Research article

Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: local fragmentation vs. vegetation structure

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Abstract

Measuring edge effects in complex landscapes is often confounded by the presence of different kinds of natural and anthropogenic edges, each of which may act differently on organisms inhabiting habitat patches. In such landscapes, proportions of different habitats surrounding nests within patches often vary and may affect nesting success independently of distance to edges. We developed methods to measure and study the effects of multiple edges and varying habitat composition around nests on the breeding success of the Acadian flycatcher (*Empidonax virescens*), an understory, open-cup nesting songbird. The Kaskaskia River in Southwestern Illinois was our study area and consists of wide (>1000-m) floodplain corridors embedded in an agricultural matrix with a variety of natural (wide rivers, backwater swamps, and oxbow lakes) and anthropogenic (internal openings, and agricultural) habitats. We also measured vegetation structure around each nest. Nest survival increased with increasing nest concealment, and probabilities of brood parasitism increased with increasing distances from anthropogenic and natural water-related openings surrounding nests. The magnitude of these effects was small, probably because the landscape is saturated with nest predators and brood parasites. These results illustrate the importance of considering both larger landscape context and details of natural and anthropogenic disturbances when studying the effects of habitat fragmentation on wildlife.

Introduction

One of the best-documented effects of habitat fragmentation is the reduced nesting success of birds along anthropogenic edges. Many studies have shown increased rates of nest predation and higher levels of brood parasitism closer to edges than in the forest interior (e.g., Brittingham and Temple 1983; Wilcove et al. 1986; Paton 1994; Suarez et al. 1997; Morse and Robinson 1999; Huhta and Jokimäki 2001), although other studies have documented no edge effects (Donovan et al. 1997), or increased brood parasitism with increasing distances from anthropogenic edges (e.g., Hahn and Hatfield 1995; Gustafson et al. 2002). More recently, however, such studies have come under

criticism because of methodological problems which include the lumping of nests into categories and the use of logistic regression (Rotella et al. 2004; Shaffer 2004). A potentially more significant problem, however, arises when analyzing edge effects on nest success in complex landscapes containing several edges of different types (e.g., Morse and Robinson 1999). In these landscapes, the magnitude and direction of the influence of different edge types on nest survival and brood parasitism may differ substantially. Some edges around anthropogenic openings, for example, have been found to negatively affect breeding birds (Wilcove et al. 1986; Paton 1994; Morse and Robinson 1999), whereas edges around natural openings appear to increase nesting success (Suarez et al. 1997; Huhta and Jokimäki 2001). Because nests may receive the simultaneous influence of more than one edge, the distance to only the closest edge may not be the most reliable predictor of nest survival and brood parasitism. Moreover, nesting success may depend more on the landscape composition (percentage of different habitats) surrounding nests within patches than on the distances to edges *per se*. The types of habitats that dominate the area around each nest may either sustain larger populations of nest predators or provide refuges from these predators (Bowman and Harris 1980; Holmes et al. 1996; Chalfoun et al. 2002).

The competing effects of multiple habitat types may underlie some of the inconsistencies among the results of edge effect studies (reviewed in Paton 1994). In floodplains, for example, flood pulses create many natural habitats such as oxbow lakes and other backwaters, some of which may be associated with unusually high probabilities of nest survival (e.g., Suarez et al. 1997; Saracco and Collazo 1999). Such natural habitats may be associated with dense vegetation that increases nest concealment (Bowman and Harris 1980; Martin 1992) and decreases predator search efficiency (Norman and Robertson 1975; Martin 1993; Uyehara 1996; Uyehara and Whitfield 2000). Within these landscapes, natural habitats may also be interspersed with anthropogenic openings such as agricultural fields and roads that may be used heavily by nest predators (e.g., Bider 1968; Angelstam 1986; Durner and Gates 1993; Chalfoun et al. 2002) and brood parasites (O'Conner and Faaborg 1992; Coker and Capen 1995). To date, there have been no studies of the relative importance of

natural and anthropogenic disturbances, and vegetation structure on nest survival of forest birds in floodplain ecosystems (Brawn et al. 2001), probably because of the difficulties posed by the analysis of such complex data sets. We propose that incorporating measures of habitat composition of the landscapes immediately around the patches into studies of the effects of edges on nesting success will improve our ability to detect the relative influence of different openings on songbird nesting success.

We compared the effects of different habitat types and lengths of different edges in circles centered on nest locations, and distance from edge and edge type on nest survival and brood parasitism of the Acadian flycatcher (*Empidonax virescens*), a forest-nesting neotropical migratory songbird. In our analysis we also included measures of vegetation structure in the immediate surroundings of nests (Martin 1992). Finally, because nest success may vary through time due to variations in populations of nest predators (Nolan 1963; Roseberry and Klimstra 1970; Best 1978; Zimmerman 1984; Vickery et al. 1992; Burhans et al. 2002; Peak et al. 2004) and parasites, we looked at temporal effects including nest initiation date, nesting stage, and year of study.

We chose the Kaskaskia River Bottoms (Figure 1) as our study region because private land owners of all the forest adjacent to the river are interested in managing to help preserve the natural resources in the region. In this landscape, within-patch habitat composition was very complex but all other larger-scale fragmentation variables were constant for the landscape as a whole (see Results section). This enabled us to determine if local effects of specific types of habitats and vegetation structure on nesting success add information to the previously documented effects of regional fragmentation in the Midwestern United Estates (Robinson et al., 1995; Donovan et al., 1997; Thompson et al., 2000). We predicted that the analysis incorporating percentages of habitat types would be more sensitive than analyses based on distance to edges and edge type, and lengths of different edge types. Based on the results of recent studies (Chapa and Robinson in press; Suarez et al. 1997; Huhta and Jokimäki 2001), we also predicted that natural habitats would positively influence nest success, and effects of
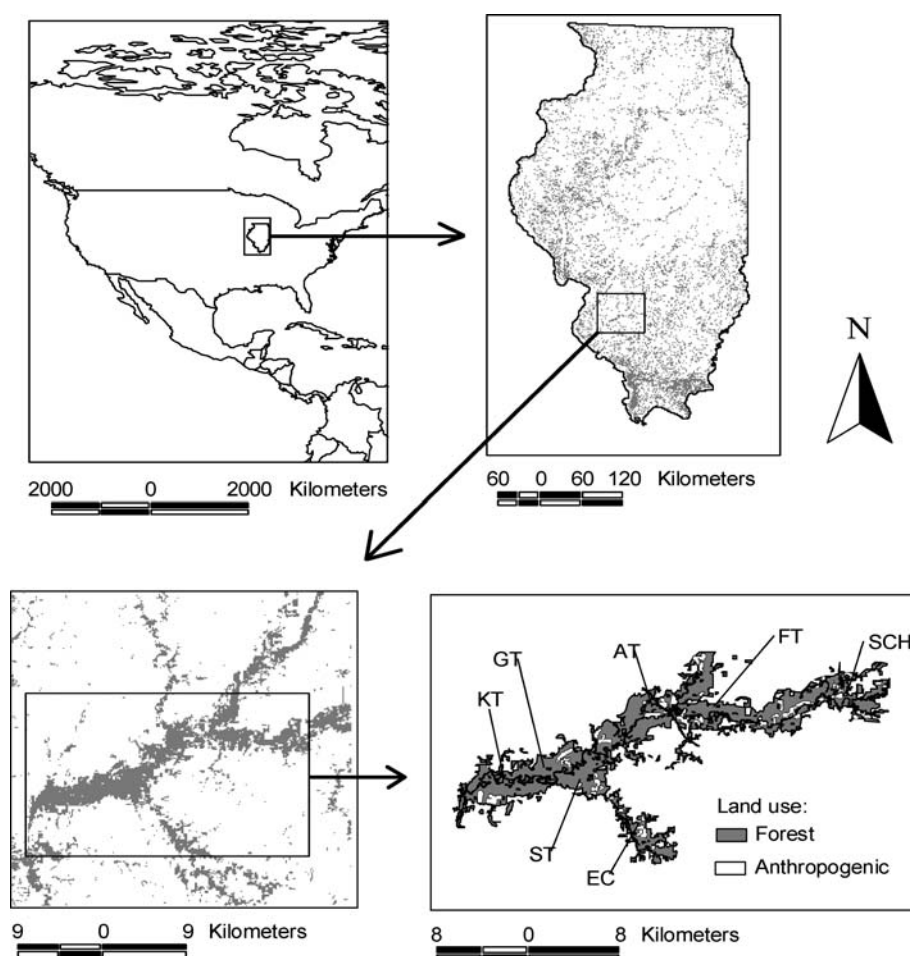
Figure 1. Study area. Site abbreviations: GT, Graul's tract; AT, Atmer's tract; FT, Founee tract; EC, Elkhorn creek; ST, Schuet's tract; SCH, Schneider's tract; KT, Kherer's tract.

anthropogenic environments would be negative. We chose the Acadian flycatcher (*Empidonax virescens*) because it is an abundant widespread species that builds typical open-cup nests and has shown to be sensitive to habitat fragmentation throughout the Midwestern United States (Robinson et al. 1995; Chapa 2001; Whitehead and Taylor 2002). This species is distributed throughout most of eastern North America from central Texas, eastern Oklahoma, Kansas and Nebraska to the east coast. Its range also extends north through the Great Lakes and southern New England and is gradually expanding north (Whitehead and Taylor 2002). Acadian flycatchers breed in wet deciduous forests such as swamps and dense riversides, and in the understory of drier woods (Whitehead and Taylor

2002), but at smaller densities in the latter habitat at least in Illinois (Chapa, personal observation).

Study area

From 1997 to 1999, we measured survival and brood parasitism of 112 Acadian flycatcher nests in the Kaskaskia River Bottoms in southern Illinois, USA (Figure 1). The Kaskaskia River is a tributary of the Mississippi River Drainage and one of the largest privately owned floodplain forests in the Midwest. Our study sites included seven wide (> 1000 m) forest corridors surrounded by an agricultural matrix (Figure 1). These forested areas were interspersed with different habitat types such as a wide river, ponds, oxbow lakes,

backwater swamps, roads, and wildlife openings (internal openings maintained in grasses and perennials to attract game species). This habitat heterogeneity allowed us to test our hypotheses concerning different edges and habitat types and their effects on nest success. A considerable proportion of these woodlots were flooded at various times during the breeding season. However, during the 3 years of our study, summer flooding was prevented by a large upriver dam and impoundment (Lake Carlyle). For the majority of the study sites, the entire area to which we were allowed access by private landowners (0.6–1.5 km^2) was searched for Acadian flycatcher nests. Some sites were too large to be searched throughout (3.0–4.1 km^2). For these sites a large (1.2–2.8 km^2) subsection of the study site was chosen randomly to concentrate searching efforts.

Methods

Reproductive success

We searched for Acadian flycatcher nests by following adult birds. Once a nest was found, a flag was attached to nearby vegetation with directions to the nest location. Using a mirror attached to a pole (Parker 1972), the number of host and cowbird eggs and/or nestlings in each nest was determined. All nests were monitored periodically (typical interval between visits was 3 days) until they became inactive either by depredation or by fledging. During each visit the nest fate and the date were recorded. Whenever a nest had nestlings nearly ready to fledge (13 days-old), and it was empty on the next visit, we used evidence such as presence of fledglings, which usually remain several days in the nest vicinity (Chapa personal observation), adults, and fresh droppings near the nest as indications of fledging events. We also looked for indications of nest predation such as shell fragments, a hole in the nest, or a nest destroyed (e.g., Martin and Geupel 1993; Manolis et al. 2000). Because we did not monitor nests daily when the date of fledging approached (e.g., Peak et al. 2004) we probably overlooked a few predation events, but we assume that these events were not biased by any edge or habitat type. The first day of egg laying was used as the first day of exposure to predation for nests that were found during nest building

(Acadian flycatchers in Illinois lay one egg per day, Chapa personal observation). Because virtually all nest mortality was due to nest predation, we attributed all of our nest survival calculations to survival from predation. Because most nests contained only a single cowbird egg (mean = 1.2 cowbird eggs/parasitized nest; Wilson and Cooper 1998; Chapa 2001), the number of cowbird eggs was not used as an independent variable. Therefore, brood parasitism was estimated as the presence or absence of parasitism.

Vegetation measurements

For each nest the tree species in which it was located was recorded and the height of the nest was estimated. Nest concealment for each nest was obtained by following the protocol used for this species by Wilson and Cooper (1998), which averages six estimates of percent nest concealment from 1 m away: one from each of the four cardinal directions on the horizontal plane, and one from directly above and below the nest. We used nest height and nest concealment because Acadian flycatcher nesting success is known to be influenced by these variables in Arkansas (Wilson and Cooper 1998).

Stem density was used as an approximation of vegetation density. For this purpose we recorded numbers of trees and shrubs within 0.04-ha circular plots (radius = 11 m) centered on each Acadian flycatcher nest (e.g., James and Shugart 1970), and calculated the number of shrubs and trees per hectare. We used number of trees and shrubs per hectare because these variables may affect nest success by altering foliage density around the nest which may, in turn, affect predator search efficiency (e.g., Martin 1992).

Geographic data entry

The outer borders of each study site and habitats within study sites were digitized. Habitats were grouped into three categories including internal water habitats (lakes, backwater swamps, and oxbow lakes), anthropogenic (agricultural fields, roads, and wildlife openings), and the Kaskaskia River. An additional coverage was created by digitizing locations of all nests. Digital Raster

Grids overlaid on Digital Ortho Quads (DOQs) were used to identify landmarks onscreen for the digitizing process. The habitat categories that we used could be easily discriminated on DOQs because they have different grey tones. Similarly, the outer borders of study sites could be easily distinguished as the borders between the forest and the external agricultural matrix.

We kept the Kaskaskia River as a separate habitat category because it formed a large (> 100 m) canopy gap, and lacked dense vegetation near its banks; therefore this edge differed structurally from the rest of the edges in the region. We grouped habitats in three general categories because keeping them separate would result in a large number of missing values due to the absence of some edge types within some study sites, considerably reducing sample sizes and statistical power. On the other hand, using these general habitat categories is unlikely to reduce the ability to detect statistical significance because habitats that were grouped in the same category were structurally similar.

Edge types and distance

We used a Geographic Information System (GIS, Arc View Version 3.3, Environmental Systems Research Institute 2002) to measure the distance of nests from the nearest edge between forest and internal water, anthropogenic, and river habitats. For this purpose we used the Arc View extension 'Nearest features, v3.7a' (Jenness 2004) and previously digitized maps of nest locations and habitat edges (see above).

Habitat cover and edge lengths

We developed a GIS-based technique to measure the combined effects of different edge and habitat types. Using a GIS, we built 500 m radius buffers centered on nest locations. We used these buffers to clip the previously digitized habitat map. Finally, within these clipped habitat maps we measured (1) percentages of different habitat types, and (2) lengths of edges between forest and other habitat types (see Appendix). We used the 500 m radius because previous studies suggest that edge effects may extend this far into the forest interior (Hoover personal communication; Wilcove 1986; Morse

and Robinson 1999). We did not use smaller radii because at smaller distances most nests were surrounded entirely by forest.

Statistical analysis of nest survival

We used PROC GENMOD in SAS (SAS institute, Cary, North Carolina) to fit logistic exposure models (Rotella et al. 2004; Shaffer 2004) to estimate daily nest success, and evaluate the effects of factors related to different habitat types, lengths of different edge types, distances from different edge types, vegetation structure, presence and absence of parasitism, and time-dependent explanatory variables on the survival of Acadian flycatcher nests from predation. We verified the fit of the logistic exposure model with the most parameters (see below) with goodness-of-fit Hosmer and Lemeshow (2000) test.

Statistical analysis of brood parasitism

We used logistic regression to estimate probabilities of brood parasitism and evaluate the effects of factors related to different habitat types, lengths of different edge types, distances from different edge types, vegetation structure, and time-dependent explanatory variables on parasitism of Acadian flycatcher nests. For this analysis, we only used nests that were found early in the nesting cycle and survived long enough to be parasitized. We verified that the assumption of linearity in the logit for continuous independent variables was met by plotting the midpoints of the independent variable quartiles vs. the average logit of the group mean (e.g., Hosmer and Lemeshow 2000). We also verified the fit of the logistic model with the most parameters (see below) with goodness-of-fit Hosmer and Lemeshow (2000) tests, and with plots of ΔX^2_j vs. π_j, ΔD_j vs. π_j, and $\Delta \beta_j$ vs. π_j (Hosmer and Lemeshow 2000).

Model selection

We used a bias-corrected version of Akaike's information criterion (AIC_c) and Akaike weights (w_i) to evaluate the support for competing *a priori* models about the factors influencing Acadian

flycatcher nest survival and brood parasitism (Burnham and Anderson 2002). To calculate AIC_c for nest survival we used the effective sample size, which is the sum of the total number of days that all nests were known to have survived plus the number of intervals that ended in failure (e.g. Rotella et al. 2004). Our set of *a priori* hypotheses were that nest survival from predation and brood parasitism are influenced by (1) habitat composition within patches, (2) amounts of edges within patches, (3) distances from edge types, (4) vegetation structure, (5) variation through time, and two-way combinations of habitat composition within patches, edge lengths, and distances-from-edge with vegetation structure, and time variation. In addition we also hypothesized that nest survival is influenced by the presence of brood parasitism, and its interaction with habitat composition within patches, edge lengths, and distances-from-edges. In all, there were a total of 15 competing hypotheses about nest survival and 11 about brood parasitism (see Appendix for a full description of explanatory variables in each model).

Our criteria to include variables in models of our *a priori* hypotheses included; knowledge of the effects of these factors on nest success and brood parasitism of Acadian flycatchers or forest birds from previous studies, results of exploratory analyses (partial correlations) that suggested that the independent variables might influence either survival or parasitism, and variables related to our hypotheses about the effects of proportions of habitat types and edge lengths within areas surrounding nests. In addition, for both nest survival and brood parasitism we built a global model with all parameters that was used to assess model fit (e.g., Burnham and Anderson 2002), and a null model with only an intercept (estimated iteratively by the method of maximum likelihood in SAS) using data for nest survival or brood parasitism from the entire data set to determine if constant-survival and constant-parasitism models received more support from the data than one including any of the remaining variables. We used Akaike's information criterion (Burnham and Anderson 2002) to rank models from most to least supported given the data on the basis of Akaike differences (ΔAIC = the difference in AIC_c between the model with the smallest AIC_c value and the current model) and Akaike weights (w_i). Each w_i is a measure of

support for each model based on ΔAIC that adds to 1 across all models. These values provide direct interpretation of the relative likelihood of a model given the data and the set of candidate models; a given w_i is considered as the weight of evidence in favor of its corresponding model. Then, to account for model-selection uncertainty, we calculated model-averaged weighted parameter estimates and their associated standard errors using w_i as weights as suggested by Burnham and Anderson (2002) and Shaffer (2004). Finally, we used these weighted parameter estimates and standard errors to calculate odd-ratios (OR) and their associated 95% confidence intervals (CI). Odd-ratios provide a direct interpretation. For example, for categorical variables, OR's of 2 or 0.5 for given categories would indicate that the probability of nest survival or brood parasitism would be twice or one half as likely, respectively, as the reference category. For continuous variables, the proportion of change in the odds of survival or parasitism as a response to each 1-unit change in the continuous independent variable can be calculated by subtracting 1 from the OR (e.g., Hosmer and Lemeshow 2000, Peak et al. 2004). We interpreted only OR's whose CI's did not include 1 unless otherwise noted (e.g. Peak et al 2004). We calculated interval nest success (percent nests surviving the entire nesting period) assuming 3, 13 and 13 days of laying, incubation, and nestling, respectively (Chapa personal observation), and brood parasitism using the most supported model and assuming a balanced population across all other factors.

Results

We collected nest survival information for 112 Acadian flycatcher nests on seven study sites (Figure 1), summing to a total of 1931 exposure days, and 565 intervals between successive visits. Predation was the leading cause of nest failure. We found no evidence of nest loss caused directly by brood parasitism. Parasitized nests, however, fledged fewer host young (mean = 0.70) than unparasitized nests (mean = 2.2). Width of study sites, area, and percentages of forest cover within 10-km radii ranged from 1050 to 4616 m, 454 to 1687 ha, and 7.5 to 22.6, respectively.

Factors influencing nest survival

Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global model adequately fit the observed values ($X^2 = 0.981$, df = 9, $p = 0.99$). We found the most support for two competing models with ΔAIC_c distances < 2; these included our vegetation structure and parasitism effects hypotheses. Additional hypotheses that received some support from the data (ΔAIC_c distances = 2.1–7) included our null, distance from edge and vegetation, habitat composition within patches and vegetation, and edge lengths and vegetation effects hypotheses (Table 1). All confidence intervals on odd ratios estimated from model-averaged parameter coefficients overlapped 1.0 (Table 2). Some of these overlaps, however, were slight and suggested that nest survival increased with increasing nest concealment (Figure 2, Table 2). The effects of all other explanatory variables were negligible (Table 2). Based on our vegetation structure model, assuming 3, 13 and 13 days of laying, incubation, and nestling, respectively, and a balanced population across all other factors, interval nest success (percent nests surviving the entire nest cycle) was 33.5% (0.0–97.4%).

Factors influencing brood parasitism

Plots of the midpoints of quartiles for continuous variables vs. the average logit of the group mean indicated that the assumption of linearity of these variables in the logit was met. Plots of ΔX^2_j vs. π_j, ΔD_j vs. π_j, and $\Delta \beta_j$ vs. π_j, and Hosmer and Lemeshow's (2000) goodness-of-fit test indicated that the global model fit the observed values ($X^2 = 5.54$, df = 8, $p = 0.59$). We found the most support from the data for two competing models with ΔAIC_c distances < 2 corresponding to our distance from edge, and distance and temporal effects hypotheses. Distance and vegetation effects, and the global model also received some support from the data (ΔAIC_c distances = 2.1–7, Table 3). All confidence intervals on odd ratios estimated from model-averaged parameter coefficients included or overlapped 1.0 (Table 4). Some of these overlaps, however, were only slight and suggested that probabilities of brood parasitism increased, but only slightly, with increasing distances from water and anthropogenic edges. Confidence intervals for these effects, however, were large (Figures 3 and 4, Table 4). Based on our distance to edge model, and assuming a

Table 1. A priori candidate models explaining variation in success of Acadian Flycatcher nests at the Kaskaskia River Bioreserve, 1997–1999.

Model	K	$Log_e(L)$	AIC_c	ΔAIC_c	w_i
Vegetation effects	5	−157.8	325.7	0.0	0.50
Parasitism effects	2	−161.8	327.7	2.0	0.18
Null model	1	−163.6	329.2	3.6	0.08
Distance from edge and vegetation effects	8	−156.8	329.6	3.9	0.07
Habitat and vegetation effects	8	−157.0	330.1	4.4	0.05
Edge length and vegetation effects	8	−157.1	330.2	4.5	0.05
Habitat and parasitism effects	5	−161.5	333.0	7.3	0.01
Distance from edge and parasitism effects	5	−161.7	333.5	7.8	0.01
Edge length and parasitism effects	5	−161.8	333.7	8.0	0.01
Distance from edge effects	4	−163.0	334.1	8.4	0.01
Edge length effects	4	−163.1	334.3	8.6	0.01
Habitat effects	4	−163.2	334.4	8.7	0.01
Temporal effects	6	−161.6	335.2	9.5	0.00
Distance from edge and temporal effects	9	−160.7	339.4	13.7	0.00
Edge length and temporal effects	9	−160.9	339.8	14.2	0.00
Habitat and temporal effects	9	−161.0	340.1	14.4	0.00
Global model	20	−151.0	342.5	16.8	0.00

K, number of estimated parameters for each model; $Log_e(L)$, maximized log-likelihood function; AIC_c, Akaike's information criterion; ΔAIC_c, scaled value of AIC_c, and w_i, Akaike weights. The model with the lowest ΔAIC_c and highest w_i had the most support by the data. The total number of intervals between successive visits to nests was $n = 565$.

Table 2. Model-averaged estimates of regression coefficients (COEFF), standard errors (SE), odd ratios (OR), and 95% confidence intervals (CI) from logistic exposure models of Acadian flycatcher nest survival.

| Effect	COEF	SE	OR	CI
bp	0.138	0.238	1.148	0.722–1.825
nh	0.057	0.068	1.058	0.926–1.208
%c	0.013	0.012	1.013	0.990–1.036
ns (laying vs nestling)	0.005	0.010	1.005	0.985–1.025
ns (incubation vs nestling)	0.003	0.007	1.003	0.990–1.016
%w	0.002	0.006	1.002	0.991–1.013
%r	0.000	0.002	1.000	0.995–1.005
ni	0.000	0.000	1.000	1.000–1.000
sha	0.000	0.000	1.000	1.000–1.000
da	0.000	0.000	1.000	1.000–1.000
bp (parasitized vs unparasitized)	0.000	0.000	1.000	1.000–1.000
la	0.000	0.000	1.000	1.000–1.000
lr	0.000	0.000	1.000	1.000–1.000
lw	0.000	0.000	1.000	1.000–1.000
dr	0.000	0.000	1.000	1.000–1.000
dw	0.000	0.000	1.000	1.000–1.000
tha	0.000	0.000	1.000	0.999–1.001
yr (1997 vs. 1999)	−0.001	0.003	1.000	0.994–1.005
%a	−0.001	0.002	0.999	0.996–1.003
yr (1998 vs. 1999)	−0.001	0.004	0.999	0.992–1.006

Parameter abbreviations as in Appendix.
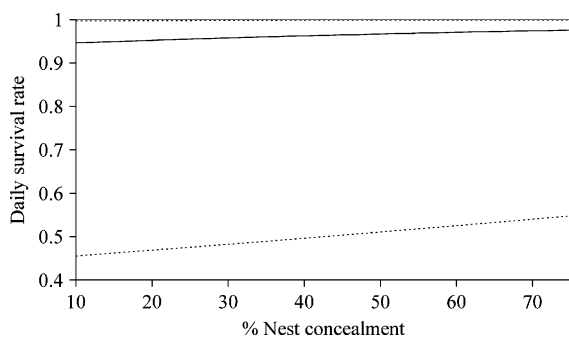
Figure 2. Estimated daily survival rates of Acadian flycatcher nests on floodplain forests at the Kaskaskia River Bottoms, Illinois as a response to percent nest concealment. Daily survival rates were estimated from model-averaged coefficients of the best supported logistic exposure model. Dotted lines indicate 95% confidence intervals.

balanced population in all factors, the proportion of broods parasitized was 0.429 (0.153–0.758).

Discussion

Contrary to our expectations, adding percentages of different habitat types and lengths of edges within 500 m of nests to our models did not explain much variation in nest survival and brood parasitism. The data suggest that nest concealment was the only variable that may have some influence on nest survival with survival increasing as percentages of nest concealment increased (Figure 2). Confidence intervals, however, were large even for this variable. Distance from natural water-related edges and from anthropogenic habitats had some influence on brood parasitism. The magnitude of the influence of these two variables, however, was small and confidence intervals were large (Figures 3 and 4). Overall, our results suggest that edge, edge types and vegetation structure add little information to predicting nesting success in this landscape saturated by nest predators and cowbirds.

The lack of edge effects in this study adds to the growing evidence that edge effects are not always strong or predictable. Studies of internal edges such as clearcuts and rivers show mixed or inconsistent effects (Ratti and Reese 1988; Gates and Griffen 1991; Suarez et al. 1997, Saracco and Collazo 1999; Morse and Robinson 1999; Peak et al. 2004). Morse and Robinson (1999) for example, found no significant effects of edges on nest survival in a similar complex upland forest landscape (see also Small and Hunter 1988; Hoover 1992; Robinson and Wilcove 1994). We also found little evidence that natural edges increased nesting success as predicted based on results of several other studies (Suarez et al. 1997; Saracco

Table 3. A priori candidate models explaining variation in parasitism of Acadian Flycatcher nests at the Kaskaskia River Bioreserve, 1997–1999.

Model	K	$\mathrm{Log_e}(L)$	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i
Distance from edge effects	4	−36.6	81.2	0.0	0.61
Distance from edge and temporal effects	7	−34.3	82.5	1.3	0.31
Distance from edge and vegetation effects	8	−35.1	86.1	5.0	0.05
Global model	17	−26.9	87.9	6.7	0.02
Edge length and temporal effects	7	−39.0	91.9	10.8	0.00
Edge length effects	4	−42.1	92.1	11.0	0.00
Edge length and vegetation effects	8	−41.3	98.6	17.4	0.00
Habitat and temporal effects	7	−42.3	98.6	17.5	0.00
Habitat effects	4	−45.8	99.7	18.5	0.00
Temporal effects	4	−47.3	102.6	21.5	0.00
Habitat and vegetation effects	8	−44.7	105.5	24.3	0.00
Null model	1	−52.4	106.7	25.6	0.00
Vegetation effects	5	−50.8	111.6	30.5	0.00

The model with the lowest $\Delta\mathrm{AIC_c}$ and highest w_i had the most support by the data. The total number of nests was $n = 112$. Abbreviations as in Table 1.

and Collazo 1999; Huhta and Jokimäki 2001). Our results were also inconsistent with the expectation that anthropogenic edges may have a negative effect (reviewed in Paton 1994). In fact, our data are more consistent with the higher probabilities of parasitism in the forest interior than near edges as reported by Hahn and Hatfield (1995) and Gustafson et al. (2002).

One possible explanation for the lack of strong local edge and vegetation effects may be that regional vegetation cover may overwhelm local edge effects as has been argued by Donovan et al. (1997) and Thompson et al. (2000). Our study areas consisted of seven wide (> 1000 m) corridors within a landscape matrix heavily dominated by row crops (see above). The large (> 100 m wide) canopy gap associated with the Kaskaskia River is directly connected with the external, agricultural matrix, and likely facilitates the movement and saturation of most portions of the forest by cowbirds and nest predators (e.g., Bider 1968; Andrén 1995; Gates and Giffen 1991; Gates and Evans 1998). This may partially account for the lack of edge effects. Because landscape composition may overwhelm local fragmentation, regional management may be necessary for breeding birds at the

Table 4. Model-averaged estimates of regression coefficients (COEFF), standard errors (SE), odd ratios (OR), and 95% confidence intervals (CI) from logistic regression models of Acadian flycatcher brood parasitism.

| Effect	COEF	SE	OR	CI
yr (1997 vs. 1999)	0.041	0.045	1.042	0.954–1.137
%*w*	0.002	0.001	1.002	1.000–1.005
da	0.001	0.000	1.001	1.000–1.002
dw	0.001	0.000	1.001	1.000–1.001
%*r*	0.001	0.001	1.001	0.999–1.002
%*a*	0.000	0.001	1.000	0.999–1.002
la	0.000	0.000	1.000	1.000–1.000
sha	0.000	0.000	1.000	1.000–1.000
lr	0.000	0.000	1.000	1.000–1.000
tha	0.000	0.000	1.000	1.000–1.000
lw	0.000	0.000	1.000	1.000–1.000
dr	0.000	0.000	1.000	0.999–1.000
%*c*	0.000	0.000	1.000	0.999–1.000
ni	−0.001	0.000	0.999	0.999–1.000
nh	−0.001	0.003	0.999	0.994–1.004
yr (1998 vs 1999)	−0.009	0.050	0.991	0.900–1.092

Parameter abbreviations as in Appendix.
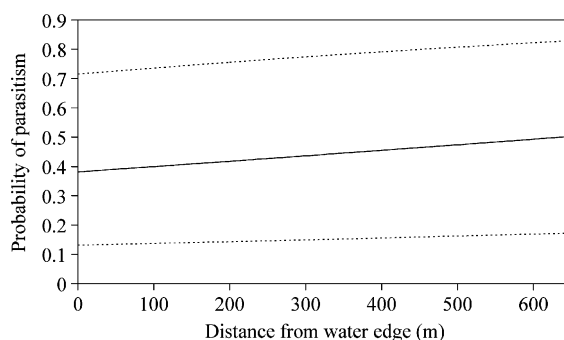
Figure 3. Estimated probabilities of Acadian flycatcher brood parasitism on floodplain forests of the Kaskaskia River Bottoms, Illinois as a response to distance from water edges. Probabilities of brood parasitism were estimated from model-averaged coefficients of the best supported logistic regression model. Dotted lines indicate 95% confidence intervals.

Kaskaskia River Bottoms. Our study landscape is located in the Prairie Peninsula Physiographic Area. The Partners in Flight Bird Conservation Plan for this area recommends increasing forest cover as much as possible and decreasing cowbird foraging opportunities in areas surrounding forest patches (Fitzgerald et al. 2000). This strategy is consistent with our suspicion that regional fragmentation is more important than local effects.

A lack of consistent variation in vegetation structure may also be in part responsible for the lack of edge effects that we encountered. We found
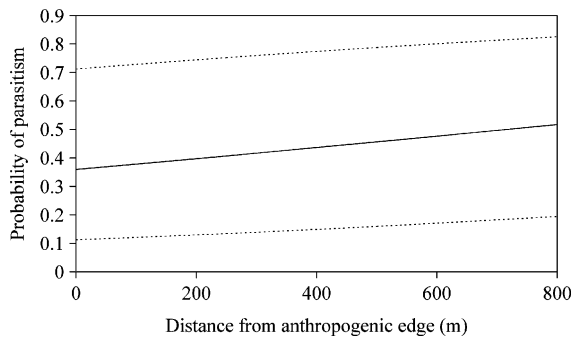
Figure 4. Estimated probabilities of Acadian flycatcher brood parasitism on floodplain forests of the Kaskaskia River Bottoms, Illinois as a response to distance from anthropogenic edges. Probabilities of brood parasitism were estimated from model-averaged coefficients of the best supported logistic regression model. Dotted lines indicate 95% confidence intervals.

some evidence that nest survival increased with increasing nest concealment (see also Moorman et al. 2002). Because vegetation structure may covary systematically with distances from various edges, we conducted exploratory data analysis using correlations of distance from different edge types vs. our measures of vegetation structure. We found that except for an effect of distance from river on tree density, all other pairs of variables had absolute Pearson correlation coefficients < 0.12, which suggests that vegetation structure surrounding nests did not vary consistently with distance from edges. Therefore, vegetation structure could hardly influence our analysis of edge effects. In many cases, failure to detect edge effects may be due to the choice of methods to measure them, or to choices of independent variables. In our study areas, most nests were surrounded entirely by forest at small scales (< 500 m radius), which suggests that Acadian flycatchers at the Kaskaskia River nested in the forest interior, and avoided edges. Therefore, we were unable to test for small-scale effects of within-site habitat composition and lengths of edge effects. In other portions of the Acadian flycatcher range, such as the Cache River Bottoms in Southern Illinois, this species nests more frequently near natural edges such as small tributaries than in the forest interior and anthropogenic edges (Chapa and Robinson, in review).

Because our study focused on a single bird species with a wide breeding distribution and a variety of habitat associations (Whitehead and Taylor 2002), our results are only applicable to this particular species in this habitat and portion of its breeding range. Some of our results, however, may apply to other birds that at least sometimes nest in the sub-canopy layer in the Kaskaskia River Bottoms such as the American redstart (*Setophaga ruticilla*), blue-gray gnatcatcher (*Polioptila caerulea*), and wood thrush (*Hylocichla mustelina*) (personal observation). Our methodology of measuring proportions and lengths of different habitat and edge types on landscapes immediately around patches can be applied to studies of other species in different geographic areas and habitats as a test of the general applicability of the method.

Conclusion

Our analysis added little explanatory information for nest success and brood parasitism, suggesting that ecological phenomena may sometimes be simpler than we think. Our estimated levels of interval nest success (0.335) suggest that Acadian flycatchers at the Kaskaskia River Bottoms are reproducing at replacement levels based on generalized population ecology of neotropical migratory songbirds (Donovan and Thompson 2001). However confidence intervals were large and included values typical of sink populations. Besides regional management actions, the positive effects of nest concealment might be promoted through some forms of management. Silvicultural techniques such as selective cutting can open up the canopy for shrubs which may increase nest concealment (Thompson et al. 1995). Although data are needed from additional species, the results of our study of the Acadian flycatcher suggest that local management of edges may have little effect on nesting success because regional forest cover is low enough that most sections of the floodplain are saturated with predators and parasites. Studies of nesting success of forest birds with a goal of developing management recommendations should first simply consider landscape composition and structure at a variety of scales before more detailed studies of vegetation structure and composition.

Acknowledgements

Appendix

Set of competing candidate *a priori* hypotheses explaining nest survival and brood parasitism of Acadian flycatcher nests at the Kaskaskia River Bottoms, and explanatory variables on each of these models. NS = nest survival; BP = brood parasitism %r, %w, and %a = % of river, water, and anthropogenic habitats within 500 m of nests; l_r, l_w, and l_a = length of river, water, and anthropogenic edges within 500 m of nests; d_r, d_w, and d_a = distance from nearest river, water, and anthropogenic edge; tha, and sha = trees and shrubs/ha within 0.04 ha of nests, n_h = nest height (m), %c = % nest concealment, bp = brood parasitism, n_i = nest initiation date, n_s = nesting stage, yr = year of study.

Nest survival

(1) Effects of habitat composition within patches: NS = %r + %w %a.
(2) Effects of edge lengths within patches: NS = l_r + l_w + l_a.
(3) Effects of distances from edges: NS = d_r + d_w + d_a.
(4) Effects of vegetation structure: NS = tha + sha + n_h + %c.
(5) Effects of brood parasitism: NS = bp.
(6) Temporal effects: NS = n_i + n_s + y_r.
(7) Habitat composition within patches and vegetation effects: NS = %r + %w + %a + tha + sha + n_h + %c.
(8) Habitat composition within patches and brood parasitism effects: NS = %r + %w + %a + bp.
9) Habitat composition within patches and temporal effects: NS = %r + %w + %a + n_i + n_s + yr.
(10) Edge lengths and vegetation effects: NS = l_r + l_w + l_a + tha + sha + n_h + %c
(11) Edge lengths and brood parasitism effects: NS = l_r + l_w + l_a + bp.
(12) Edge lengths and temporal effects: NS = l_r + l_w + l_a n_i n_s + yr.
(13) Distance from edges and vegetation effects: NS = d_r + d_w + d_a + tha + sha + n_h + %c.
(14) Distance from edges and brood parasitism effects: NS = d_r + d_w + d_a + bp.
(15) Distance from edges and temporal effects: NS = d_r + d_w + d_a + n_i + n_s + yr.
(16) Global model: NS = all variables from previous models.
(17) Null model: NS = intercept.

Brood parasitism

(1) Effects of habitat composition within patches: BP = %r + %w + %a.
(2) Effects of edge lengths within patches: BP = l_r + l_w + l_a.
(3) Effects of distances from edges: BP = d_r + d_w + d_a.
(4) Effects of vegetation structure: BP = tha + sha + n_h + %c.
(5) Temporal effects: BP = n_i + yr.
(6) Habitat composition within patches and vegetation effects: BP = %r + %w + %a + tha + sha + n_h + %c
(7) Habitat composition within patches and temporal effects: BP = %r + %w + %a + n_i + yr.
(8) Edge lengths and vegetation effects: BP = l_r + l_w + l_a + tha + sha + n_h + %c.

536

(9) Edge lengths and temporal effects:
$BP = l_r + l_w + l_a + n_i + yr$.
(10) Distance from edges and vegetation effects:
$BP = d_r + d_w + d_a + tha + sha + n_h + \%c$
(11) Distance from edges and temporal effects:
$BP = d_r + d_w + d_a + n_i + yr$.
(12) Global model: BP = all variables from previous models.
(13) Null model: BP = intercept.

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