



Use of landscape metrics to predict avian nest survival in a fragmented midwestern forest landscape

Michael R. Cottam^{a,1}, Scott K. Robinson^{a,*}, Edward J. Heske^b, Jeffrey D. Brawn^c, Kevin C. Rowe^{b,2}

^a Florida Museum of Natural History, P.O. Box 117800, University of Florida, Gainesville, FL 32611, USA

^b Illinois Natural History Survey, University of Illinois, Urbana-Champaign, 1816 South Oak Street, MC 652, Champaign, IL 61820, USA

^c Department of Natural Resources and Environmental Sciences, University of Illinois, 606 E. Healey Champaign, IL 61820, USA

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ABSTRACT

Habitat fragmentation fundamentally affects trophic interactions and ecosystem function. Understanding how the landscape matrix modulates such interactions can improve our understanding of fragmentation ecology. Studies of breeding birds provide clear examples of the consequences of habitat fragmentation, but the landscape context of these effects are unclear. We sampled avian nesting success in 12 moderately-large forest patches (>250 ha) embedded in different types of landscapes in southern Illinois, USA. We then evaluated eight models that predicted the probability of nest success and brood parasitism by Brown-headed Cowbirds. These models incorporated landscape composition (% grassland, % agriculture, fragmentation), year and seasonal effects, conspecific density, predator density, and combinations of these variables. Temporal factors (stage of nesting cycle, seasonal effects, annual variation) had the most effect on nesting success; landscape factors had little influence on nesting success. The rate and intensity of brood parasitism were significantly influenced by the amount of grassland for the Wood Thrush, but not for the Acadian Flycatcher. Fine-scale management of the matrix surrounding the patches may dictate the local abundance and movements of nest predators and parasites. Other major nest predators may prefer the forest interior and at least partially compensate for the lower abundance of nest predators that depend upon the matrix. Overall, landscape metrics were weak predictors of avian nesting success in complex landscapes that have diverse predator communities.

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1. Introduction

Habitat fragmentation fundamentally affects ecosystem function and trophic interactions (Fahrig, 2003; Hedlund et al., 2004; Lindenmayer and Fischer, 2006; Noss and Csuti, 1997; Tscharrntke and Brandl, 2004). Numerous studies of forest birds support the widely held notion that fragmentation of breeding habitat significantly decreases annual reproductive success and viability (reviewed in Faaborg et al., 1995; Lloyd et al., 2005; Robinson and Wilcove, 1994). Mechanisms underlying the reduction of breeding success include changes in the local abundances and assemblage of predators (Brawn and Robinson, 1996; Chalfoun et al., 2002; Hoover et al., 1995; Porneluzi et al., 1993; Robinson, 1992), invasive species (reviewed in Cronin and Haynes, 2004; Knick et al., 2003), and brood parasites (reviewed in Chace et al., 2005) associ-

ated with edges and the matrix surrounding the fragments. Many forest species nesting in small habitat patches or close to edges experience increased rates of nest loss and brood parasitism (reviewed in Faaborg et al., 1995; Hoover, 2006; Robinson and Wilcove, 1994; Weldon and Haddad, 2005). Differential nesting success in fragmented landscapes may result in a mosaic of population sources and sinks (sensu Pulliam, 1988; Pulliam and Danielson, 1991; With and King, 2001) at local (e.g. Temple and Cary, 1988; Urban and Shugart, 1986) or regional scales (e.g. Donovan et al., 1995a,b; Hochachka et al., 1999; Lloyd et al., 2005; Robinson et al., 1995; Trine, 1998). These findings have been widely incorporated into conservation and land management plans (Beissinger et al., 2000; Bonney et al., 1999; Carter et al., 2000; Finch and Stangel, 1993; Larson et al., 2004; Marzluff and Sallabanks, 1993; Petit and Petit, 2000; Rich et al., 2004; Thompson, 1996).

The effects of habitat fragmentation on forest birds, however, are not uniform within or among regions and many studies have reported few or no edge effects (reviewed in Batary and Baldi, 2004; Hartley and Hunter, 1998; Lahti, 2001; Laurance, 2000; Paton, 1994). Moreover, recent papers have proposed that landscape composition (percentage cover of forest and non-forest habitats or total core habitat) may be as important as landscape structure (patch size, shape, and isolation) in determining avian

* Corresponding author. Tel.: +1 352 253 1965; fax: +1 352 392 0479.

E-mail addresses: michael.cottam@sdm.unlv.edu (M.R. Cottam), srobinson@flmnh.ufl.edu (S.K. Robinson), eheske@uiuc.edu (E.J. Heske), jbrawn@uiuc.edu (J.D. Brawn), rattus@berkeley.edu (K.C. Rowe).

¹ Present address: School of Dental Medicine, University of Nevada, Las Vegas, 1001 Shadov Lane, Las Vegas, NV 89106, USA.

² Present address: Museum of Vertebrate Zoology, University of California, Berkeley, Valley Life Science Building #4151, Berkeley, CA 94720, USA.

nesting success (Andren, 1994, 1995; Donovan et al., 1997, 1995a; Driscoll et al., 2005; Howell et al., 2000; Kupfer et al., 2006; Robinson et al., 1995; Rodewald, 2003; Rodewald and Yahner, 2001b). Edge effects, for example, are demonstrably highest in landscapes with intermediate forest cover in the agricultural Midwest (Donovan et al., 1997; Thompson et al., 2000), a pattern replicated in the northeastern US (Driscoll and Donovan, 2004). Several other studies also failed to detect negative edge effects in mostly forested landscapes (Bayne and Hobson, 1997; Darveau et al., 1997; Hanski et al., 1996; Hawrot and Niemi, 1996; Keyser et al., 1998; Rudnicki and Hunter, 1993; Small and Hunter, 1988; Yahner and Delong, 1992; Yahner and Wright, 1985). Rates of nest predation have been shown to be high even in the interior of forest patches in mainly agricultural (>60% cover) landscapes (Bayne and Hobson, 1997; Hartley and Hunter, 1998; Heske, 1995; Marini et al., 1995; Robinson and Wilcove, 1994; Trine, 1998). Agricultural edges generally appear to exert stronger negative effects on birds than edges of regenerating forest patches (Darveau et al., 1997; Hanski et al., 1996; Hartley and Hunter, 1998; Hawrot and Niemi, 1996; Morse and Robinson, 1999; Rodewald, 2002).

The landscape matrix may also have a strong mediating influence on the effects of forest fragmentation through the movements of predators in and out of habitats (Freemark et al., 1995; Rodewald, 2002, 2003; Rodewald and Yahner, 2001a; Wiens, 1995; Wiens et al., 1993). Agricultural regions may support greater abundances of some important generalist predators (Andren, 1992, 1995; Angelstam, 1986; Bayne and Hobson, 1997; Dijak, 1996; Haskell, 1995; Moller, 1989; Oehler and Litvaitis, 1996; Pedlar et al., 1997; Warner, 1994; Wegner and Merriam, 1990, 1979) than regions where the matrix consists primarily of grasslands or pasture. Crop fields provide increased cover and food later in the growing season, and predators increase their use of these areas at that time (EJH, unpublished data). In contrast, grasslands retain some cover throughout the year and some resources (small mammals, insects, fruit, and green plant material) are available during the winter and early spring. Thus, predator activity may be more dispersed throughout the landscape (via both lower overall predator density and allowing some individual predators to subsist on resources in locations where forest birds do not nest) during the time of songbird nesting.

Effects of fragmentation on avian productivity may therefore be conditional on landscape composition (Kupfer et al., 2006), but what exactly the effects would be of a given matrix type on avian nesting success are not immediately clear, especially if the matrix contains a mixture of both agricultural and grassland land uses. As agriculture is the principle matrix type for mid-continental North America, an understanding of how an agricultural matrix may modulate avian nesting success in forest fragments could greatly improve our understanding of fragmentation ecology. Most studies, however, have only looked at percentage of forest and non-forest cover and none have distinguished among the effects of different kinds of agriculturally influenced landscape matrices (e.g., row crops vs. rural grassland).

We explored the extent to which landscape composition mediates the effects of forest fragmentation on songbird nesting success and, secondarily, abundances of their nest predators and parasites. We worked in southern Illinois, a region where traditional fragmentation variables (tract size, distance to edge) appear to explain little variation in songbird nesting success (Chapa-Vargas and Robinson, 2006, 2007; Marini et al., 1995; Morse and Robinson, 1999; Peak et al., 2004; Robinson and Wilcove, 1994; Trine et al., 1998). We asked three different questions: (1) What are the effects of the composition of the landscape matrix (% of different kinds of non-forest cover) on nest success when controlling for fragmentation? (2) What are the effects of forest fragmentation on nesting success when the composition of the matrix is held constant? (3) How does

landscape composition affect the abundance of important nest predators and brood parasites that determine nesting success? We predicted higher depredation rates of avian nests in landscapes with high cover of row crops (Andren, 1995), and higher levels of brood parasitism in landscapes with higher cover of grasses where cowbirds feed.

2. Materials and methods

2.1. Study sites

We sampled in the southern 11 counties of Illinois, an area that contains the 108,000-ha Shawnee National Forest (SNF) (Fig. 1). The SNF consists of hundreds of forest tracts of various sizes dominated by oak-hickory forests on steep hillsides and narrow ridge tops. The western half of the SNF includes the easternmost extension of the Ozark Mountains and the eastern section of the SNF lies mostly in the Shawnee Hills region. We restricted our studies to areas of upland oak-hickory and avoided pine plantations and floodplain forest, which tend to have different communities of birds and potential nest predators (SKR, unpublished data).

We used a stratified random process for site selection. We used the program FRAGSTATS (McGarigal and Marks, 1995) in conjunction with digital land cover maps for Illinois derived from Landsat imagery (Luman et al., 1996) to characterize land cover (% forest, % row crop, % rural grassland) within a 3-km radius of each forested pixel in southern Illinois. Each pixel represented a 28 m × 28 m square of actual land area. We then identified candidate forest tracts for study sites, starting with the criteria that each site had to comprise >250 ha of contiguous forest and include at least one major ravine to serve as the focus for nest searching. We chose 250 ha as a criterion to control for effects of tract size on patch occupancy by focal study species (all species nesting in this region occur in tracts of greater than 200 ha (Robinson et al., 1997)) and we wanted to have a wide range of distances from edges to look for deep (>500 m) edge effects, which have been documented for both cowbird parasitism and nest predation in the Shawnee National Forest (Hoover, 2006; Morse and Robinson, 1999). On a purely practical level, smaller tracts simply did not have enough nests to give us statistical power to conduct analyses (Martin and Geupel, 1993).

We categorized each site in terms of the amount of forested land within 3 km of the central pixel, and the amount of non-forested land comprised of row-crop agriculture or grassland (primarily pasture, but including other native and non-native grasslands). We further classified sites as high (<50% overall forest cover within the 3-km radius area, and <10% of the forest >50 m from a forest edge) and low (>50% overall forest cover and >40% of the forest >50 m from a forest edge) forest fragmentation, and whether the non-forested matrix was primarily row-crop agriculture or grassland (Table 1). This combination of percent landscape cover and percent forest interior provided the best index of forest fragmentation that we found. We then randomly selected between two and four sites that were separated from other sites in the same category (Table 1) by at least 20 km, and from all other sites by at least 10 km, while distributing replicates as evenly as possible across the SNF (Fig. 1). When more than one candidate site was considered in a region (e.g., the western SNF), we used a coin toss to select among sites. An unanticipated problem was that extensive row-crop agriculture occurred primarily in the Mississippi River floodplain, Cache River floodplain, and till plains northeast of the SNF. When stratifying our sites in the low forest fragmentation, high row-crop matrix category, we had only one choice of site in the northeastern SNF (Cave Hills), which had approximately equal proportions of row crop and grassland (Table 2).

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