006	casto	2006	604133	180130586	198100305	0	1	2.8	39	103	1.3	11	38	1.25	5.62	0.9332
casto812007	casto	2007	707021	180130586	198100422	0	.	2.0	17	34	.	.	.	1.25	9.04	0.9457
casto812007	casto	2007	704052	180130586	198100422	0	0	15.0	10	30	13.0	-7	-4	1.25	9.04	0.9457
casto212009	casto	2009	904035	198100381	198100594	1	.	2.0	63	.	.	.	.	1.25	6.22	0.9516
casto212009	casto	2009	908031	198100381	198100594	1	1	3.8	20	67	1.8	-43	.	1.25	6.22	0.9516
casto312009	casto	2009	904013	198100539	.	0	.	2.0	48	22	.	.	.	1.25	6.22	0.9516
casto312009	casto	2009	904066	198100539	.	1	0	1.8	50	55	-0.3	2	33	1.25	6.22	0.9516
casto312009	casto	2009	908022	198100539	.	0	1	2.6	55	48	0.9	5	-7	1.25	6.22	0.9516
casto112010	casto	2010	1003004	198107163	198100538	1	.	1.9	43	119	.	.	.	1.25	3.77	0.9584
casto112010	casto	2010	1003065	198107163	198100538	0	1	2.2	63	104	0.3	20	-15	1.25	3.77	0.9584
casto112010	casto	2010	1003117	198107163	198100538	1	0	2.1	68	63	-0.1	5	-41	1.25	3.77	0.9584
casto512010	casto	2010	1003012	.	.	1	.	1.8	60	65	.	.	.	1.25	3.77	0.9584
casto512010	casto	2010	1003099	.	.	0	1	5.8	48	44	4.0	-13	-21	1.25	3.77	0.9584
casto512010	casto	2010	1003111	.	.	0	0	5.0	70	48	-0.8	23	4	1.25	3.77	0.9584
cherry212006	cherry	2006	611061	180130562	180130582	0	.	1.5	45	52	.	.	.	0.76	6.77	0.9136
cherry212006	cherry	2006	610084	180130562	180130582	0	0	1.8	19	40	0.3	-26	-12	0.76	6.77	0.9136
cherry212007	cherry	2007	710021	.	180130580	0	.	1.0	.	49	.	.	.	0.76	15.73	0.9541
cherry212007	cherry	2007	707039	.	180130580	0	0	1.5	6	59	0.5	.	10	0.76	15.73	0.9541
cherry512008	cherry	2008	805035	.	198100580	1	.	1.5	50	184	.	.	.	0.76	2.54	0.9593
cherry512008	cherry	2008	804121	.	198100580	0	1	5.5	64	58	4.0	14	-126	0.76	2.54	0.9593
cherry212009	cherry	2009	904003	198100331	198100599	0	.	1.4	46	89	.	.	.	0.76	4.99	0.9086
cherry212009	cherry	2009	903018	198100331	198100599	0	0	1.0	58	40	-0.4	11	-49	0.76	4.99	0.9086
cherry212009	cherry	2009	908006	198100331	198100599	1	0	2.0	46	66	1.0	-11	26	0.76	4.99	0.9086
cherry212009	cherry	2009	903086	198100331	198100599	1	1	1.6	55	42	-0.4	9	-24	0.76	4.99	0.9086
cherry312009	cherry	2009	908001	198100524	198100525	0	.	1.0	100	19	.	.	.	0.76	4.99	0.9086
cherry312009	cherry	2009	903040	198100524	198100525	0	0	1.6	81	69	0.6	-19	50	0.76	4.99	0.9086
cherry122010	cherry	2010	1004018	198100331	.	1	.	0.8	48	64	.	.	.	0.76	3.83	0.9696
cherry122010	cherry	2010	1003101	198100331	.	1	1	1.8	43	121	1.0	-5	57	0.76	3.83	0.9696

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
cherry312010	cherry	2010	1004005	198107124	198107125	0	.	1.4	56	78	.	.	.	0.76	3.83	0.9696
cherry312010	cherry	2010	1003070	198107124	198107125	0	0	1.4	50	102	0.0	-6	24	0.76	3.83	0.9696
cherry312010	cherry	2010	1009027	198107124	198107125	0	0	3.6	54	77	2.2	4	-25	0.76	3.83	0.9696
cherry412010	cherry	2010	1003020	.	.	1	.	1.5	49	112	.	.	.	0.76	3.83	0.9696
cherry412010	cherry	2010	1003108	.	.	1	1	8.0	84	38	6.5	35	-74	0.76	3.83	0.9696
creeks1112007	creeks	2007	701073	.	198100282	0	.	8.0	53	76	.	.	.	-0.71	8.57	0.9339
elkrun112006	elkrun	2006	610002	189199303	.	0	.	1.3	20	52	.	.	.	-0.16	4.62	0.7727
elkrun112006	elkrun	2006	610018	189199303	.	0	0	1.0	30	57	-0.3	10	5	-0.16	4.62	0.7727
elkrun112006	elkrun	2006	604069	189199303	.	0	0	9.0	70	24	8.0	40	-33	-0.16	4.62	0.7727
elkrun212009	elkrun	2009	902010	.	199167448	0	.	2.3	28	60	.	.	.	-0.16	3.36	0.9262
elkrun212009	elkrun	2009	902045	.	199167448	0	0	1.5	15	52	-0.8	-13	-8	-0.16	3.36	0.9262
elkrun212009	elkrun	2009	905037	.	199167448	1	0	1.5	12	49	0.0	-4	-3	-0.16	3.36	0.9262
elkrun412009	elkrun	2009	905008	.	199100537	0	.	1.8	24	46	.	.	.	-0.16	3.36	0.9262
elkrun412009	elkrun	2009	906150	.	198100537	0	0	3.0	83	106	1.3	59	60	-0.16	3.36	0.9262
elkrun112010	elkrun	2010	1005002	198107405	198107404	0	.	1.3	39	104	.	.	.	-0.16	6.02	0.9232
elkrun112010	elkrun	2010	1001050	198107405	198107404	0	0	1.5	46	71	0.3	8	-33	-0.16	6.02	0.9232
galena212006	galena	2006	603028	198100401	198100184	0	.	2.0	10	96	.	.	.	-0.48	5.35	0.9589
galena212006	galena	2006	604046	198100401	198100184	0	0	1.5	78	86	-0.5	68	-10	-0.48	5.35	0.9589
galena512007	galena	2007	703037	.	198100364	1	.	1.8	33	60	.	.	.	-0.48	6.61	0.9527
galena512007	galena	2007	701101	.	198100364	1	1	2.0	4	52	0.3	-29	-8	-0.48	6.61	0.9527
galena112009	galena	2009	909006	.	198100486	0	.	2.0	55	28	.	.	.	-0.48	5.98	0.9114
galena112009	galena	2009	903075	.	198100486	0	0	7.0	56	16	5.0	1	-12	-0.48	5.98	0.9114
galena112009	galena	2009	903083	.	198100486	1	0	4.3	21	45	-2.8	-35	29	-0.48	5.98	0.9114
galena112010	galena	2010	1004013	198100584	.	1	.	2.1	24	22	.	.	.	-0.48	4.83	0.9572
galena112010	galena	2010	1005053	198100584	.	0	1	4.0	76	18	1.9	53	-4	-0.48	4.83	0.9572
kennyn512006	kenny	2006	604036	198100211	.	0	.	3.0	44	89	.	.	.	0.89	7.77	0.9511
kennyn512006	kenny	2006	608002	198100211	.	0	0	1.8	34	83	-1.3	-10	-6	0.89	7.77	0.9511
kennys412006	kenny	2006	603013	198100291	198100172	1	.	1.5	65	297	.	.	.	0.89	7.77	0.9511
kennys412006	kenny	2006	610067	198100291	198100172	1	1	2.3	83	144	0.8	18	-153	0.89	7.77	0.9511
kennyn612007	kenny	2007	705001	.	198100204	0	.	2.4	49	41	.	.	.	0.89	7.91	0.9480
kennyn612007	kenny	2007	710170	.	198100204	0	0	4.5	70	11	2.1	21	-30	0.89	7.91	0.9480
kennys1012007	kenny	2007	710199	198100301	.	0	.	3.0	.	53	.	.	.	0.89	7.91	0.9480
kennys312007	kenny	2007	702010	198100291	198100172	0	.	1.5	31	89	.	.	.	0.89	7.91	0.9480
kennys312007	kenny	2007	701045	198100291	198100172	0	0	1.5	45	57	0.0	14	-32	0.89	7.91	0.9480
kennys312007	kenny	2007	702044	198100291	198100172	0	0	1.9	91	26	0.4	46	-31	0.89	7.91	0.9480
kennys412007	kenny	2007	710063	.	198100151	0	.	0.7	35	24	.	.	.	0.89	7.91	0.9480
kennys412007	kenny	2007	701044	.	198100151	1	0	1.4	21	10	0.7	-14	-14	0.89	7.91	0.9480

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
kennys512007	kenny	2007	704006	.	198100346	0	.	1.5	54	107	.	.	.	0.89	7.91	0.9480
kennys512007	kenny	2007	710102	.	198100346	0	0	3.0	30	108	1.5	-24	1	0.89	7.91	0.9480
kennys612007	kenny	2007	702036	198100300	198100173	0	.	3.7	69	26	.	.	.	0.89	7.91	0.9480
kennys612007	kenny	2007	704064	198100300	198100173	0	0	9.0	58	21	5.3	-11	-5	0.89	7.91	0.9480
kennyn1112008	kenny	2008	801004	198100557	.	0	.	1.8	10	42	.	.	.	0.89	5.07	0.9391
kennyn1112008	kenny	2008	801034	198100557	.	0	0	1.3	.	28	-0.5	.	-14	0.89	5.07	0.9391
kennyn1112008	kenny	2008	807047	198100557	.	1	0	3.0	43	55	1.7	.	27	0.89	5.07	0.9391
kennys312008	kenny	2008	801033	180144890	.	0	.	2.3	43	27	.	.	.	0.89	5.07	0.9391
kennys312008	kenny	2008	803071	180144890	.	1	0	3.0	58	57	0.8	15	30	0.89	5.07	0.9391
kennys612008	kenny	2008	801025	198100300	.	0	.	1.2	48	22	.	.	.	0.89	5.07	0.9391
kennys612008	kenny	2008	801045	198100300	.	0	0	0.9	11	43	-0.3	-37	21	0.89	5.07	0.9391
kennyn912009	kenny	2009	901018	.	198100363	1	.	1.3	23	55	.	.	.	0.89	7.99	0.9116
kennyn912009	kenny	2009	906014	.	198100363	0	1	1.3	86	40	-0.1	63	-15	0.89	7.99	0.9116
kennyn912009	kenny	2009	901110	.	198100363	1	0	3.0	53	58	1.8	-34	18	0.89	7.99	0.9116
kennys112009	kenny	2009	901020	.	198100241	0	.	0.7	89	46	.	.	.	0.89	7.99	0.9116
kennys112009	kenny	2009	901055	.	198100241	0	0	1.7	30	62	1.0	-59	16	0.89	7.99	0.9116
kennys112009	kenny	2009	906016	.	198100241	0	0	2.3	54	37	0.6	24	-25	0.89	7.99	0.9116
kennys112009	kenny	2009	901126	.	198100241	1	0	1.8	57	48	-0.5	3	11	0.89	7.99	0.9116
kennys112009	kenny	2009	913008	.	198100241	0	1	2.5	49	71	0.8	-8	23	0.89	7.99	0.9116
kennys812009	kenny	2009	904009	198100450	198100208	0	.	0.8	6	10	.	.	.	0.89	7.99	0.9116
kennys812009	kenny	2009	901039	.	198100208	0	0	4.3	9	21	3.5	3	11	0.89	7.99	0.9116
kennys812009	kenny	2009	901121	.	198100208	1	0	3.5	75	30	-0.8	67	9	0.89	7.99	0.9116
kennys812009	kenny	2009	913010	.	198100208	1	1	5.5	73	32	2.0	-3	2	0.89	7.99	0.9116
kennyn1112010	kenny	2010	1006009	.	198107108	1	.	4.5	75	79	.	.	.	0.89	10.10	0.9225
kennyn1112010	kenny	2010	1002148	.	198107108	0	1	6.3	63	155	1.8	-13	76	0.89	10.10	0.9225
kennyn2012010	kenny	2010	1002104	198100532	198100442	1	.	2.4	63	83	.	.	.	0.89	10.10	0.9225
kennyn2012010	kenny	2010	1013015	198100532	198100442	1	1	4.2	55	90	1.8	-8	7	0.89	10.10	0.9225
kennys422010	kenny	2010	1013008	198100300	198100208	0	.	6.0	59	12	.	.	.	0.89	10.10	0.9225
kennys422010	kenny	2010	1002122	198100300	198100208	0	0	3.9	94	111	-2.1	35	99	0.89	10.10	0.9225
kennys422010	kenny	2010	1006028	198100300	198100208	1	0	6.0	65	137	2.1	-29	26	0.89	10.10	0.9225
loun112006	lou	2006	604008	.	198100218	0	.	2.0	.	93	.	.	.	1.26	5.28	0.9536
loun112006	lou	2006	604043	.	198100218	0	0	0.5	56	38	-1.5	.	-55	1.26	5.28	0.9536
loun112006	lou	2006	604064	.	198100218	0	0	1.3	25	121	0.8	-31	83	1.26	5.28	0.9536
loun112006	lou	2006	603092	.	198100218	0	0	2.3	75	186	1.0	50	65	1.26	5.28	0.9536
loun112006	lou	2006	603126	.	198100218	0	0	1.5	88	120	-0.8	13	-66	1.26	5.28	0.9536
loun112006	lou	2006	612094	.	198100218	1	0	2.5	56	137	1.0	-31	17	1.26	5.28	0.9536
loun212006	lou	2006	603007	180130513	198100287	0	.	2.0	13	69	.	.	.	1.26	5.28	0.9536

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
loun212006	lou	2006	612555	180130513	198100287	0	0	2.0	93	77	0.0	80	8	1.26	5.28	0.9536
loun212006	lou	2006	603117	180130513	198100287	0	0	2.0	64	177	0.0	-29	100	1.26	5.28	0.9536
lous112006	lou	2006	603001	189199304	198100181	0	.	1.5	28	38	.	.	.	1.26	5.28	0.9536
lous112006	lou	2006	612013	189199304	198100181	0	0	1.3	85	198	-0.3	57	160	1.26	5.28	0.9536
lous112006	lou	2006	603074	189199304	198100181	1	0	1.8	49	203	0.5	-36	5	1.26	5.28	0.9536
lous112006	lou	2006	604119	189199304	198100181	1	1	1.5	38	162	-0.3	-11	-41	1.26	5.28	0.9536
loun312007	lou	2007	701036	180130513	180130566	0	.	1.3	71	151	.	.	.	1.26	6.21	0.9373
loun312007	lou	2007	701088	180130513	180130566	0	0	6.0	81	139	4.8	10	-12	1.26	6.21	0.9373
loun612007	lou	2007	708035	198100404	198100218	0	.	5.0	38	11	.	.	.	1.26	6.21	0.9373
loun612007	lou	2007	701098	198100404	198100218	1	0	1.5	44	106	-3.5	6	95	1.26	6.21	0.9373
lous212007	lou	2007	706006	.	180130574	0	.	4.0	29	7	.	.	.	1.26	6.21	0.9373
lous212007	lou	2007	708042	.	180130574	0	0	2.5	53	18	-1.5	24	11	1.26	6.21	0.9373
lous212007	lou	2007	708067	.	180130574	0	0	4.5	20	43	2.0	-33	25	1.26	6.21	0.9373
lous312007	lou	2007	708028	.	198100379	0	.	2.5	36	23	.	.	.	1.26	6.21	0.9373
lous312007	lou	2007	701086	.	198100379	0	0	1.5	14	64	-1.0	-23	41	1.26	6.21	0.9373
lous712007	lou	2007	702046	.	198100185	0	.	2.0	31	71	.	.	.	1.26	6.21	0.9373
lous712007	lou	2007	708066	.	198100185	1	0	4.0	25	75	2.0	-6	4	1.26	6.21	0.9373
loun312008	lou	2008	803035	198100252	198100500	0	.	1.6	26	89	.	.	.	1.26	4.69	0.9541
loun312008	lou	2008	808055	198100252	198100500	1	0	2.3	45	70	0.7	19	-19	1.26	4.69	0.9541
loun312008	lou	2008	804106	198100252	198100500	0	1	2.6	59	38	0.3	14	-32	1.26	4.69	0.9541
loun512008	lou	2008	803014	180130513	198100218	0	.	1.0	92	24	.	.	.	1.26	4.69	0.9541
loun512008	lou	2008	808056	180130513	198100218	0	0	1.8	76	59	0.8	-16	35	1.26	4.69	0.9541
lous212008	lou	2008	803026	198100371	180130574	0	.	1.6	16	57	.	.	.	1.26	4.69	0.9541
lous212008	lou	2008	801079	198100371	180130574	1	0	2.5	85	40	0.9	69	-17	1.26	4.69	0.9541
loun212009	lou	2009	904031	198130513	198100218	0	.	1.0	50	63	.	.	.	1.26	5.97	0.9396
loun212009	lou	2009	904074	180130513	198100218	0	0	1.0	58	153	0.0	8	90	1.26	5.97	0.9396
loun212009	lou	2009	906010	180130513	198100218	0	0	1.8	29	72	0.8	-29	-81	1.26	5.97	0.9396
loun212009	lou	2009	906093	180130513	198100218	1	0	2.5	31	60	0.8	3	-12	1.26	5.97	0.9396
loun312009	lou	2009	907064	198100252	198100500	1	.	2.4	28	37	.	.	.	1.26	5.97	0.9396
loun312009	lou	2009	906109	198100252	198100500	0	1	3.3	33	74	0.9	5	37	1.26	5.97	0.9396
lous212010	lou	2010	1001039	.	198100378	0	.	2.5	46	49	.	.	.	1.26	4.24	0.9459
lous212010	lou	2010	1001076	.	198100378	1	0	3.3	74	107	0.8	28	58	1.26	4.24	0.9459
ngalena212006	ngalena	2006	604040	180130557	198100205	0	.	1.5	.	32	.	.	.	-1.27	5.76	0.9263
ngalena212006	ngalena	2006	604055	180130557	198100205	0	0	2.5	56	32	1.0	.	0	-1.27	5.76	0.9263
ngalena612006	ngalena	2006	603101	198100170	.	0	.	5.5	34	37	.	.	.	-1.27	5.76	0.9263
ngalena612006	ngalena	2006	604160	198100170	.	1	0	3.5	69	10	-2.0	35	-27	-1.27	5.76	0.9263
ngalena112010	ngalena	2010	1003063	198100408	198100394	1	.	2.3	50	44	.	.	.	-1.27	6.80	0.9805

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
ngalena112010	ngalena	2010	1003120	198100408	198100394	0	1	7.0	74	15	4.8	24	-29	-1.27	6.80	0.9805
prairie112007	prairie	2007	701059	.	180144865	0	.	2.3	44	38	.	.	.	-1.12	7.32	0.9457
prairie112007	prairie	2007	708054	.	180144865	0	0	2.5	48	58	0.3	4	20	-1.12	7.32	0.9457
prairie212007	prairie	2007	708012	.	198100338	0	.	1.5	100	124	.	.	.	-1.12	7.32	0.9457
prairie212007	prairie	2007	701034	.	198100338	0	0	1.0	50	90	-0.5	-50	-34	-1.12	7.32	0.9457
prairie412009	prairie	2009	901008	.	198100561	0	.	2.0	86	.	.	.	.	-1.12	9.06	0.9434
prairie412009	prairie	2009	907034	.	198100561	0	0	1.4	45	105	-0.6	-41	.	-1.12	9.06	0.9434
prairie412009	prairie	2009	907084	.	198100561	0	0	2.0	56	109	0.6	11	4	-1.12	9.06	0.9434
prairie412009	prairie	2009	901123	.	198100561	0	0	1.8	54	132	-0.3	-3	23	-1.12	9.06	0.9434
prairie512009	prairie	2009	907019	198100507	.	1	.	1.8	10	43	.	.	.	-1.12	9.06	0.9434
prairie512009	prairie	2009	907153	198100507	.	0	1	9.0	59	120	7.3	49	77	-1.12	9.06	0.9434
prairie212010	prairie	2010	1007148	198107157	.	0	.	3.2	53	136	.	.	.	-1.12	10.76	0.9540
prairie212010	prairie	2010	1002177	198107157	.	1	0	5.0	34	99	1.8	-19	-37	-1.12	10.76	0.9540
prairie312010	prairie	2010	1007111	198107161	.	0	.	4.0	60	54	.	.	.	-1.12	10.76	0.9540
prairie312010	prairie	2010	1007138	198107161	.	0	0	1.4	61	76	-2.6	1	22	-1.12	10.76	0.9540
prairie312010	prairie	2010	1007170	198107161	.	0	0	2.5	84	167	1.1	23	91	-1.12	10.76	0.9540
prairie412010	prairie	2010	1007046	.	198107133	1	.	1.0	53	89	.	.	.	-1.12	10.76	0.9540
prairie412010	prairie	2010	1007156	.	198107133	1	1	3.1	38	59	2.1	-15	-30	-1.12	10.76	0.9540
prairie712010	prairie	2010	1007047	198107136	.	0	.	1.5	63	84	.	.	.	-1.12	10.76	0.9540
prairie712010	prairie	2010	1007070	198107136	.	1	0	1.5	48	40	0.0	-15	-44	-1.12	10.76	0.9540
pubhunt212006	pubhunt	2006	604024	198100116	.	0	.	0.5	.	42	.	.	.	-1.15	6.64	0.9451
pubhunt212006	pubhunt	2006	612091	198100116	.	0	0	2.5	71	145	2.0	.	103	-1.15	6.64	0.9451
pubhunt412006	pubhunt	2006	603046	.	198100114	0	.	1.0	48	79	.	.	.	-1.15	6.64	0.9451
pubhunt112007	pubhunt	2007	708015	.	198100176	0	.	1.5	10	163	.	.	.	-1.15	7.74	0.9677
pubhunt112007	pubhunt	2007	708046	.	198100176	1	0	.	.	194	.	.	31	-1.15	7.74	0.9677
pubhunt412007	pubhunt	2007	708022	198100343	198100360	1	.	2.0	74	56	.	.	.	-1.15	7.74	0.9677
pubhunt412007	pubhunt	2007	708050	198100343	198100360	1	1	15.0	73	30	13.0	-1	-26	-1.15	7.74	0.9677
pubhunt612008	pubhunt	2008	807022	198100505	198100360	1	.	1.5	91	60	.	.	.	-1.15	5.13	0.9490
pubhunt612008	pubhunt	2008	807059	198100505	198100360	1	1	3.1	63	33	1.6	-29	-27	-1.15	5.13	0.9490
pubhunt112009	pubhunt	2009	907026	.	198100567	0	.	1.3	80	60	.	.	.	-1.15	6.51	0.9290
pubhunt112009	pubhunt	2009	901047	.	198100567	1	0	1.0	30	96	-0.3	-50	36	-1.15	6.51	0.9290
pubhunt112009	pubhunt	2009	907128	.	198100567	0	1	1.5	79	197	0.5	49	101	-1.15	6.51	0.9290
pubhunt112009	pubhunt	2009	907146	.	198100567	0	0	2.0	51	39	0.5	-28	-158	-1.15	6.51	0.9290
pubhunt112009	pubhunt	2009	907151	.	198100567	1	0	2.8	54	88	0.8	3	49	-1.15	6.51	0.9290
pubhunt312009	pubhunt	2009	901022	.	198100571	0	.	1.8	54	116	.	.	.	-1.15	6.51	0.9290
pubhunt312009	pubhunt	2009	907049	.	198100571	1	0	1.2	73	38	-0.5	18	-78	-1.15	6.51	0.9290
pubhunt112010	pubhunt	2010	1007042	.	198100566	0	.	2.3	66	65	.	.	.	-1.15	7.18	0.9759

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
pubhunt112010	pubhunt	2010	1007084	.	198100566	1	0	1.5	36	59	-0.8	-30	-6	-1.15	7.18	0.9759
pubhunt112010	pubhunt	2010	1007143	.	198100566	0	1	13.0	86	12	11.5	50	-47	-1.15	7.18	0.9759
pubhunt112010	pubhunt	2010	1007178	.	198100566	1	0	11.0	89	54	-2.0	3	42	-1.15	7.18	0.9759
pubhunt212010	pubhunt	2010	1007069	198100467	198100568	0	.	0.7	91	46	.	.	.	-1.15	7.18	0.9759
pubhunt212010	pubhunt	2010	1007090	198100467	198100568	1	0	1.2	61	56	0.6	-30	10	-1.15	7.18	0.9759
pubhunt212010	pubhunt	2010	1002150	198100467	198100568	1	1	4.5	60	20	3.3	-1	-36	-1.15	7.18	0.9759
pubhunt312010	pubhunt	2010	1007067	198107118	.	1	.	0.9	54	32	.	.	.	-1.15	7.18	0.9759
pubhunt312010	pubhunt	2010	1007177	198107118	.	1	1	2.3	19	34	1.4	-35	2	-1.15	7.18	0.9759
pubhunt612010	pubhunt	2010	1007108	198107162	198107148	1	.	1.9	69	98	.	.	.	-1.15	7.18	0.9759
pubhunt612010	pubhunt	2010	1007168	198107162	198107148	0	1	1.7	31	103	-0.2	-38	5	-1.15	7.18	0.9759
rushrunn112006	rushrun	2006	604006	180130516	.	0	.	2.7	45	51	.	.	.	0.75	8.17	0.9375
rushrunn112006	rushrun	2006	610007	180130516	.	0	0	2.0	49	38	-0.7	4	-13	0.75	8.17	0.9375
rushrunn112006	rushrun	2006	611049	180130516	.	0	0	2.8	45	35	0.8	-4	-3	0.75	8.17	0.9375
rushrunn112006	rushrun	2006	611072	180130516	.	1	0	2.8	68	22	0.0	23	-13	0.75	8.17	0.9375
rushruns612006	rushrun	2006	610100	180130585	.	0	.	1.0	50	191	.	.	.	0.75	8.17	0.9375
rushruns612006	rushrun	2006	610063	180130585	.	1	0	2.5	.	121	1.5	.	-70	0.75	8.17	0.9375
rushrunn112007	rushrun	2007	704022	.	198100359	0	.	2.0	3	52	.	.	.	0.75	8.00	0.9515
rushrunn112007	rushrun	2007	704033	.	198100359	0	0	2.0	8	60	0.0	5	8	0.75	8.00	0.9515
rushrunn112007	rushrun	2007	702048	.	198100359	0	0	2.0	17	66	0.0	9	6	0.75	8.00	0.9515
rushruns112007	rushrun	2007	704008	180130587	.	0	.	1.2	53	85	.	.	.	0.75	8.00	0.9515
rushruns112007	rushrun	2007	701054	180130587	.	0	0	2.5	30	65	1.3	-23	-20	0.75	8.00	0.9515
rushrunn112008	rushrun	2008	803025	198100322	198100465	0	.	3.0	48	65	.	.	.	0.75	4.87	0.9349
rushrunn112008	rushrun	2008	806004	198100322	198100465	0	0	3.0	53	48	0.0	5	-17	0.75	4.87	0.9349
rushruns101200	rushrun	2008	804040	180144896	198100572	0	.	1.8	26	22	.	.	.	0.75	4.87	0.9349
rushruns101200	rushrun	2008	809048	180144896	198100572	1	0	3.0	41	14	1.2	16	-8	0.75	4.87	0.9349
rushrunn141200	rushrun	2009	907041	198100322	198100497	1	.	1.3	23	39	.	.	.	0.75	7.13	0.9264
rushrunn141200	rushrun	2009	901122	198100322	198100497	0	1	8.0	31	17	6.7	8	-22	0.75	7.13	0.9264
rushrunn151200	rushrun	2009	901005	.	.	0	.	1.0	74	44	.	.	.	0.75	7.13	0.9264
rushrunn151200	rushrun	2009	905027	.	.	0	0	1.8	20	76	0.8	-54	32	0.75	7.13	0.9264
rushrunn151200	rushrun	2009	901085	.	.	1	0	2.0	39	22	0.3	19	-54	0.75	7.13	0.9264
rushruns812009	rushrun	2009	901011	.	198100543	1	.	0.8	.	43	.	.	.	0.75	7.13	0.9264
rushruns812009	rushrun	2009	901100	.	198100543	0	1	6.0	38	21	5.2	.	-22	0.75	7.13	0.9264
rushrunn21201	rushrun	2010	1006001	198100542	198100543	1	.	2.9	39	122	.	.	.	0.75	12.69	0.9187
rushrunn21201	rushrun	2010	1013026	198100542	198100543	0	1	2.9	28	49	0.0	-11	-73	0.75	12.69	0.9187
rushrunn71201	rushrun	2010	1007017	198100322	.	0	.	1.8	75	47	.	.	.	0.75	12.69	0.9187
rushrunn71201	rushrun	2010	1007056	198100322	.	0	0	1.8	39	30	0.1	-36	-17	0.75	12.69	0.9187
rushruns16120	rushrun	2010	1006025	198107151	.	0	.	3.2	48	86	.	.	.	0.75	12.69	0.9187

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
rushruns16120	rushrun	2010	1006033	198107151	.	1	0	2.6	28	86	-0.6	-20	0	0.75	12.69	0.9187
sgalena112006	sgalena	2006	603037	198100154	198100186	0	.	1.0	53	103	.	.	.	-0.57	7.38	0.9207
sgalena112006	sgalena	2006	604066	198100154	198100186	0	0	1.0	38	32	0.0	-15	-71	-0.57	7.38	0.9207
sgalena112006	sgalena	2006	612073	198100154	198100186	0	0	1.0	38	128	0.0	0	96	-0.57	7.38	0.9207
sgalena612006	sgalena	2006	612010	.	198100156	0	.	2.3	50	80	.	.	.	-0.57	7.38	0.9207
sgalena612006	sgalena	2006	612032	.	198100156	0	0	1.5	48	66	-0.8	-3	-14	-0.57	7.38	0.9207
sgalena112007	sgalena	2007	703023	198100154	198100186	0	.	2.5	11	41	.	.	.	-0.57	11.54	0.9285
sgalena112007	sgalena	2007	709028	198100154	198100186	0	0	1.4	58	32	-1.1	46	-9	-0.57	11.54	0.9285
sgalena112008	sgalena	2008	805023	180130549	198100493	0	.	1.0	59	58	.	.	.	-0.57	4.61	0.9187
sgalena112008	sgalena	2008	804095	180130549	198100493	0	0	4.0	88	43	3.0	29	-15	-0.57	4.61	0.9187
sgalena112009	sgalena	2009	903009	.	198100569	0	.	1.8	50	21	.	.	.	-0.57	6.28	0.9336
sgalena112009	sgalena	2009	903063	.	198100569	0	0	3.5	48	50	1.7	-3	29	-0.57	6.28	0.9336
sgalena112009	sgalena	2009	903073	.	198100569	0	0	6.0	50	9	2.5	3	-41	-0.57	6.28	0.9336
sgalena112009	sgalena	2009	909042	.	198100569	1	0	4.3	36	34	-1.8	-14	25	-0.57	6.28	0.9336
sgalena212009	sgalena	2009	904042	.	198100586	0	.	2.0	48	61	.	.	.	-0.57	6.28	0.9336
sgalena212009	sgalena	2009	903034	.	198100586	1	0	1.2	43	37	-0.8	-5	-24	-0.57	6.28	0.9336
sgalena212009	sgalena	2009	903105	.	198100586	1	1	2.5	60	127	1.3	18	90	-0.57	6.28	0.9336
sgalena312009	sgalena	2009	903021	.	198100570	0	.	1.4	78	23	.	.	.	-0.57	6.28	0.9336
sgalena312009	sgalena	2009	906050	.	198100570	1	0	1.0	45	115	-0.4	-33	92	-0.57	6.28	0.9336
sgalena412009	sgalena	2009	903010	198100597	.	0	.	2.0	53	15	.	.	.	-0.57	6.28	0.9336
sgalena412009	sgalena	2009	903035	198100597	198100541	0	0	1.7	60	16	-0.3	8	1	-0.57	6.28	0.9336
sgalena112010	sgalena	2010	1003022	180130576	.	0	.	2.0	49	48	.	.	.	-0.57	7.08	0.9160
sgalena112010	sgalena	2010	1003038	180130576	.	0	0	1.8	49	47	-0.3	0	-1	-0.57	7.08	0.9160
sgalena112010	sgalena	2010	1002080	180130576	.	0	0	1.3	44	38	-0.5	-5	-9	-0.57	7.08	0.9160
sgalena112010	sgalena	2010	1004020	180130576	.	0	0	1.5	58	93	0.3	14	55	-0.57	7.08	0.9160
sgalena112010	sgalena	2010	1004033	180130576	.	0	0	4.8	40	107	3.3	-18	14	-0.57	7.08	0.9160
sgalena112010	sgalena	2010	1009026	180130576	.	1	0	2.1	61	57	-2.7	21	-50	-0.57	7.08	0.9160
sgalena212010	sgalena	2010	1003030	198100540	198100570	0	.	1.7	41	133	.	.	.	-0.57	7.08	0.9160
sgalena212010	sgalena	2010	1004021	198100540	198100570	0	0	3.5	34	24	1.8	-8	-109	-0.57	7.08	0.9160
sgalena212010	sgalena	2010	1003107	198100540	198100570	0	0	2.6	41	8	-0.9	8	-16	-0.57	7.08	0.9160
sgalena312010	sgalena	2010	1003031	.	198100586	0	.	1.1	55	40	.	.	.	-0.57	7.08	0.9160
sgalena312010	sgalena	2010	1002076	.	198100586	1	0	.	.	.	.	.	.	-0.57	7.08	0.9160
sgalena312010	sgalena	2010	1003100	.	198100586	0	1	2.1	44	160	.	.	.	-0.57	7.08	0.9160
tuttlen112006	tuttle	2006	604013	189199382	198100223	0	.	2.5	64	214	.	.	.	1.61	7.39	0.9585
tuttlen112006	tuttle	2006	612020	189199382	198100223	1	0	2.0	56	104	-0.5	-8	-110	1.61	7.39	0.9585
tuttlen212006	tuttle	2006	604005	198100409	198100160	0	.	2.0	89	132	.	.	.	1.61	7.39	0.9585
tuttlen212006	tuttle	2006	604056	198100409	198100160	1	0	2.5	65	67	0.5	-24	-65	1.61	7.39	0.9585

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
tuttlen312006	tuttle	2006	604014	198100259	198199381	0	.	1.0	83	49	.	.	.	1.61	7.39	0.9585
tuttlen312006	tuttle	2006	604051	198100259	189199381	1	0	2.5	18	139	1.5	-65	90	1.61	7.39	0.9585
tuttlen112007	tuttle	2007	704001	198100259	189199381	0	.	3.0	30	36	.	.	.	1.61	14.60	0.9600
tuttlen112007	tuttle	2007	709003	198100259	189199381	0	0	1.8	70	55	-1.3	40	19	1.61	14.60	0.9600
tuttlen112007	tuttle	2007	703030	198100259	189199381	0	0	3.0	58	71	1.3	-13	16	1.61	14.60	0.9600
tuttlen112007	tuttle	2007	701051	198100259	189199381	0	0	2.5	21	26	-0.5	-36	-45	1.61	14.60	0.9600
tuttlen112007	tuttle	2007	709056	198100259	189199381	0	0	2.5	59	73	0.0	38	47	1.61	14.60	0.9600
tuttles112007	tuttle	2007	701005	198100340	198100555	0	.	1.5	59	47	.	.	.	1.61	14.60	0.9600
tuttles112007	tuttle	2007	701039	198100340	198100555	0	0	2.5	18	58	1.0	-41	11	1.61	14.60	0.9600
tuttlen612008	tuttle	2008	809007	198100259	.	0	.	1.2	55	82	.	.	.	1.61	3.66	0.9592
tuttlen612008	tuttle	2008	809023	198100259	.	0	0	1.6	65	24	0.4	10	-58	1.61	3.66	0.9592
tuttlen612008	tuttle	2008	806005	198100259	.	0	0	1.8	73	74	0.2	8	50	1.61	3.66	0.9592
tuttlen612008	tuttle	2008	807058	198100259	.	1	0	3.5	50	34	1.8	-23	-40	1.61	3.66	0.9592
tuttles412008	tuttle	2008	803032	.	198100559	1	.	1.3	68	25	.	.	.	1.61	3.66	0.9592
tuttles412008	tuttle	2008	803066	.	198100559	1	1	2.5	5	31	1.3	-63	6	1.61	3.66	0.9592
tuttlen112009	tuttle	2009	902005	198100417	.	1	.	1.5	16	35	.	.	.	1.61	5.20	0.9413
tuttlen112009	tuttle	2009	901090	198100417	.	1	1	3.3	40	117	1.8	24	82	1.61	5.20	0.9413
tuttlen312009	tuttle	2009	902025	198100259	.	0	.	3.1	86	81	.	.	.	1.61	5.20	0.9413
tuttlen312009	tuttle	2009	902075	198100259	.	0	0	2.8	54	31	-0.3	-33	-50	1.61	5.20	0.9413
tuttlen312009	tuttle	2009	906089	198100259	.	1	0	3.5	59	47	0.7	5	16	1.61	5.20	0.9413
tuttles212009	tuttle	2009	902034	.	198100188	0	.	4.5	53	44	.	.	.	1.61	5.20	0.9413
tuttles212009	tuttle	2009	902071	.	198100188	0	0	2.3	50	34	-2.3	-3	-10	1.61	5.20	0.9413
tuttles212009	tuttle	2009	906087	.	198100188	1	0	3.6	5	35	1.4	-45	1	1.61	5.20	0.9413
tuttles512009	tuttle	2009	902012	.	198100334	0	.	1.5	9	50	.	.	.	1.61	5.20	0.9413
tuttles512009	tuttle	2009	902074	.	198100334	0	0	2.0	64	37	0.5	55	-13	1.61	5.20	0.9413
tuttles512009	tuttle	2009	906100	.	198100334	1	0	3.5	64	12	1.5	0	-25	1.61	5.20	0.9413
tuttlen112010	tuttle	2010	1001005	198100259	198100560	0	.	2.8	65	55	.	.	.	1.61	6.09	0.9582
tuttlen112010	tuttle	2010	1001028	198100259	198100560	1	0	1.9	36	78	-0.9	-29	23	1.61	6.09	0.9582
tuttlen112010	tuttle	2010	1001078	198100259	198100560	0	1	3.5	50	65	1.6	14	-13	1.61	6.09	0.9582
tuttlen112010	tuttle	2010	1001082	198100259	198100560	0	0	4.1	90	72	0.6	40	7	1.61	6.09	0.9582
tuttlen112010	tuttle	2010	1011004	198100259	198100560	1	0	1.8	73	36	-2.4	-18	-36	1.61	6.09	0.9582
tuttlen112010	tuttle	2010	1001106	198100259	198100560	0	1	2.0	55	77	0.3	-18	41	1.61	6.09	0.9582
tuttles712010	tuttle	2010	1002101	.	198100188	1	.	2.5	41	46	.	.	.	1.61	6.09	0.9582
tuttles712010	tuttle	2010	1009018	.	198100188	1	1	2.5	33	32	0.0	-9	-14	1.61	6.09	0.9582
tuttles812010	tuttle	2010	1001059	198100294	198100334	1	.	2.0	63	48	.	.	.	1.61	6.09	0.9582
tuttles812010	tuttle	2010	1001080	198100294	198100334	0	1	3.8	74	70	1.8	11	22	1.61	6.09	0.9582
tuttles812010	tuttle	2010	1008007	198100294	198100334	0	0	3.2	36	55	-0.6	-38	-15	1.61	6.09	0.9582

Continued

Table D.1 Continued

Terr ID	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
tuttles812010	tuttle	2010	1011013	198100294	198100334	1	0	3.5	34	49	0.3	-3	-6	1.61	6.09	0.9582
woodside112006	tuttle	2006	604011	180130565	.	0	.	1.0	18	36	.	.	.	0.32	7.58	0.9320
woodside112006	wdside	2006	610037	180130565	.	0	0	1.0	39	45	0.0	21	9	0.32	7.58	0.9320
woodside112006	wdside	2006	611080	180130565	.	1	0	0.5	6	14	-0.5	-33	-31	0.32	7.58	0.9320
woodside412006	wdside	2006	610012	180130544	.	0	.	2.0	29	39	.	.	.	0.32	7.58	0.9320
woodside412006	wdside	2006	611040	180130544	.	1	0	5.0	40	8	3.0	11	-31	0.32	7.58	0.9320
woodside112009	wdside	2009	904002	180130534	180130527	0	.	2.5	69	2	.	.	.	0.32	5.43	0.8989
woodside112009	wdside	2009	904018	180130534	180130527	0	0	1.4	38	45	-1.1	-31	43	0.32	5.43	0.8989
woodside112009	wdside	2009	903016	180130534	180130527	0	0	2.0	38	12	0.6	0	-33	0.32	5.43	0.8989
woodside112009	wdside	2009	903041	180130534	180130527	0	0	2.0	53	5	0.0	15	-7	0.32	5.43	0.8989
woodside112009	wdside	2009	903067	180130534	180130527	0	0	7.0	38	8	5.0	-15	3	0.32	5.43	0.8989
woodside212009	wdside	2009	904001	198100392	198100589	0	.	2.5	46	18	.	.	.	0.32	5.43	0.8989
woodside212009	wdside	2009	903015	198100392	198100589	0	0	1.0	68	37	-1.5	21	19	0.32	5.43	0.8989
woodside212009	wdside	2009	903088	198100392	198100589	0	0	4.5	65	30	3.5	-3	-7	0.32	5.43	0.8989
woodside112010	wdside	2010	1003047	198100350	198107104	0	.	1.5	21	43	.	.	.	0.32	4.90	0.9326
woodside112010	wdside	2010	1003073	198100350	198107104	0	0	2.0	60	44	0.5	39	1	0.32	4.90	0.9326
woodside112010	wdside	2010	1003092	198100350	198107104	0	0	1.3	90	15	-0.8	30	-29	0.32	4.90	0.9326
woodside212010	wdside	2010	1003028	.	199167443	1	.	1.4	23	26	.	.	.	0.32	4.90	0.9326
woodside212010	wdside	2010	1004035	.	199167443	0	1	7.0	71	66	5.6	49	40	0.32	4.90	0.9326
woodside312010	wdside	2010	1003029	198107121	.	0	.	1.3	70	23	.	.	.	0.32	4.90	0.9326
woodside312010	wdside	2010	1003046	198107121	.	0	0	1.5	29	50	0.2	-41	27	0.32	4.90	0.9326
woodside312010	wdside	2010	1001098	198107121	.	1	0	5.0	59	13	3.5	30	-37	0.32	4.90	0.9326
woodside512010	wdside	2010	1003001	198100392	.	0	.	2.3	45	55	.	.	.	0.32	4.90	0.9326
woodside512010	wdside	2010	1004008	198100392	.	0	0	1.8	55	12	-0.5	10	-43	0.32	4.90	0.9326
woodside512010	wdside	2010	1004039	198100392	.	0	0	1.8	59	42	0.0	4	30	0.32	4.90	0.9326
woodside512010	wdside	2010	1003109	198100392	.	1	0	7.0	54	12	5.2	-5	-30	0.32	4.90	0.9326

Table D.2 Data for analyses to determine effect of previous nest fate, perceived and actual risk on changes in Acadian flycatcher (*Empidonax virescens*) nest characteristics between successive nest attempts at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2006-2010. Terr ID = Territory ID for pairs used in the analysis, Male ID = male USGS band number, Female ID = female USGS band number, Fate = nest fate (0 = failed, 1 = fledged), Pfate = fate of previous nest, Nh = nest height, Nc = nest concealment, Vd = vegetation density, ΔNh = change in nest height between successive nests, ΔNc = change in nest concealment between successive nests, ΔVd = change in vegetation density between successive nests, Urb = urban index, Predrd = relative detections of predators (perceived predation risk), DSR = daily survival rate of flycatcher nests by site and year (1 – DSR = actual predation risk). See Chapter 3 for additional details.

Table D.2 Continued

Terr Id	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
casto112008	casto	2008	803046	.	.	0	.	1.6	1	4	.	.	.	1.25	3.45	0.7803
casto112008	casto	2008	804087	.	.	1	0	4	16	29	2.4	15	25	1.25	3.45	0.7803
casto112009	casto	2009	903064	.	240094088	1	.	3.6	10	17	.	.	.	1.25	6.22	1
casto112009	casto	2009	909037	.	240094088	1	1	5	18	22	1.4	8	5	1.25	6.22	1
cherry112009	cherry	2009	903060	240094047	.	0	.	6	45	8	.	.	.	0.76	4.99	0.5005
cherry112009	cherry	2009	903087	240094047	.	1	0	15	60	14	9	15	6	0.76	4.99	0.5005
cherry712010	cherry	2010	1003069	240094047	.	0	.	5	21	48	.	.	.	0.76	3.83	0.9084
cherry712010	cherry	2010	1003091	240094047	.	0	0	.	.	.	.	.	.	0.76	3.83	0.9084
cherry712010	cherry	2010	1003106	240094047	.	0	0	13	40	25	.	.	.	0.76	3.83	0.9084
creeks212006	creeks	2006	604072	232051586	.	0	.	.	26	53	.	.	.	-0.71	3.91	0.7459
creeks212006	creeks	2006	603143	232051586	.	0	0	7	45	0	.	19	-53	-0.71	3.91	0.7459
creeks112007	creeks	2007	711031	240094066	.	0	.	4	15	44	.	.	.	-0.71	8.57	0.8216
creeks112007	creeks	2007	701072	240094066	.	0	0	5.5	31	20	1.5	16	-24	-0.71	8.57	0.8216
creeks112007	creeks	2007	711069	240094066	.	1	0	8	1	16	2.5	-30	-4	-0.71	8.57	0.8216
creeks412007	creeks	2007	711045	.	232051578	1	.	4	19	13	.	.	.	-0.71	8.57	0.8216
creeks412007	creeks	2007	701096	.	232051578	1	1	5.5	13	20	1.5	-7	7	-0.71	8.57	0.8216
creeks312008	creeks	2008	808048	240094089	.	0	.	6.4	18	11	.	.	.	-0.71	1.13	0.7418
creeks312008	creeks	2008	804073	240094089	.	0	0	5.5	61	8	-0.9	44	-3	-0.71	1.13	0.7418
creeks312009	creeks	2009	905041	240094089	.	0	.	3.2	40	37	.	.	.	-0.71	1.71	0.9686
creeks312009	creeks	2009	906098	240094089	.	1	0	4.5	33	21	1.3	-8	-16	-0.71	1.71	0.9686
creeks112010	creeks	2010	1005045	240094063	240094062	0	.	4	0	15	.	.	.	-0.71	4.21	0.9411
creeks112010	creeks	2010	1001077	240094063	240094062	0	0	8	63	12	4	63	-3	-0.71	4.21	0.9411
creeks112010	creeks	2010	1011007	240094063	240094062	0	0	6	16	0	-2	-46	-12	-0.71	4.21	0.9411
creeks112010	creeks	2010	1009020	240094063	240094062	1	0	8	23	10	2	6	10	-0.71	4.21	0.9411
elkrun112010	elkrun	2010	1005043	240094054	.	0	.	3.5	5	6	.	.	.	-0.16	6.02	1
elkrun112010	elkrun	2010	1009002	240094054	.	1	0	4	1	34	0.5	-5	28	-0.16	6.02	1
elkrun112010	elkrun	2010	1009024	240094054	.	1	1	4	24	55	0	23	21	-0.16	6.02	1
galena112006	galena	2006	604068	232051595	.	0	.	3.5	61	25	.	.	.	-0.48	5.35	0.6834
galena112006	galena	2006	604097	232051595	.	0	0	2.5	23	26	-1	-39	1	-0.48	5.35	0.6834
galena312006	galena	2006	603083	240094014	229058059	1	.	8	30	4	.	.	.	-0.48	5.35	0.6834
galena312006	galena	2006	604144	240094014	229058059	1	1	8	41	5	0	11	1	-0.48	5.35	0.6834
galena512006	galena	2006	604117	240094004	232051596	0	.	4.8	9	17	.	.	.	-0.48	5.35	0.6834
galena512006	galena	2006	604154	240094004	232051596	1	0	6.5	63	25	1.8	54	8	-0.48	5.35	0.6834
galena612006	galena	2006	604098	240094022	240094021	0	.	3.5	54	37	.	.	.	-0.48	5.35	0.6834

Continued

Table D.2 Continued

Terr Id	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
galena612006	galena	2006	603199	240094022	240094021	0	0	6	61	21	2.5	8	-16	-0.48	5.35	0.6834
galena612006	galena	2006	604147	240094022	240094021	1	0	4	9	38	-2	-53	17	-0.48	5.35	0.6834
galena312007	galena	2007	709042	240094022	240094021	0	.	10	25	12	.	.	.	-0.48	6.61	0.7508
galena122008	galena	2008	804056	.	.	0	.	3.5	33	16	.	.	.	-0.48	3.98	0.7472
galena122008	galena	2008	804074	.	.	0	0	5	60	16	1.5	28	0	-0.48	3.98	0.7472
galena132008	galena	2008	804079	.	240094048	1	.	2	43	61	.	.	.	-0.48	3.98	0.7472
galena132008	galena	2008	804098	.	240094048	1	1	4	34	17	2	-9	-44	-0.48	3.98	0.7472
galena122009	galena	2009	903074	240094065	.	0	.	3.7	10	10	.	.	.	-0.48	5.98	0.9667
galena122009	galena	2009	903095	240094065	.	1	0	6	19	11	2.3	9	1	-0.48	5.98	0.9667
galena212009	galena	2009	909024	.	.	0	.	6	35	5	.	.	.	-0.48	5.98	0.9667
galena212009	galena	2009	908015	.	229058059	1	0	5.2	28	16	-0.8	-8	11	-0.48	5.98	0.9667
galena212009	galena	2009	908033	.	229058059	0	1	4.5	36	27	-0.7	9	11	-0.48	5.98	0.9667
galena312010	galena	2010	1003072	.	240094021	0	.	2.8	15	18	.	.	.	-0.48	4.83	0.9397
galena312010	galena	2010	1003094	.	240094021	0	0	4.1	49	20	1.4	34	2	-0.48	4.83	0.9397
ngalena112006	ngalena	2006	603085	232051585	229058051	0	.	5	29	48	.	.	.	-1.27	5.76	0.6888
ngalena112006	ngalena	2006	612078	232051585	229058051	1	0	5	31	4	0	3	-44	-1.27	5.76	0.6888
ngalena212006	ngalena	2006	604075	232051579	.	0	.	10	90	63	.	.	.	-1.27	5.76	0.6888
ngalena212006	ngalena	2006	612079	232051579	.	1	0	8	70	16	-2	-20	-47	-1.27	5.76	0.6888
ngalena222006	ngalena	2006	604092	232051579	.	0	.	5	54	45	.	.	.	-1.27	5.76	0.6888
ngalena222006	ngalena	2006	604141	232051579	.	1	0	6	74	9	1	20	-36	-1.27	5.76	0.6888
ngalena412006	ngalena	2006	604091	183014617	240094019	1	.	3.5	30	18	.	.	.	-1.27	5.76	0.6888
ngalena412006	ngalena	2006	604140	183014617	240094019	1	1	9	66	26	5.5	36	8	-1.27	5.76	0.6888
ngalena112007	ngalena	2007	711035	232051585	.	0	.	5	3	7	.	.	.	-1.27	7.72	0.8045
ngalena112007	ngalena	2007	711051	232051585	.	1	0	7	40	24	2	37	17	-1.27	7.72	0.8045
ngalena512008	ngalena	2008	805047	240094040	240094046	0	.	3.3	10	19	.	.	.	-1.27	2.75	0.7751
ngalena512008	ngalena	2008	805057	240094040	240094046	0	0	6	43	16	2.8	33	-3	-1.27	2.75	0.7751
ngalena412010	ngalena	2010	1003080	249074154	.	0	.	4.3	23	42	.	.	.	-1.27	6.8	0.9612
ngalena412010	ngalena	2010	1003090	249074154	.	1	0	5	56	5	0.8	34	-37	-1.27	6.8	0.9612
ngalena412010	ngalena	2010	1009025	249074154	.	1	1	4.7	23	49	-0.3	-34	44	-1.27	6.8	0.9612
ngalena422010	ngalena	2010	1003096	249074154	.	1	.	4.3	55	64	.	.	.	-1.27	6.8	0.9612
ngalena422010	ngalena	2010	1003123	249074154	.	1	1	7	45	179	2.8	-10	115	-1.27	6.8	0.9612
prairie112006	prairie	2006	603077	229058062	240094027	1	.	2.8	41	48	.	.	.	-1.12	7.87	0.8539
prairie112006	prairie	2006	604139	229058062	240094027	0	1	8	55	37	5.3	14	-11	-1.12	7.87	0.8539
prairie212006	prairie	2006	603078	240094036	240094028	1	.	3	17	54	.	.	.	-1.12	7.87	0.8539
prairie212006	prairie	2006	603161	240094036	240094028	1	1	4.5	28	74	1.5	10	20	-1.12	7.87	0.8539
prairie112007	prairie	2007	708033	229058062	.	0	.	2.5	11	69	.	.	.	-1.12	7.32	0.7519
prairie112007	prairie	2007	701093	229058062	.	1	0	5	98	38	2.5	86	-31	-1.12	7.32	0.7519

Continued

Table D.2 Continued

Terr Id	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
prairie122007	prairie	2007	708049	229058062	240094016	1	.	10	46	52	.	.	.	-1.12	7.32	0.7519
prairie122007	prairie	2007	708065	229058062	240094016	0	1	13	30	41	3	-16	-11	-1.12	7.32	0.7519
prairie112008	prairie	2008	804045	229058062	.	0	.	3.2	36	60	.	.	.	-1.12	4.36	0.8989
prairie112008	prairie	2008	803057	229058062	.	1	0	4	24	32	0.8	-12	-28	-1.12	4.36	0.8989
prairie112009	prairie	2009	907119	240094049	.	1	.	3.3	20	78	.	.	.	-1.12	9.06	0.9338
prairie112009	prairie	2009	907148	240094049	.	0	1	7	55	89	3.8	35	11	-1.12	9.06	0.9338
prairie112009	prairie	2009	907155	240094049	.	0	0	2.5	48	153	-4.5	-8	64	-1.12	9.06	0.9338
prairie112010	prairie	2010	1007115	240094049	.	0	.	2.8	8	89	.	.	.	-1.12	10.76	0.9855
prairie112010	prairie	2010	1007146	240094049	.	1	0	4.5	31	7	1.8	24	-82	-1.12	10.76	0.9855
pubhunt112006	pubhunt	2006	608004	229058046	.	0	.	7	26	50	.	.	.	-1.15	6.64	0.807
pubhunt112006	pubhunt	2006	603099	229058046	.	0	0	4	45	55	-3	20	5	-1.15	6.64	0.807
pubhunt212006	pubhunt	2006	604090	232051537	240094017	1	.	3.3	44	57	.	.	.	-1.15	6.64	0.807
pubhunt212006	pubhunt	2006	612090	232051537	240094017	0	1	4.5	70	116	1.3	26	59	-1.15	6.64	0.807
pubhunt312006	pubhunt	2006	604105	240094007	.	0	.	2	28	50	.	.	.	-1.15	6.64	0.807
pubhunt312006	pubhunt	2006	604142	240094007	.	1	0	1.5	38	15	-0.5	10	-35	-1.15	6.64	0.807
pubhunt112008	pubhunt	2008	807037	240094070	.	0	.	5	18	33	.	.	.	-1.15	5.13	0.8157
pubhunt112008	pubhunt	2008	807050	240094070	.	1	0	4	54	17	-1	36	-16	-1.15	5.13	0.8157
pubhunt112009	pubhunt	2009	907100	240094063	.	0	.	2.8	6	32	.	.	.	-1.15	6.51	0.9298
pubhunt112009	pubhunt	2009	907122	240094063	.	1	0	4.8	18	15	2	12	-17	-1.15	6.51	0.9298
pubhunt122009	pubhunt	2009	907136	240094063	.	0	.	2.5	19	42	.	.	.	-1.15	6.51	0.9298
pubhunt122009	pubhunt	2009	907163	240094063	.	0	0	5	38	43	2.5	18	1	-1.15	6.51	0.9298
pubhunt212009	pubhunt	2009	901076	.	240094085	1	.	4	20	40	.	.	.	-1.15	6.51	0.9298
pubhunt212009	pubhunt	2009	907145	.	240094085	0	1	3	19	88	-1	-1	48	-1.15	6.51	0.9298
pubhunt112010	pubhunt	2010	1007106	249074152	240094085	0	.	3.4	11	95	.	.	.	-1.15	7.18	0.9747
pubhunt112010	pubhunt	2010	1007123	249074152	240094085	0	0	2.5	59	152	-0.9	48	57	-1.15	7.18	0.9747
pubhunt112010	pubhunt	2010	1007144	249074152	240094085	0	0	15	26	.	12.5	-33	.	-1.15	7.18	0.9747
pubhunt112010	pubhunt	2010	1007171	249074152	240094085	1	0	2.5	11	101	-12.5	-15	.	-1.15	7.18	0.9747
pubhunt212010	pubhunt	2010	1007114	249074151	.	1	.	4	8	80	.	.	.	-1.15	7.18	0.9747
pubhunt212010	pubhunt	2010	1007150	249074151	.	1	1	4	8	47	0	0	-33	-1.15	7.18	0.9747
rushrunsouth1	rushrun	2007	704054	240094076	.	0	.	4	21	33	.	.	.	0.75	8	0.8929
rushrunsouth1	rushrun	2007	704066	240094076	.	1	0	4	59	41	0	38	8	0.75	8	0.8929
rushrunsouth1	rushrun	2008	802036	.	.	0	.	3.1	23	13	.	.	.	0.75	4.87	0.7795
rushrunsouth1	rushrun	2008	803068	.	.	0	0	7	89	30	3.9	66	17	0.75	4.87	0.7795
sgalena112006	sgalena	2006	604081	229058032	.	1	.	3.5	60	41	.	.	.	-0.57	7.38	0.8232
sgalena112006	sgalena	2006	604137	229058032	.	1	1	3.3	56	46	-0.3	-4	5	-0.57	7.38	0.8232
sgalena122006	sgalena	2006	603091	229058032	240094001	0	.	1.8	17	78	.	.	.	-0.57	7.38	0.8232

Continued

Table D.2 Continued

Terr Id	Site	Year	Nest ID	Male ID	Female ID	Fate	Pfate	Nh	Nc	Vd	ΔNh	ΔNc	ΔVd	Urb	Predrd	DSR
sgalena122006	sgalena	2006	603129	229058032	240094001	1	0	5.5	63	29	3.8	46	-49	-0.57	7.38	0.8232
sgalena112007	sgalena	2007	701070	229058032	240094001	0	.	2.3	60	12	.	.	.	-0.57	11.54	0.807
sgalena112007	sgalena	2007	711068	229058032	240094001	0	0	3	4	28	0.7	-56	16	-0.57	11.54	0.807
sgalena112007	sgalena	2007	703058	229058032	240094001	1	0	1.4	5	51	-1.6	1	23	-0.57	11.54	0.807
sgalena112009	sgalena	2009	906051	240094050	.	0	.	3.8	43	64	.	.	.	-0.57	6.28	0.975
sgalena112009	sgalena	2009	909035	240094050	.	1	0	5	46	28	1.3	4	-36	-0.57	6.28	0.975
tuttlenorth11	tuttle	2010	1001081	249074115	.	0	.	5.5	64	34	.	.	.	1.61	6.09	0.9668
tuttlenorth11	tuttle	2010	1001102	249074115	.	1	0	3.5	46	77	-2	-18	43	1.61	6.09	0.9668
woodside112006	woodside	2006	604116	240094025	240094026	0	.	3.5	10	27	.	.	.	0.32	7.58	0.5838
woodside112006	woodside	2006	604148	240094025	240094026	1	0	6	8	34	2.5	-3	7	0.32	7.58	0.5838
woodside112007	woodside	2007	710105	240094025	240094026	1	.	3	28	22	.	.	.	0.32	15.58	0.8143
woodside112007	woodside	2007	704068	240094025	240094026	1	1	5.2	2	7	2.2	-26	-15	0.32	15.58	0.8143
woodside122007	woodside	2007	710124	240094025	240094023	0	.	9	21	17	.	.	.	0.32	15.58	0.8143
woodside122007	woodside	2007	710173	240094025	240094023	1	0	8	.	37	-1	.	20	0.32	15.58	0.8143
woodside112008	woodside	2008	804044	240094045	240094026	1	.	4	43	8	.	.	.	0.32	4.41	0.764
woodside112008	woodside	2008	804081	240094045	240094026	0	1	4	23	11	0	-20	3	0.32	4.41	0.764
woodside112008	woodside	2008	804099	240094045	240094026	1	0	2	37	6	-2	14	-5	0.32	4.41	0.764
woodside112010	woodside	2010	1003084	249074128	.	0	.	2	50	11	.	.	.	0.32	4.9	0.9307
woodside112010	woodside	2010	1004038	249074128	.	1	0	11	56	17	9	6	6	0.32	4.9	0.9307
woodside122010	woodside	2010	1004027	249074128	.	0	.	9	40	15	.	.	.	0.32	4.9	0.9307
woodside122010	woodside	2010	1009019	249074128	.	1	0	10	44	7	1	4	-8	0.32	4.9	0.9307

Appendix E – Supplement to Chapter 4

Table E.1 Data for analyses to explain provisioning rates (visits per hour) of northern cardinals (*Cardinalis cardinalis*) at riparian forest sites in Franklin and Delaware Counties, Ohio, USA, 2008-2010, *n* = 60. Young = number of nestlings, Julian date = date of nest observation, nest cover = % of nest concealed by vegetation, veg density = vegetation density within 11.3 m radius circle of the nest, predrd = relative detections of predators at each site by year (i.e. perceived predation risk), DSR = site-level daily survival rates of cardinal nests at the respective site by year (1 – DSR = actual predation risk), urban index = index of urbanization.

Nest ID	Year	Site	Visits per Hour	Nest Fate	Young	Julian Date	Nest Cover %	Veg Density	Pred Rd	DSR	Urban Index
802025	2008	casto	6.50	failed	2	151	50	78	3.45	0.9511	1.25
804091	2008	casto	3.00	fledged	1	197	38	33	3.45	0.9511	1.25
903050	2009	casto	4.50	fledged	2	154	39	39	6.22	0.9516	1.25
904014	2009	casto	5.00	fledged	2	126	74	43	6.22	0.9516	1.25
1003117	2010	casto	5.33	fledged	2	213	60	63	3.77	0.9584	1.25
805014	2008	cherry	3.33	fledged	2	137	54	92	2.54	0.9593	0.76
805035	2008	cherry	4.00	fledged	3	156	48	184	2.54	0.9593	0.76
909033	2009	cherry	5.17	failed	2	196	33	103	4.99	0.9086	0.76
1004018	2010	cherry	3.17	fledged	2	149	49	64	3.83	0.9696	0.76
803012	2008	elkrun	1.82	failed	2	125	15	102	2.72	0.9558	-0.16
803078	2008	elkrun	5.43	fledged	2	217	18	131	2.72	0.9558	-0.16
808026	2008	elkrun	7.50	fledged	3	142	27	109	2.72	0.9558	-0.16
905008	2009	elkrun	1.33	failed	1	116	17	46	3.36	0.9262	-0.16
803071	2008	kenny	2.73	fledged	1	205	53	57	5.07	0.9391	0.89
804041	2008	kenny	3.67	failed	3	159	43	42	5.07	0.9391	0.89
901110	2009	kenny	3.50	fledged	1	192	52	58	7.99	0.9116	0.89
901128	2009	kenny	6.67	fledged	3	200	54	67	7.99	0.9116	0.89
906018	2009	kenny	8.67	fledged	3	169	53	53	7.99	0.9116	0.89
1002018	2010	kenny	2.89	fledged	1	120	98	88	10.10	0.9225	0.89

Continued

Table E.1 Continued

Nest ID	Year	Site	Visits per Hour	Nest Fate	Young	Julian Date	Nest Cover %	Veg Density	Pred Rd	DSR	Urban Index
1002057	2010	kenny	4.17	fledged	2	144	69	136	10.10	0.9225	0.89
1002104	2010	kenny	3.33	fledged	1	149	64	83	10.10	0.9225	0.89
1002122	2010	kenny	3.00	failed	3	169	86	111	10.10	0.9225	0.89
1002146	2010	kenny	4.50	fledged	3	201	53	61	10.10	0.9225	0.89
1013032	2010	kenny	6.17	fledged	3	232	22	96	10.10	0.9225	0.89
904049	2009	lou	4.17	fledged	2	129	4	126	5.97	0.9396	1.26
906109	2009	lou	3.50	failed	3	233	42	74	5.97	0.9396	1.26
901042	2009	prairie	4.00	fledged	3	133	47	25	9.06	0.9434	-1.12
907105	2009	prairie	4.50	fledged	2	170	50	70	9.06	0.9434	-1.12
1007070	2010	prairie	2.50	fledged	2	137	47	40	10.76	0.9540	-1.12
1007110	2010	prairie	2.33	fledged	1	160	49	126	10.76	0.9540	-1.12
801062	2008	pubhunt	2.77	failed	3	169	66	100	5.13	0.9490	-1.15
807022	2008	pubhunt	3.33	failed	2	152	84	60	5.13	0.9490	-1.15
907049	2009	pubhunt	2.33	fledged	1	149	60	38	6.51	0.9290	-1.15
907151	2009	pubhunt	4.17	fledged	2	211	54	88	6.51	0.9290	-1.15
1007067	2010	pubhunt	4.67	fledged	3	145	52	32	7.18	0.9759	-1.15
1007090	2010	pubhunt	4.83	fledged	3	153	56	56	7.18	0.9759	-1.15
1007108	2010	pubhunt	4.33	fledged	2	163	69	98	7.18	0.9759	-1.15
1007112	2010	pubhunt	3.83	fledged	2	168	43	75	7.18	0.9759	-1.15
804012	2008	rushrun	5.17	fledged	2	148	43	22	4.87	0.9349	0.75
804022	2008	rushrun	6.00	failed	2	139	13	16	4.87	0.9349	0.75
901085	2009	rushrun	2.83	fledged	1	164	43	22	7.13	0.9264	0.75
901099	2009	rushrun	3.83	failed	2	170	52	21	7.13	0.9264	0.75
907041	2009	rushrun	2.50	fledged	1	143	30	39	7.13	0.9264	0.75
907074	2009	rushrun	6.33	fledged	3	151	52	14	7.13	0.9264	0.75
914008	2009	rushrun	5.00	fledged	3	228	50	10	7.13	0.9264	0.75
1002153	2010	rushrun	5.67	fledged	3	212	52	7	12.69	0.9187	0.75
1002155	2010	rushrun	3.67	failed	2	219	35	60	12.69	0.9187	0.75
1006005	2010	rushrun	6.83	failed	3	162	37	121	12.69	0.9187	0.75
805027	2008	sgalena	2.71	failed	2	141	48	68	4.61	0.9187	-0.57
805077	2008	sgalena	3.83	fledged	3	229	27	77	4.61	0.9187	-0.57
903034	2009	sgalena	6.67	fledged	3	153	45	37	6.28	0.9336	-0.57
903105	2009	sgalena	5.17	fledged	3	228	60	127	6.28	0.9336	-0.57
901090	2009	tuttle	1.00	fledged	2	168	52	117	5.20	0.9413	1.61
1001059	2010	tuttle	3.50	fledged	1	149	62	48	6.09	0.9582	1.61
1001079	2010	tuttle	6.83	fledged	2	177	49	67	6.09	0.9582	1.61
1001083	2010	tuttle	3.17	fledged	2	182	79	125	6.09	0.9582	1.61
1001106	2010	tuttle	4.17	failed	3	235	59	77	6.09	0.9582	1.61
1008010	2010	tuttle	4.33	failed	2	233	45	72	6.09	0.9582	1.61
1009018	2010	tuttle	4.50	fledged	3	203	42	32	6.09	0.9582	1.61
1011013	2010	tuttle	5.33	fledged	2	240	43	49	6.09	0.9582	1.61