

Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales

Scott E. Stephens^{a,b,*}, David N. Koons^{a,c}, Jay J. Rotella^a, David W. Willey^a

^a*Department of Ecology, Montana State University, Bozeman, MT 59717, USA*

^b*Ducks Unlimited, Inc., Great Plains Regional Office, 2525 River Road, Bismarck, ND 58503, USA*

^c*School of Forestry and Wildlife Sciences, 108 M. White Smith Hall, Auburn University, AL 36849, USA*

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Abstract

We reviewed published literature to examine the effect of habitat fragmentation on avian nesting success at three spatial scales (i.e., edge, patch, and landscape scales). We identified 86 relevant manuscripts that provided 117 individual tests of hypotheses regarding the effects of habitat fragmentation on nesting success. Most papers and reviews on this topic have been narrow in scope and have not examined multiple spatial scales. However, our results suggest that the scale at which fragmentation is measured (i.e., edge, patch and landscape) and the duration of the study do influence the probability that a study will detect a fragmentation effect. Studies that measured fragmentation at landscape scales and studies conducted over several years were more likely to detect effects of fragmentation on nesting success. A recent review of research on nest predators and habitat fragmentation found a very similar scale-dependent pattern; predator effects were more prevalent when fragmentation occurs at landscape scales than patch or edge scales. Based on these findings, we recommend future research on the topic should be conducted at the landscape scale, over several years, and incorporate accompanying work on nest-predator ecology. Correspondingly, conservation actions that limit fragmentation at landscape scales should have positive impacts on nesting success rates and bird populations.

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1. Introduction

Fragmentation of wintering and breeding habitats for birds has been extensive and continues to occur at a rapid rate across many areas (Richards, 1990; Skole and Tucker, 1993; Hansen et al., 2002) with negative demographic implications (e.g., Terborgh, 1989; Saunders et al., 1991; Robinson et al., 1995; Donovan et al., 1997; Askins, 2000; Boulonier et al., 2001). Habitat fragmentation typically reduces total habitat area, size of individual habitat patches, and proximity of habitat patches, and it can increase the amount of habitat edge. Reduction in the area of suitable habitat can result in population declines by simply reducing adequate space for territories, nest sites, and other critical

resources (Rolstad, 1991). Changes in habitat patch size, proximity of habitat patches, and the amount of edge-habitat also can affect bird populations by negatively impacting reproductive success, survival, emigration and/or immigration rates in the remaining habitat (Rolstad, 1991; Lawton, 1995; Franklin et al., 2000).

Because of the importance of nesting success to avian population dynamics (Lack, 1954; Ricklefs, 1969; Sæther and Bakke, 2000), many empirical studies have attempted to address the effects of habitat fragmentation on nest survival (e.g., Martin, 1988; Robinson et al., 1995; Donovan et al., 1997; Marzluff et al., 2000). However, different studies have considered fragmentation at different scales, and results have been inconsistent. Thus, an overall theory about the effects of habitat fragmentation on nesting success has remained elusive; although such theory is further developed for some regions and orders (Robinson et al., 1995; Donovan et al., 1997).

In this review, we examine patterns among studies of habitat fragmentation and avian nesting success with a

* Corresponding author. Fax: +1-701-355-3547.

E-mail address: sstephens@ducks.org (S.E. Stephens).

focus on the spatial scale at which habitat fragmentation was measured. After considering which scales had been examined in previous research, we determined that past research could be effectively categorized as having examined three spatial scales (edge, patch, and landscape scale). A study was classified as having been done at the edge scale if it quantified fragmentation by measuring factors such as distance from a nest to a habitat edge. Patch-scale studies quantified metrics of fragmentation such as the size and shape of the habitat patch where nests were located. Landscape-scale studies quantified metrics of fragmentation such as the amount of habitat, edge, and variation in patch size across a defined spatial extent (e.g., 1 km, 10 km). Each of these distinct scales suggests different scale-specific hypotheses about the effects of fragmentation on nesting success. The first hypothesis predicts that nest-predation rate is a function of proximity to a habitat edge (edge-scale effects) (e.g., Gates and Gysel, 1978; Wilcove et al., 1986; Yahner and Scott, 1988; Paton, 1994; Cooper and Francis, 1998; Lahti, 2001). The second hypothesis states that patch-level attributes are key determinants of nest-predation rate within a patch (patch-scale effects) (Duebbert and Lokemoen, 1976; Wilcove, 1985; Faaborg et al., 1995). Debate about edge-scale versus patch-scale hypotheses continues because some authors have found a relationship between nesting success and patch area without detecting an edge effect (Small and Hunter, 1988; Arango-Velez and Kattan, 1997), while others have found the opposite (Rudnicki and Hunter, 1993). The third hypothesis suggests that it is critical to consider fragmentation in a broader context (landscape-scale effects; e.g., total amount of edge in a landscape, density of habitat patches, configuration of habitat patches, and variance of habitat patch size) when trying to predict nest-predation rate (Andr n et al., 1985; Robinson et al., 1995; Dooley and Bowers, 1998; Hartley and Hunter, 1998; Tewksbury et al., 1998). Several previous studies found effects of landscape-level factors. However some did not detect patch or edge effects while others found that patch and/or edge effects were landscape dependent (Kurki and Linden, 1995; Donovan et al., 1997). Also, Chalfoun et al. (2002) suggest that factors operating at larger scales may be more influential than smaller-scale factors on the abundance and behavior of nest predators.

Although Lahti (2001) conducted a thorough review of studies that examined the edge-scale hypothesis, no review has evaluated patterns in findings across multiple scales. Thus, we used the numerous studies that have been conducted on the effects of habitat fragmentation on nesting success to search for scale-dependent patterns in results, and provide suggestions for conservation and future research.

2. Methods

Our overall approach was to (1) choose taxonomic groups of interest, (2) review the relevant literature and locate studies that examined habitat fragmentation and nesting success, (3) summarize the results of all studies, and (4) evaluate the evidence for a consistent relationship between habitat fragmentation and nesting success with respect to spatial scales. We focused our review on avian taxa (e.g., anseriformes, ciconiiformes, galliformes, passeriformes, and tinamiformes) where nesting success is highly variable, strongly influenced by predation, and has the potential to strongly affect population growth rate and mean fitness (S tther and Bakke, 2000). Therefore, we excluded studies of raptors and cavity- or colonial-nesting species (e.g., cavity nesting songbirds, colonial nesting waterbirds) from our search.

Because we primarily were interested in the effect of habitat fragmentation on avian nesting success, we limited our search to 22 peer-reviewed journals that we believed were most likely to contain articles on the subject. We searched each issue of the 22 journals published from January 1990 through January 2000 to locate articles and then examined the citations of each article to ensure adequate sampling coverage of previously published relevant articles. As a result, our review encompassed studies published as early as 1984.

For each study that examined habitat fragmentation and avian nesting success, we recorded the following: (1) taxonomic order of birds studied, (2) nest type(s) used in the study (i.e., real and artificial), (3) study duration (i.e., the number of years in the study), (4) sample size of nests monitored, (5) geographic region of study, (6) physiographic habitat type of study, (7) scale(s) at which habitat fragmentation was examined (i.e., edge, patch, or landscape recorded on an ordinal scale) with respect to nesting success, and (8) whether an effect of habitat fragmentation on nesting success was detected at each scale considered. Studies that detected effects counter to the hypothesized predictions were classified as finding an effect but were noted in the Appendix. Some studies that used artificial nests did not make it clear which taxonomic order they were attempting to mimic. Additionally, several have shown that artificial nests cannot accurately represent the nests of any specific taxa (Martin, 1987; Willebrand and Marstrom, 1988; Roper, 1992; Haskell, 1995; Major and Kendal, 1996; Butler and Rotella, 1998; Ortega et al., 1998). Thus, we categorized artificial nests by the type of eggs [e.g., domestic chicken (*Gallus gallus*) or Japanese quail (*Coturnix japonica*)] used in the study. We used the following geographic regions: Canada/Alaska, Fennoscandia, Eurasia, Eastern US, Middle US, Western US, and Other. For our purposes, we considered the Eastern US to include the states of Ohio, Kentucky, Tennessee, Mississippi and all states east; the Western US to

include the states of Montana, Wyoming, Colorado, New Mexico and all states west; and the Middle US to include those states between the Eastern and Western states. We classified physiographic habitat types as forest, grassland, marsh, and shrubland dominated systems (excluding agricultural activity). For studies that examined hypotheses across multiple spatial scales or nest types, we used the individual hypothesis test at each scale and for each nest type as a sample in our analysis.

Because field and statistical methodologies were inconsistent across reviewed publications, we could not conduct a formal statistical meta-analysis. Instead, we modeled the probability of a study detecting an effect of habitat fragmentation on nesting success with logistic regression (McCulloch and Nelder, 1989; Collett, 1991). In the modeling process, we predicted that the aforesaid probability would increase with the spatial scale examined. We then evaluated the amount of support in our data for this hypothesis by comparing it to the support for alternative a priori hypotheses (Platt, 1964). Our list of a priori hypotheses (models) included the univariate spatial-scale model, a null model, as well as additive and interaction models that considered (1) spatial scale and (2) one of the following covariates: nest type, study duration, geographic region, and physiographic habitat type. We considered these additive and interaction models to see if these covariates added information to our primary hypothesis regarding spatial scale. Further, with the subset of studies that examined real nests, we examined the support for the aforementioned models alongside additive and interaction models of spatial scale and taxonomic order. To evaluate the amount of support in our data for each model in our candidate list, we used Akaike's Information Criterion adjusted for sample size (AIC_c) (Akaike, 1973, Burnham and Anderson, 1998: 51, 124), which employs maximum-likelihood theory, information theory, and the principle of parsimony (Akaike, 1973). Among the models in our candidate list, we considered the best approximating and most informative model to be that with the lowest AIC_c value. To assess the goodness-of-fit of each candidate model, we used the area under the receiver-operating-characteristic (ROC) curve, which ranges from 0 to 1 and measures the ability of the model to discriminate between effect and no-effect (i.e., success and failure) detections given the covariate values (Hosmer and Lemeshow, 2000).

Although our vote-counting strategy has problems if publication biases exist, we agree with Chalfoun et al. (2002) that potential biases should be similar across studies at the three spatial scales of interest. Additionally, the probability of detecting significant results could be confounded with sample size of nests (Gurevitch and Hedges, 1993). Therefore, we considered models that examined whether sample size of nests was related to detection of significant results.

3. Results

Our literature survey identified 86 publications with 117 hypothesis tests of the effects of habitat fragmentation on avian nesting success. Of these, 33 examined real nests yielding a total of 42 hypothesis tests. Among the studies that examined artificial nests, 40% of the hypothesis tests were done using chicken eggs and 60% with Japanese quail eggs. Four orders of birds were represented in the literature that examined real nests: Anseriformes (7.1% of tests), Ciconiiformes (2.4%), Galliformes (14.3%), and Passeriformes (76.2%). The mean duration of study was only 2 years (S.E. = 0.17). Many geographic regions and physiographic habitat types were represented poorly in the literature (Table 1). However, the journals we selected to review likely introduced a North American bias into our results.

Most studies ($n = 62$ hypothesis tests) examined effects of habitat fragmentation on nesting success at the edge scale, whereas fewer studies examined effects at patch ($n = 35$) or landscape ($n = 20$) scales (see Appendix for details of studies that examined multiple scales and nest types). The spatial-scale model was a better model than the null model ($\Delta AIC_c = 10.78$). However, when covariates were considered in addition to spatial scale, only the model with spatial scale and study duration (Fig. 1) performed better than the spatial-scale model ($\Delta AIC_c = 1.42$; $\beta_0 = -1.82$, S.E. = 0.55; $\beta_{\text{spatial scale}} = 0.93$, S.E. = 0.28; $\beta_{\text{study duration}} = 0.22$, S.E. = 0.13; ROC = 0.62) making it the best approximating model in our candidate list.

Table 1

The number of hypothesis tests contained in the studies at each spatial scale^a and nest type across the geographic regions and physiographic habitat types

	Edge		Patch		Landscape	
	Nest type		Nest type		Nest type	
	Real	Artificial	Real	Artificial	Real	Artificial
<i>Region</i>						
Canada/Alaska	4	7	1	3	1	1
Eurasia	0	3	0	3	0	0
Fennoscandia	2	6	2	3	0	3
Eastern US	5	10	3	8	1	6
Middle US	10	6	6	1	4	2
Western US	1	2	1	1	1	1
Other	0	6	0	3	0	0
Total	22	40	13	22	7	13
<i>Physiographic habitat type</i>						
Forest	13	33	8	17	5	12
Grassland	9	5	5	4	2	0
Marsh	0	1	0	0	0	0
Shrubland	0	1	0	1	0	1
Total	22	40	13	22	7	13

^a Some studies examined multiple nest types and spatial scales of habitat fragmentation and the results for each nest type and scale examined are included in the table. See Appendix for specific studies.

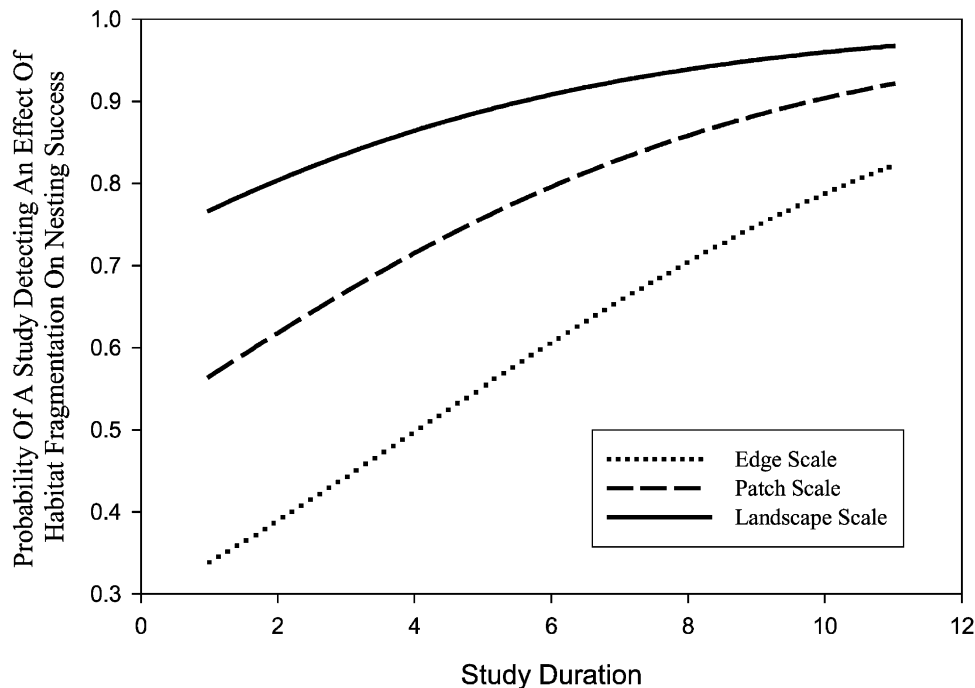


Fig. 1. The effect of the spatial scale of study, and the duration of study (measured in years) on the probability of detecting a significant effect of habitat fragmentation on nesting success for studies that used real and artificial nests ($n = 117$).

When we examined the subset of studies that used real nests, the results were similar to those using the complete data set. Again, the spatial-scale model was better than the null model ($\Delta AIC_c = 4.70$). When models with other covariates were considered, the model with spatial scale and study duration (Fig. 2) performed better than the spatial-scale model ($\Delta AIC_c = 4.00$; $\beta_0 = -3.48$, S.E. = 1.20; $\beta_{\text{spatial scale}} = 1.19$, S.E. = 0.53; $\beta_{\text{study duration}} = 0.46$, S.E. = 0.24) and had better predictive power than the same model using the complete data set (ROC = 0.77). The model with an interaction between spatial scale and study-duration was better than the spatial scale model ($\Delta AIC_c = 2.60$). However, the model that contained spatial scale and study duration without the interaction term was still the best model by 1.42 AIC_c units. We did not find support for models that included geographic region, physiographic habitat type, or nest type ($\Delta AIC_c \geq 2.58$). Additionally, the trends observed did not appear to be confounded by sample size ($\Delta AIC_c \geq 2.47$).

4. Discussion

From our review of the literature, it is evident that habitat fragmentation studies have not been evenly distributed across species, geographic regions, or physiographic habitat types. In addition to Lahti's (2001) review on the edge-effect hypothesis, our multi-scale review of habitat fragmentation and its effect on avian

nesting success provides a broad-based perspective that illuminates gaps in our knowledge. Based on this information, we identify directions for continued research on the topic and implications for conservation programs.

Overall, the proportion of studies detecting relationships between habitat fragmentation and nesting success increased as the scale at which habitat fragmentation was measured increased from edge, to patch, to landscape scale. We believe this trend represents compelling evidence that fragmentation effects are manifest at the larger landscape scales that have only recently begun to receive attention (Robinson et al., 1995; Donovan et al., 1997; Tewksbury et al., 1998). Interestingly, Chalfoun et al. (2002) recently conducted a literature review of nest predator responses to habitat fragmentation and noted the following general pattern across studies: nest predators were more likely to show a positive response to fragmentation (increased abundance, activity, or species richness) when fragmentation was measured at the landscape scale than at finer scales. Responses at local scales were more variable and dependent upon the landscape context within which the study was conducted, as was previously suggested by Andr n (1995) and Donovan et al. (1997). We believe our results, coupled with Chalfoun et al.'s (2002) findings, provide new insight into the scale-dependent mechanism responsible for fragmentation effects on nesting success. Specifically, it appears that the response of nest predators is most sensitive to fragmentation at a landscape scale, and consequently, variation in nesting success is best

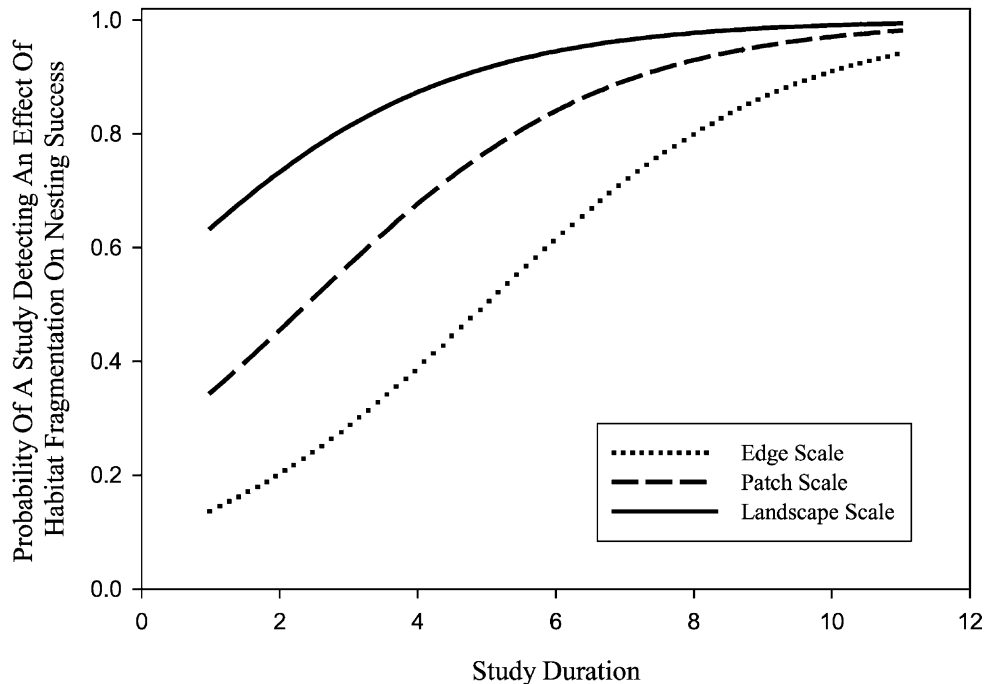


Fig. 2. The effect of the spatial scale of study, and the duration of study (measured in years) on the probability of detecting a significant effect of habitat fragmentation on nesting success for studies that used real nests ($n = 42$).

explained by landscape-level metrics of fragmentation. When fragmentation only occurs at a local scale, however, the results are less predictable. Despite the consistent findings between our study and that of Chalfoun et al. (2002), it is important to realize that (1) the appropriate landscape scale (e.g., 1-, 10-, 100-km) will likely vary for different groups of nest predators and has not been explicitly examined (Mitchell et al., 2001); (2) some studies of nesting success conducted at the landscape scale failed to detect effects of fragmentation; and (3) many landscape settings, biogeographic regions, species groups, and physiographic habitat types remain poorly studied (see later).

Chalfoun et al. (2002) found no studies that examined species richness of nest predators in relation to landscape type. But, it seems plausible that patterns of predation on nests may be driven by the diversity of nest predators present in a landscape. We hypothesize that in settings with diverse predator communities, it will be important to consider multiple landscape scales when trying to predict nesting success rates because different species or groups of nest predators (e.g., squirrels vs. coyotes) likely respond to fragmentation at different scales. Thus, empirical investigations that concurrently examine predator–community composition and nesting-success rates across a range of landscape types at multiple spatial scales may be necessary to elucidate the true effect of habitat fragmentation on nest predators and nesting success.

Our results also suggest that the short duration of most studies may be partly responsible for the inconsistent results among studies. Given the nature of temporal variation in predator populations, alternate prey populations, and thus, predation rates (see Holmes and Sherry, 2001), research conducted for at least 4 years will offer greater ability to separate real effects of fragmentation from those due to inherent environmental stochasticity. Additionally, spatially and temporally replicated studies will be necessary to accomplish the important task of partitioning variance into process and sampling components (White, 2000; Franklin et al., 2000). Thus, conservation decisions will be best informed by longer-term efforts to monitor the effects of fragmentation on nesting success, and correspondingly, decisions made based upon short-term evaluations may be misleading.

There is little information on the effects of habitat fragmentation on nesting success for most orders of birds, making it difficult to draw conclusions across taxa even in the same geographic regions or physiographic habitat types (see Results). For example, this is particularly relevant in the western US where the rate of habitat loss is accelerating (Hansen et al., 2002) but where few studies on habitat fragmentation effects have been conducted (Franklin et al., 2000).

Chalfoun et al. (2002) found that nest–predator response was inconsistent and variable across geo-

graphic areas. Thus, for reliable inference and conservation decisions to be made across poorly studied regions and physiographic habitats, more work will be required. To improve our understanding of the relationship between habitat fragmentation and nesting success, future studies should consider studying avian species and orders where little or no information currently exists. Also, future study designs should focus on using real nests (Butler and Rotella, 1998), consider necessary sample sizes of nests (Rotella et al., 2000), and ensure spatial and temporal replication of sites to rigorously examine alternative hypotheses.

Because our review strongly indicated that landscape scale is important to consider when examining the effect of habitat fragmentation on nesting success (e.g., $\geq 85\%$ of studies that examined landscape-scale habitat fragmentation detected an effect of habitat fragmentation on avian nesting success), we believe that an underlying paradigm of “habitat fragmentation effects on nesting success” may exist at the landscape scale. Furthermore, the effects of habitat fragmentation on avian demographics at smaller spatial scales may be dependent on the larger landscape context (Andr n, 1994; Donovan et al., 1997; Chalfoun et al., 2002). However, the lack of an experimental design across the available studies prevents strong inference on the causal nature of the association between fragmentation, scale, and avian nesting success. We strongly believe that future studies designed to address fragmentation effects on nesting success should: (1) focus on sampling across landscape gradients, (2) measure predictor variables at

multiple landscape-scales, and (3) as suggested by Lahti (2001), conduct corresponding research on the dominant nest predators.

Based on our results we conclude that habitat fragmentation at larger scales may affect nesting success more than fragmentation at smaller scales. If true, then management of avian populations will have to consider management of human development as well. Based on our findings, we suggest that avian conservation plans should focus on developing reserves comprised of large blocks of unfragmented habitats. Negative impacts on bird populations will be minimized if human-induced fragmentation (e.g., home development, logging, agriculture) is concentrated in one locale rather than dispersed across a large spatial extent. Furthermore, the cumulative effects of multiple small anthropogenic developments, which may occur across socio-political boundaries of ownership and management, will have to be considered in the landscape context when trying to manage fragmentation of avian habitat to minimize demographic impacts.

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Appendix A. Nest-type and spatial scale of habitat fragmentation examined by 86 studies used in this review

Nest type	Scale studied and resulting effect					Sources	
	Edge	Effect	Patch	Effect	Landscape		Effect
Artificial	X	Yes					Andr�n and Angelstam, 1988; M�ller, 1989; Burkey, 1993; Linder and Bollinger, 1995; Marini et al., 1995; Pasitschniak-Arts and Messier, 1995; Fenske-Crawford and Niemi, 1997; Niemuth and Boyce, 1997; King et al., 1998; Wong et al., 1998; Brand and George, 2000
Artificial	X	No					Boag et al., 1984; Yahner and Wright, 1985; Angelstam, 1986; Ratti and Reese, 1988; Yahner et al., 1989; Telleria and Santos, 1992; Esler and Grand, 1993; Laurance et al., 1993; Picman et al., 1993; Yahner et al., 1993; Berg, 1996; Russo and Young, 1997
Artificial			X	Yes			M�ller, 1988; Haskell, 1995 ^a ; Yahner and Mahan, 1996; Darveau et al., 1997 ^a ; Clawson and Rotella, 1998; Wilson et al., 1998
Artificial			X	No			Santos and Telleria, 1992; DeGraaf and Angelstam, 1993; DeGraaf, 1995
Artificial					X	Yes	Andr�n et al., 1985; Yahner and Scott, 1988; Langen et al., 1991 ^a ; Andr�n, 1992; Gering and Blair, 1999 ^b
Artificial					X	No	Seitz and Zegers, 1993
Artificial	X	Yes	X	Yes			Gibbs, 1991; Burger et al., 1994
Artificial	X	Yes	X	No			Storch 1991 ^c ; Pasitschniak-Arts and Messier, 1996

(continued on next page)

Appendix A (continued)

Nest type	Scale studied and resulting effect						Sources
	Edge	Effect	Patch	Effect	Landscape	Effect	
Artificial	X	No	X	No			Rudnický and Hunter, 1993; Huhta et al., 1998; Matthews et al., 1999
Artificial	X	No	X	Yes			Nour et al., 1993; Arango-Velez and Kattan, 1997; Hannon and Cotterill, 1998 ^a ; Keyser et al., 1998
Artificial			X	Yes	X	Yes	Wilcove, 1985
Artificial	X	Yes			X	Yes	Donovan et al., 1997; Hartley and Hunter, 1998
Artificial	X	No			X	Yes	Bayne and Hobson, 1997; Sargent et al., 1998
Artificial	X	Yes	X	No	X	Yes	Huhta et al., 1996
Artificial	X	No	X	Yes	X	No	Small and Hunter, 1988
Real	X	Yes					Bjorklund, 1990; King et al., 1996; Suarez et al., 1997; Clark and Shutler, 1999
Real	X	No					Vickery et al., 1992; Lutz et al., 1994; Robinson and Wilcove, 1994; Berg, 1996; Hanski et al., 1996; D'Eon, 1997; Drobney et al., 1998; Fleming and Giuliano, 1998; McKee et al., 1998; Pasitschniak-Arts et al., 1998; Morse and Robinson, 1999
Real			X	Yes			Møller, 1988; Møller, 1991; Burhans and Thompson, 1999
Real			X	No			Bryan and Best, 1994; Gale et al., 1997; Hughes et al., 1999; Taylor et al., 1999
Real					X	Yes	Donovan et al., 1995; Greenwood et al., 1995; Robinson et al., 1995
Real					X	No	Porneluzi and Faaborg, 1999
Real	X	Yes	X	Yes			Johnson and Temple, 1990; Winter and Faaborg, 1999
Real	X	No	X	No			Friesen et al., 1999
Real	X	No	X	Yes			Hoover et al., 1998
Real	X	Yes			X	Yes	Clark et al., 1999
Real	X	No	X	Yes	X	Yes	Hoover et al., 1995
Real	X	No	X	No	X	Yes	Tewksbury et al., 1998 ^d

^aHannon and Cotterill 1988, Langen et al. (1991), Haskell (1995) and Darveau et al. (1997) detected lower nestling success in larger patches.

^bGering and Blair (1999) found lower nesting success in “natural” habitats than urbanized habitats.

^cStorch (1991) reported higher nesting success near edges than in the interior of forests.

^dTewksbury et al. (1998) detected lower nesting success in unfragmented landscapes than in fragmented agricultural landscapes.

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