Nest Predation and Population Declines in Illinois Songbirds: a Case for Mesopredator Effects

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Abstract: *Mesopredator release has typically been examined at small spatial scales; however, processes such as habitat fragmentation, suppression of top predators, and changes in land use that lead to higher meso-predator densities typically occur at large spatial scales. In Illinois, raccoon (Procyon lotor) numbers have increased since the early 1980s, with unknown consequences for breeding songbirds. I examined population trends between 1979 and 2001 for songbirds inhabiting woodland and scrub-successional habitats within Illinois by using data from the North American Breeding Bird Survey (BBS). I assigned species a priori into two groups: (1) raccoon-vulnerable species that nest low and thus are highly vulnerable to nest predation by raccoons and (2) raccoon-invulnerable species that nest high and largely escape nest predation by raccoons. The mean number of raccoon-vulnerable species per Illinois BBS route declined by approximately 10%, whereas the number of raccoon-invulnerable species increased approximately 15% through the early 1990s. Population trends of the two groups also diverged. Raccoon-vulnerable species had predominantly negative population trends from 1980 to 2001, whereas raccoon-invulnerable species show roughly equal numbers of positive and negative trends. In contrast, population trends prior to 1980 did not show this divergence. A survey of studies from Illinois that report nesting success connects these divergent patterns between the two groups to substantially higher nest-predation rates for raccoon-vulnerable species. Taken together, results of these studies and mine suggest that large-scale changes in the abundance of raccoons have had demonstrable consequences for songbird populations and communities in Illinois.*

Depredación de Nidos y Declinación Poblacional de Aves Canoras en Illinois: Validación del Efecto de los Meso-depredadores

Resumen: *La liberación de meso-depredadores se ha examinado por lo general a escalas espaciales pequeñas; sin embargo, los procesos tales como la fragmentación del hábitat, la supresión de depredadores superiores y los cambios en el uso de la tierra que conducen a densidades altas de meso-depredadores, por lo general ocurren a escalas espaciales grandes. En Illinois, el número de mapaches (Procyon lotor) ha aumentado desde la década de los 80 con consecuencias desconocidas para la reproducción de aves canoras. Se examinaron las tendencias poblacionales entre 1979 y 2001 de aves canoras en hábitats de bosque y matorral secundarios en Illinois usando datos del Relevamiento Norteamericano de Aves Reproductivas (North American Breeding Bird Survey, BBS). Se asignaron a-priori especies a dos grupos: (1) especies vulnerables a mapaches que anidan a poca altura y por lo tanto son depredados por estos y (2) especies invulnerables a mapaches que anidan a mayor altura y por lo general no son depredados por estos. El número promedio de especies vulnerables a mapaches en las rutas del BBS de Illinois bajó en aproximadamente un 10%, mientras que el número de especies invulnerables a mapaches aumentó aproximadamente un 15% al inicio de los años 90. Las tendencias poblacionales de los dos grupos también divergieron. Las especies vulnerables a mapaches tuvieron tendencias predominantemente negativas entre 1980 y 2001, mientras que las especies invulnerables tuvieron tendencias positivas y negativas con casi la misma frecuencia. En contraste, las tendencias de la población previas a 1980 no mostraron esta divergencia. Una revisión bibliográfica de estudios realizados en Illinois indicó que estos patrones de divergencia se vincularían a tasas de depredación de nidos signif-*

icativamente mayores en especies vulnerables a mapaches. Al integrar esta información con los resultados de este estudio, surge que los cambios a gran escala en la abundancia de mapaches afectarían las poblaciones y comunidades de aves canoras en Illinois.

Introduction

Songbird predators may affect the population dynamics and community composition of songbirds through predation on adults directly or on their eggs and nestlings (Newton 1993; Jędrejewska & Jędrejewski 1998). Typically, the largest effects are seen in island populations of birds previously unexposed to predators (Savidge 1987; Monteiro et al. 1996; Fritts & Rodda 1998). However, populations may also be exposed to unnaturally high densities of native predators. Examples of the latter include instances of mesopredator release (Soulé et al. 1988; Rogers & Caro 1998; Crooks & Soulé 1999) and apparent competition (or hyperpredation; sensu Courchamp et al. 1999, 2000). Mesopredator release involves the "release" or increased density of a consumer species, usually following a decline in predation by species at higher trophic levels. The increased abundance of mesopredators is experienced by species in the next lower trophic level in the form of higher predation rates, which in turn can cause prey populations to decline and can potentially alter community structure (Terborgh et al. 1999).

One of the better-documented cases of mesopredator effects on songbird populations involves the absence of coyotes (*Canis latrans*) from small, fragmented scrub ravines in coastal southern California (Crooks & Soulé 1999). Cats (*Felis sylvestris*), raccoons (*Procyon lotor*), and other medium-sized predators subsequently occur at higher densities in the absence of coyotes, and the result has been declining songbird abundance and diversity. Mesopredator release from predation by coyotes was also implicated in studies by Rogers and Caro (1998) and Soulé et al. (1988). Each of these studies was conducted at a small spatial scale. However, the eradication of top carnivores and other anthropogenic influences promoting an increase in mesopredators has often occurred on a regional to continental scale but the consequences rarely have been investigated (Terborgh et al. 1999, 2001; Micheli et al. 2001).

Fragmentation (including accompanying edge effects), the regional extinction or suppression of top predators, and the conversion of natural habitats to agricultural land—resulting in large quantities of unharvested grain—are all known to increase densities of mesopredators (Soulé et al. 1988; Palomares et al. 1995; Pedlar et al. 1997; Crooks & Soulé 1999; Heske et al. 1999; Dijak & Thompson 2000). In Illinois these processes have been rampant. Of 6 million ha of forest present in Illi-

nois during presettlement times, only 1.7 million ha remain (Iverson & Schwartz 1994). Most remaining forest occurs in small woodlots. For instance, Heske et al. (1999) determined that >23,000 (approximately 95%) woodlots in 12 counties in east-central Illinois were ≤10 ha in size. In contrast, only 8 woods (approximately 0.03%) were >2000 ha in size. The prairie and forest habitats that once dominated this area have been converted to row-crop agriculture that currently covers approximately 50% of the land. This habitat conversion and the loss of top carnivores have allowed mesopredators, including raccoons, to flourish (Engels & Sexton 1994; Pedlar et al. 1997; Heske et al. 1999), in turn creating a hostile landscape for songbirds (Askins 1995, 2000).

Results of studies of local breeding productivity in central, southern, and northeastern Illinois suggest that the entire state may be a population sink for numerous species of songbirds, particularly open-cup, low-nesting Neotropical migrants (Robinson et al. 1995; Brawn & Robinson 1996). In an investigation conducted in northeastern Illinois, Schmidt and Whelan (1999*a*) found extremely high rates of nest predation on artificial ground nests designed to exclude all but medium-sized nest predators (e.g., raccoons and opossums [*Didelphis virginiana*]). Based on these high predation rates, they conjectured that the decline in ground-nesting species of songbirds widely observed in forests in northeastern Illinois (De Vore 1996; S. Hickman, personal communication) may be linked to nest predation by raccoons. Although they found disproportionate numbers of extinctions of ground- and low-nesting species, an increase in raccoon populations is a statewide phenomenon (Gehrt et al. 2002). If increasing raccoon populations have contributed to declines in Illinois' songbird populations, the evidence may be found in the Breeding Bird Survey (BBS). Thus, I used BBS data to conduct an examination of the effects of raccoons on songbird populations at the state level.

Beginning in 1981, raccoons have been surveyed in Illinois through annual spring spotlight surveys conducted in over 40 counties (Gehrt et al. 2002). These censuses have documented an approximately threefold increase in the number of raccoon sightings since the survey began (Gehrt et al. 2002), with the greatest increase occurring from 1987 to 1996, which was sustained at high numbers thereafter. Although the effectiveness of spotlight surveys in measuring population trends remains unquantified, two additional trends support the spotlight results: (1) increased raccoon sight-

ings parallel the decline in the estimated annual raccoon harvest in Illinois, from a high of >380,000 animals in 1979 to a low in 1990 of about 71,000 animals, and (2) the spotlight index is highly correlated with indices based on road-kill surveys (Gehrt et al. 2002).

Several recent studies, including a review by Söderström et al. (1998), have reported differences in the identity of nest predators on ground- and shrub-nesting songbirds (e.g., Nour et al. 1993; Hannon & Cotterill 1998; Schmidt 1999; Boulet et al. 2000). Schmidt and Whelan (1999*b*) tested for an effect of nest height on nest predation in a population of American Robins nesting in deciduous woodland in northeastern Illinois over a range of nest heights from approximately 0.5 m to 12 m. (Scientific names of birds are provided in Appendix 1.) Both the daily nest mortality rate and the proportion of depredated nests ascribed to mesopredators (raccoons and possibly opossums) were inversely related to nest height ($r^2 = 0.496$, $p = 0.001$, and $r^2 = 0.291$, $p = 0.02$, respectively). Two other results from this study warrant additional comment. First, nests built at heights of ≤ 2.5 m had an average daily mortality rate of $\geq 5\%$, which corresponds to a >75% nest failure rate (Fig. 2b in Schmidt & Whelan 1999*b*). Second, because nest predation increased exponentially with a decline in nest height, as nests were built ever closer to ground level (<2.5 m) predation rates rapidly increased beyond 75%. Although one should be cautious in generalizing these results from robins (for a similar study with Field Sparrows and Indigo Buntings, see Burhans et al. 2002), the conclusions were further supported by predation rates on artificial nests designed to exclude all but medium-sized predators. Ground nests were depredated approximately four times more frequently by raccoons than were shrub nests (Schmidt & Whelan 1999*a*). Taken together, the results from Schmidt and Whelan (1999*a*, 1999*b*) and from other nest-predation studies in which comparisons were made across predator types (see citations above) suggest that raccoons and other ground-for-aging mammals are typically the dominant predators on low nests.

The studies summarized above indicate (1) increasing populations of raccoons; (2) very high rates of nest predation by raccoons on low-nesting species; and (3) lower nest-predation rates, likely by avian predators such as Blue Jays, on high-nesting species. Based on these conclusions, I hypothesized that increasing populations of raccoons are most likely to negatively affect ground- and low-nesting songbird populations. In contrast, high-nesting species would be relatively invulnerable to nest predation by raccoons, and, given much lower overall predation rates, should not be susceptible to population declines due to increasing numbers of raccoons. To test these hypotheses, I used records of the BBS to examine population trends in Illinois songbirds between 1979 and 2001. I categorized songbird species based on their vulnerability to nest predation from raccoons and tested the prediction that declines in vulnerable, low-nesting songbird species in Illinois have paralleled increases in raccoon populations.

Methods

Breeding Bird Survey

The Breeding Bird Survey (Robbins et al. 1986) is a roadside survey that uses permanent sampling routes randomly located in physiographic strata within the United States and Canada. Each route is 39.4 km long and is surveyed in late May or early June. An observer makes 3-minute stops at 0.8-km intervals, for a total of 50 stops along the route, and records all birds seen or heard within 0.4 km. The total count of each species at the 50 stops is used as an index of species abundance for that combination of route and year. The raw data are available on the BBS website (Sauer et al. 1999).

Eighty-one routes have been regularly surveyed in Illinois, although approximately 25% of these were added in 1990. To ensure as high a quality of route selection as possible, I limited my analyses to 41 routes that were surveyed continuously from 1979 to 2001 or that had no more than 1 year of data missing over this period. I chose a subset of 44 species (Appendix 1) nesting in woodland or scrub-successional habitats, excluding cavity or ledge nesters (e.g., Eastern Phoebe). I eliminated species that often nest in association with wetlands (e.g., Red-winged Blackbird, Swamp Sparrow) and those that primarily inhabit prairie or grassland habitats (e.g., Bobolink, Savannah Sparrow). The American Goldfinch and Common Grackle were not included because these species nest outside the typical breeding season of most other species (i.e., grackles in March and goldfinches in August–September) and because grackles are known to sometimes nest in loose colonies.

I expected low-nesting species, but not high-nesting species, to be strongly affected by increases in raccoon abundance. Therefore, I used nest height as the sole trait by which to divide the 44 species into two groups that I a priori expected to show divergent population trends with respect to raccoon abundance. I grouped the species as raccoon-vulnerable (Appendix 1) if they were low-nesting and raccoon-invulnerable if they were high-nesting. Low-nesting species typically nest <2.5 m above the ground. To aid in classifying species by nest height, I used Peterjohn and Sauer (1993) as my single, consistent source.

Population Trends

I used two different data sets to examine patterns in population trends. First, I used the BBS's long-term trend

estimates (not available for the Veery, Hooded Warbler, Ovenbird, and Least Flycatcher) for the periods 1980–2001 and 1966–1979. I examined the earlier trends to determine whether later trends were simply a continuation of a pattern established prior to 1980 when raccoon harvest was at its peak. These data were obtained from the BBS website (Sauer et al. 1999) and subjected to a different selection criterion than I used above (Geissler & Sauer 1990). For instance, trend estimates were not inclusive of the 41 routes that met my selection criteria. In addition, the BBS analysis uses the route-regression method that also includes an observer effect to prevent biases due to improving observer quality over time. Similarly, I tested for differences in the distribution of population trends between species that are hosts to the brood parasitic Brown-headed Cowbird and between species' migratory strategies (Neotropical migrant vs. short-distance migrant or permanent resident). I used Ehrlich et al. (1988) to determine which species served as cowbird hosts, and Peterjohn and Sauer's (1993) grouping of birds by migratory strategy.

Second, I used linear-regression analysis to calculate population trends between 1979 and 2001 for my set of 41 selected routes. I used Kolmogorov-Smirnov and Fisher's exact test to compare the frequency of negative trends between low- and high-nesting species for all trend estimates or, in a separate analysis, only for significant ($p < 0.10$) trend estimates. I used one-tailed statistical tests for all analyses comparing low- versus high-nesting groups of birds.

The above analyses may be biased toward positive results by the categorization based on nest height or the inclusion of species whose population trends may be unrelated to nest mortality. The two species of cuckoo are known to follow episodic eruptions of their prey and are therefore potentially regulated by regional prey abundance. Similarly, populations of the Whip-poor-will and the Loggerhead Shrike may fluctuate dramatically in response to forest regeneration and habitat loss, respectively. Finally, the Yellow Warbler and Willow Flycatcher, more so than other species, do not fall cleanly into either vulnerability category. These criticisms do not explain the shift in cuckoo population trends before and after the 1980s, and it is entirely possible that high rates of nest predation have hastened their decline. Moreover, several ground-nesting species were too uncommon to allow calculation of population trends (Veery, Hooded Warbler, Ovenbird), yet given their nest placement they are among the mostly likely to suffer from high rates of raccoon predation. These species have some of the highest reported nest mortality rates from studies conducted in Illinois. Thus, whether the analyses are biased and in which direction is difficult to ascertain. Nonetheless, I deleted the six species singled out above and repeated the analyses. For these tests I used the less conservative $p \leq 0.10$ as the estimate of statistical significance.

Species Richness

I summed the total number of species recorded over the 41 routes separately within the two vulnerability categories and tested for a trend in species richness between 1979 and 2001 via regression analysis. I included a quadratic term in the regression model but subsequently dropped the term from the analysis if it was not significant and reran the reduced linear model. For this analysis, I included additional woodland species that occurred too infrequently to allow estimation of population trends (e.g., Veery, Least Flycatcher).

Daily Survival Rates in Illinois

I searched the literature for published data sets reporting daily nest survival rates (DSRs) for woodland and scrub-successional breeding songbird species in Illinois. I used data sets from the following studies: Robinson (1992); Brawn and Robinson (1996); Robinson et al. (1997); Suarez et al. (1997; Indigo Bunting); Trine (1998; Wood Thrush); and C. J. Whelan and K.A.S. (unpublished data; Wood Thrush, Northern Cardinal, Blue Jay, American Robin). I augmented the data set with two unpublished reports on songbird nest survival (S. K. Robinson, unpublished reports). Daily survival rates were used for a wider range of species than were available for population trend estimates, including the Veery, ground-nesting warblers (e.g., Ovenbird, Worm-eating Warbler), and canopy-nesting species (e.g., Cerulean Warbler).

I tallied the number of studies reporting DSRs and placed DSRs into the following classes: <0.940; 0.941–0.955; 0.956–0.965; and >0.965. The cut-offs for these classes were chosen to correspond to >80%, 70–80%, 60–70%, and <60% of nests depredated, assuming a 26-day nesting cycle. In one report, survival rates were reported as a percentage without nest-exposure days provided; therefore, I placed the studies into the above categories based on the percentage values. I used, when possible, DSRs pooled over time but treated separate sites as independent samples. I used DSRs regardless of the number of nests (often not reported) or nest-exposure days (Mayfield 1975) from which they were calculated. Because many DSRs were based on a small number of nest-exposure days (<100), this greatly increased the number of data points and species used for the analysis. Daily survival rates calculated from <20 nests may have larger errors associated with them, but there should be no systematic bias in the distribution of these errors with regard to categorization of species, and it is not likely that total errors were biased from mean DSRs. Nonetheless, I did not use the individual DSRs to calculate means. Rather I used chi-square analysis to examine differences in the frequency distribution of DSRs between low- and high-nesting species.
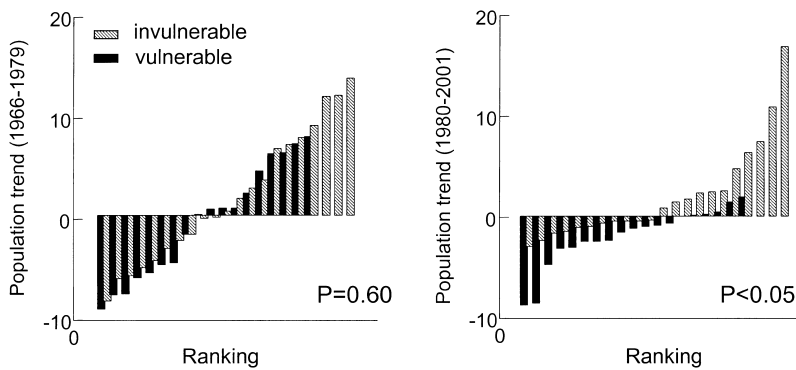
Figure 1. Breeding Bird Survey population trends (ranked from most negative to most positive) for raccoon-vulnerable (low-nesting) and invulnerable (high-nesting) species during the periods 1966–1979 and 1980–2001.

Results

Population Trends

Population trend estimates from 1980 to 2001 of the Breeding Bird Survey showed that 13 of 18 raccoon-vulnerable species had negative population trends (trend for the Northern Mockingbird = 0.00), whereas only 11 of 22 invulnerable species had negative population trends ($p = 0.033$; one-tailed Kolmogorov-Smirnov test; Fig. 1). In contrast, there was no significant difference ($p > 0.50$) in the distribution of population trends between these two groups prior to 1980 (Fig. 1).

Likewise, population trend estimates from the 41 selected routes showed that 15 of 19 raccoon-vulnerable species had negative population trends, whereas only 11 of 22 invulnerable species did ($p = 0.052$, one-tailed Fisher's exact test). Repeating the analysis with only significant trend regressions (using $p < 0.10$) also resulted in a significant difference (11 of 13 vs. 7 of 17; $p = 0.026$, one-tailed Fishers exact test).

In contrast, there was no evidence of differences in the distribution of BBS population trends between cowbird hosts and nonhosts (Kolmogorov-Smirnov test, $p > 0.90$) or between Neotropical migrants and short-distance migrants or permanent residents (Kolmogorov-Smirnov test, $p > 0.80$).

The Kolmogorov-Smirnov test for differences in the distribution of BBS population trends from 1980 to 2001 between the two vulnerability categories remained significant ($p = 0.026$) after the removal of the six disputed species. Likewise, the number of significant population trends based on linear-regression results of the 41 selected routes indicated a significant difference in the frequency of negative trends (vulnerable = 7 of 9; invulnerable = 6 of 15; $p = 0.053$, one-tailed Fisher's exact test).

Species Richness and Daily Survival Rates

The species richness of the raccoon-vulnerable group declined significantly ($r^2 = 0.629$, $p = <0.001$; Fig. 2) by approximately one species per BBS route from 1979 to 2001. In contrast, the species richness of the raccoon-invulnerable group exhibited a quadratic relationship ($r^2 = 0.703$; both the linear and quadratic terms, $p = 0.001$; Fig. 2), peaking in the mid-1990s and changing little afterward.

From the literature review, I found 217 daily survival rates for the two groups of species (raccoon-vulnerable, 119; raccoon-invulnerable, 98). The analysis of DSRs from Illinois songbirds indicated that nest mortality was significantly greater for raccoon-vulnerable than rac-
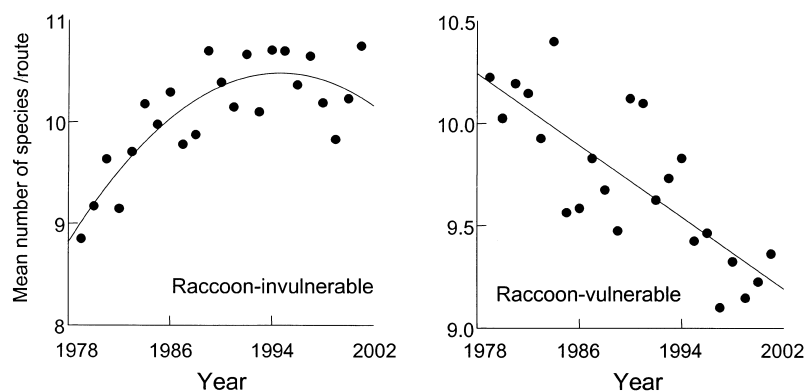

Figure 2. Trends in the mean number of raccoon-vulnerable (low-nesting) and invulnerable (high-nesting) species recorded from the 41 selected Illinois Breeding Bird Survey routes from 1979 to 2001.

coon-invulnerable species ($\chi^2 = 19.18$, df = 3, $p < 0.001$; Fig. 3). Approximately 50% of nest DSRs reported for vulnerable species were below 0.940 (i.e., >80% nest mortality over a 26-day nest cycle), and only 24% exceeded 0.965 (i.e., <60% nest mortality) (Fig. 3). These patterns were essentially reversed for raccoon-invulnerable species (Fig. 3).

Discussion

There have been dramatic changes over the last 20 years in the songbird assemblages inhabiting woodland and scrub-successional habitats in Illinois. Population trends of most low-nesting species are negative, and their species richness on BBS routes has declined in the last two decades. In contrast, there are nearly equal numbers of negative and positive trends among high-nesting species, and this group shows a strong rise in the number of species per route throughout most of the time period. Regardless of the causes of these patterns, such a strong, demonstrated decline of this large and important group of songbirds is alarming and suggests that conditions in Illinois have become less suitable for low-nesting songbirds in recent years.

I believe these patterns in part reflect underlying changes in the abundance of raccoons in Illinois over the last 20 years. This is supported by three lines of evidence. First, I placed species into a priori groups that re-
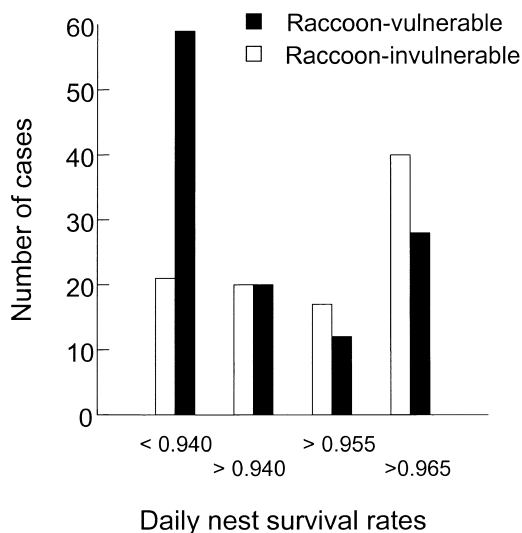

Figure 3. Number of reported daily survivorship cases (based on a literature review of Illinois studies) broken down into four classifications. Species for which the daily survivorship rates were reported are divided into raccoon-vulnerable (low-nesting) and invulnerable (high-nesting) categories.

flect their susceptibility to different predator guilds (Nour et al. 1993; Söderström et al. 1998; Schmidt & Whelan 1999b). In all the analyses I conducted there were consistent divergences between low-nesting, raccoon-vulnerable species and high-nesting, raccoon-invulnerable species. The distribution of population trends between 1980 and 2001 was heavily skewed in favor of negative trends for vulnerable species, whereas invulnerable species were less heavily skewed in the opposite direction (Fig. 1). The mean number of vulnerable species inhabiting woodland and scrub-successional habitats (excluding cavity nesters) declined approximately 10% throughout the time period, whereas the mean number of invulnerable species increased by approximately 15% before reaching a plateau in the 1990s (Fig. 2).

Second, my survey of studies reporting breeding success in Illinois connects these divergent patterns in songbird population trends and species richness to patterns of nest predation. Low-nesting species had dramatically higher nest-predation rates than did high-nesting species. In fact, approximately 75% of the nest survival rates were below levels likely to be sustainable based on the analyses of Schmidt and Whelan (1999b). Third, my analysis of BBS population trends between 1966 and 1979 demonstrated that these trends were not a simple continuation of earlier declines among low-nesting species. Instead, the number of negative population trends among the vulnerable species increased after the 1980s. Although some of the population trends may reflect the existence of additional environmental factors, when I eliminated several species for which nest mortality may be only marginally to blame, the patterns still persisted. The addition of other ecological processes that may be negatively affecting low-nesting species—habitat fragmentation, non-native plant invasions, community succession—only exacerbates their plight.

One drawback of my study is the inability to separate potential effects of time from raccoon abundance. A stronger test for examining the effect of raccoons on songbird abundance would attempt to factor out any possible long-term trend and examine the effects of raccoons on the residual variation. However, strong colinearity between the independent variables, year and raccoon abundance (Gehrt et al. 2002), precludes such analysis. Furthermore, raccoons may be contributing to songbird population trends in multiple ways. Sustained high raccoon density may influence long-term trends, and annual variation in raccoon densities may contribute to annual variation in breeding bird densities. Thus, although raccoon populations apparently leveled off in the mid-1990s (Gehrt et al. 2002), continuing high nest mortality may perpetuate songbird declines.

There are a number of Illinois birds for which I was unable to estimate population trends, including the Hooded Warbler, Veery, and Ovenbird (1966–1979). These species are likely restricted to larger forest tracts

(e.g., Herkert 1995a), which may be poorly surveyed by a roadside survey such as the BBS. It is possible that these ground-nesting species are not declining because mesopredator abundance is typically lower in larger forest blocks. In northeastern Illinois, however, populations of Ovenbirds have been declining (De Vore 1996; Schmidt & Whelan 1999a; S. Hickman, personal communication). Furthermore, the DSRs of these species are the lowest among all the songbirds in this study. For example, all seven DSRs reported for Veeries were <0.94 (i.e., >80% predation), and four of five DSRs for Ovenbirds were below 0.90. Similarly, low DSRs were seen among Hooded, Worm-eating, and Kentucky warblers. These results suggest that species nesting on or slightly above the ground are the most seriously threatened songbirds and that more information on the population trends of these species in Illinois would likely bolster the conclusion that raccoons are negatively affecting Illinois' songbird populations. Because these species are both less common and highly vulnerable to nest predation, more population studies are urgently needed.

Population dynamics are influenced by multiple factors, and I acknowledge that high mesopredator density is only one of several possible factors contributing to the patterns demonstrated here. Additional biotic or abiotic changes in the last 20 years may have affected these groups of songbirds differently. First, increased habitat fragmentation and the avoidance of small habitat fragments by area-sensitive species (Herkert 1995a; Robinson et al. 1997; Rosenberg et al. 1999) may contribute to population declines. Interestingly, among Illinois' area-sensitive species as listed in the study by Robinson et al. (1997), there is no consistency between increases or decreases of an individual species' numbers with area and the direction of the species' population trend over the last 20 years. In fact, positive population trends were noted for those species that require larger forests, whereas negative trends were seen for those species found in small fragments (K.A.S., unpublished data). Similarly, Rosenberg et al. (1999) found that tanager abundance decreased in smaller forests, yet both Summer and Scarlet tanagers have positive population trends in Illinois between 1980 and 2001. Second, brood parasitism by the Brown-headed Cowbird is severe across Illinois and certainly affects songbird reproductive success (Robinson 1992; Brawn & Robinson 1996; Trine 1998). There is no consistency, however, between susceptibility to brood parasitism and population decline among the species I examined. Finally, there was no evidence for an effect of migratory strategy. Thus, I found no evidence for several commonly proposed alternative hypotheses for songbird declines (e.g., Brittingham & Temple 1983; Böhning-Gaese et al. 1993).

Other factors that can potentially affect the abundance of Illinois' songbirds may reinforce the patterns seen here. For instance, the invasion of exotic plants, such as garlic mustard (*Alliaria petiolata*), and shrubs, such as Amur honeysuckle (*Lonicera maackii*), may dramatically alter forest structure and composition (Nuzzo 1991; Meekins & McCarthy 1999) and lead to increased predation by raccoons on nests built in these species (Schmidt & Whelan 1999c). Forest fragments also show reduced food supply (Burke & Nol 1998), which may in turn lead to higher nest-predation rates if predators turn more frequently to nests as alternative prey or if nests are left undefended as adult birds forage more widely for food (Schmidt 1999). Other alternatives may be complementary. Global climate change or weather patterns (Sillett et al. 2000) may alter summer food abundance, over-winter survivorship, or species' ranges (Parmesan 1996). If complementary or compensatory sources of songbird mortality or decline are strong enough, the control of nest-predator densities—those involving raccoons in particular—may be limited in its effectiveness to restore songbird diversity in Illinois.

Lastly, the patterns I report here for Illinois may be representative of patterns noted previously for the eastern United States as a whole (Böhning-Gaese et al. 1993; Peterjohn et al. 1995; Askins 2000). Herkert (1995b), on the other hand, found no evidence for population declines among midwestern (U.S.) bird populations in relation to nest location. His study differed considerably from my analysis, however, in that he pooled species across eight states, multiple habitats, and taxa (i.e., nonpasserines).

Mesopredators have been implicated in several studies conducted at smaller spatial scales, including those by Rogers and Caro (1998), Soulé et al. (1988), Crooks and Soulé (1999), and Terborgh et al. (2001). My analysis of the relationship between Illinois songbird communities and raccoon abundance suggests that increased nest predation may scale up to region-wide effects on the population dynamics, abundance, and diversity of songbirds. The spread of raccoon rabies north and westward from its epicenter on the border between West Virginia and Virginia (Jenkins et al. 1998) may have similar—in this case beneficial—large-scale effects on songbirds Documentation of the potential impact of rabies on raccoons and songbirds would complement my analyses and help reveal large-scale patterns and processes influencing songbird population dynamics.

States Geological Survey researchers and managers who helped compile the data.

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Appendix 1.   Species and classification.

Common name	Scientific name	Brown-headed Cowbird host	Neotropical migrant
Low-nesting species			
Black-billed Cuckoo	*Coccyzus erythropthalmus*	+	+
Yellow-billed Cuckoo	*Coccyzus americanus*	+	+
Whip-poor-will	*Caprimulgus vociferous*		+
White-eyed Vireo	*Vireo griseus*	+	+
Bell's Vireo	*Vireo bellii*	+	+
Gray Catbird	*Dumetella carolinensis*		+
Kentucky Warbler	*Oporornis formosus*	+	+
Common Yellowthroat	*Geothlypis trichas*	+	+
Yellow-breasted Chat	*Icteria virens*	+	+
Eastern Towhee	*Pipilo erythrpthalmus*	+	+
Blue Grosbeak	*Guiraca caerulea*	+	+
Indigo Bunting	*Passerina cyanea*	+	+
Brown Thrasher	*Toxostoma rufum*		
Field Sparrow	*Spizella pusilla*	+	
Song Sparrow	*Melospiza melodia*	+	
Willow Flycatcher	*Empidonax trailii*	+	+
Veery*	*Catharus fuscescens*	+	+
Hooded Warbler*	*Wilsonia citrine*	+	+
Ovenbird*	*Seiurus aurocapillus*	+	+
Northern Cardinal	*Cardinalis cardinalis*	+	
High-nesting species			
Mourning Dove	*Zenaida macroura*		
Chipping Sparrow	*Spizella passerina*	+	+
Blue Jay	*Cyanocitta cristata*		
Loggerhead Shrike	*Lanius ludovicianus*		
Northern Mockingbird	*Mimus polyglottos*		
American Robin	*Turdus migratorius*		
Eastern Wood Pewee	*Contopus virens*		+
Eastern Kingbird	*Tyrannus tyrannus*		+
Acadian Flycatcher	*Empidonax virescens*	+	+
Wood Thrush	*Hylocichla mustelina*	+	+
Blue-gray Gnatcatcher	*Polioptila caerulea*	+	+
Yellow-throated Vireo	*Vireo flavifrons*	+	+
Warbling Vireo	*Vireo gilvus*	+	+
Red-eyed Vireo	*Vireo olivaceous*	+	+
American Redstart	*Setophaga ruticilla*	+	+
Yellow-throated Warbler	*Dendroica dominica*		+
Yellow Warbler	*Dendroica petechia*	+	+
Northern Parula	*Parula Americana*		+
Summer Tanager	*Piranga rubra*	+	+
Scarlet Tanager	*Piranga olivacea*	+	+
Baltimore Oriole	*Icterus galbula*		+
Orchard Oriole	*Icterus spurious*	+	+
Rose-breasted Grosbeak	*Pheucticus lidovicianus*	+	+
Least Flycatcher*	*Empidonax minimus*	+	
Other species mentioned in the text			
American Goldfinch	*Carduelis tristis*		
Common Grackle	*Quiscalus quiscula*		
Brown-headed Cowbird	*Molothrus ater*		
Red-winged Blackbird	*Agelaius phoeniceus*		
Bobolink	*Dolichonyx oryzivorus*		
Savannah Sparrow	*Passerculus sandwichensis*		
Eastern Phoebe	*Sayornis pheobe*		

Some trend estimates not available.