
Nest Predators and Fragmentation: a Review and Meta-Analysis

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Abstract: *Population declines of many avian species are often attributed to increased rates of nest predation in fragmented landscapes, yet mechanisms underlying these effects have rarely been examined. We reviewed the literature to determine the extent to which hypotheses about nest predators and fragmentation have been invoked and compared this to the number of direct tests of predators with respect to habitat edge, patch size, or landscape type. We also conducted a meta-analysis of tested predator effects to evaluate whether predator responses—numerical, functional, or species richness—to fragmentation depend on spatial scale (edge, patch, or landscape), landscape type, geographic region, or predator taxa. We found 120 papers containing hypotheses about nest predators and fragmentation, but only 31 with hypothesis tests. Most tests were of a single predator species or guild, whereas most cited hypotheses generalized across broader taxonomic groups. Results of predator tests were variable, but some general patterns were evident. Predator effects, including increased abundance, activity, or species richness in edges, small patches, or certain landscapes, were more prevalent (1) in tests conducted at the landscape scale than at the local scale, (2) in agricultural landscapes than in predominantly forested landscapes, (3) in certain biogeographic regions, and (4) for avian predators than for mammalian predators. Local-scale (edge and patch) effects were most common when the land surrounding patches was agricultural and when tests were conducted within agricultural landscapes. The response of nest predators to fragmentation is complex, taxon-specific, and context-dependent. Conservation efforts for declining avian species may therefore need to be customized according to the nest-predator species primarily responsible for local nest mortality and the nature of the landscape mosaic.*

Depredadores de Nidos y Fragmentación: una Revisión y Meta-Análisis

Resumen: *A menudo se atribuyen las declinaciones de poblaciones de muchas especies de aves al incremento de las tasas de depredación de nidos en paisajes fragmentados, pero raras veces se han analizado los mecanismos subyacentes a estos efectos. Revisamos la literatura para determinar los alcances de las hipótesis de depredadores de nidos y fragmentación que se han postulado y los comparamos con el número de pruebas directas de depredadores con respecto al borde del hábitat, tamaño del fragmento o el tipo de paisaje. También realizamos un meta-análisis de los efectos comprobados de depredadores para evaluar si la respuesta del depredador (numérica, funcional o riqueza de especies) a la fragmentación depende de la escala espacial (borde, fragmento o paisaje), tipo de paisaje, región geográfica o taxa de depredadores. Encontramos 120 trabajos con hipótesis sobre depredadores de nidos y fragmentación, pero solo 31 con pruebas de hipótesis. La mayoría de las pruebas fueron con una sola especie o gremio de depredador, mientras que la mayoría citó hipótesis generalizadas para grupos taxonómicos más amplios. Los resultados de pruebas de depredadores fueron variables, pero algunos patrones generales fueron evidentes. Los efectos de depredador (es decir, incremento de abundancia, actividad o riqueza de especies en bordes, fragmentos o ciertos paisajes)*

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fueron más prevalentes (1) en pruebas conducidas al nivel de paisaje que en escala local, (2) en paisajes agrícolas que en paisajes predominantemente boscosos, (3) en ciertas regiones biogeográficas y, (4) para aves depredadoras más que para mamíferos depredadores. Los efectos a escala local (borde y fragmento) fueron más comunes cuando los fragmentos circundantes eran agrícolas y cuando las pruebas fueron llevadas a cabo en paisajes agrícolas. La respuesta de los depredadores de nidos a la fragmentación es compleja, específica al taxón y dependiente del contexto. Por lo tanto, los esfuerzos de conservación para especies de aves en declinación deberán planearse dependiendo de las principales especies depredadoras de nidos responsables de la mortalidad local de nidos y de la naturaleza del mosaico paisajístico.

Introduction

Avian nest-predation rates are affected by regional patterns of habitat fragmentation and local-scale attributes such as patch size and edges (Robinson et al. 1995; Thompson et al. 2002). Several studies report elevated rates of nest predation in fragmented landscapes (e.g., Robinson et al. 1995; Donovan et al. 1997; Hartley & Hunter 1998), small habitat remnants (e.g., Small & Hunter 1988; Wilcove 1985), and habitat edges (e.g., Gates & Gysel 1978; Andrén & Angelstam 1988; Fenske-Crawford & Niemi 1997). Few studies, however, have evaluated causal mechanisms for such patterns via direct studies of nest predators and fragmentation. This is surprising considering the widespread agreement among researchers that understanding rates of nest predation ultimately requires a better knowledge of the autecology of predators (e.g., Paton 1994; Keyser et al. 1998; Marzluff & Restani 1999).

Understanding factors affecting nest-predation rates is important because nest predation is the primary agent of avian nest mortality and, on average, accounts for 80% of nest losses (Martin 1993). Moreover, along with brood parasitism, nest predation is an important factor limiting the reproduction and population viability of many Neotropical migrant landbird species in fragmented landscapes (Robinson & Wilcove 1994). Many species of Neotropical migrant birds are experiencing population declines (Robbins et al. 1989; Askins et al. 1990; Robinson et al. 1995), which are frequently attributed to factors associated with habitat fragmentation.

Many studies have proposed hypotheses about nest predators to explain elevated nest-predation rates. Some of the more common hypotheses are that predators are more abundant in small habitat patches and fragmented landscapes and are more active and/or abundant in edges. These hypotheses, however, have rarely been tested empirically. We reviewed the extent to which various hypotheses about nest predators have been cited and the number of studies that directly tested hypotheses about nest predators with respect to edge, patch size, or landscape effects. We also performed a meta-analysis of the results of studies that conducted tests of these effects. We tested the predictions that (1) nest-predator response to habitat fragmentation is de-

pendent on scale and context and that (2) nest-predator response to fragmentation is taxon-specific. Also, because other researchers suggest that ecological processes at larger spatial scales constrain effects at a local scale (Thompson et al. 2002), we tested whether the expression of local-scale (edge and patch) predator effects depend on the adjacent land-cover type and landscape composition.

Methods

Cited and Tested Hypotheses

We included in the review only peer-reviewed, published literature, including journal articles, book chapters, and government technical reports. We retrieved papers through computer literature searches using appropriate key words. No limits were imposed with respect to year of publication or specific journals. Our criteria for inclusion of papers mentioning hypotheses about nest predators and fragmentation (hereafter referred to as "cited" hypotheses) were that the author(s) referred to a numerical, functional, or species-richness response of one or more documented species of avian nest predator in relation to edge, patch size, or landscape type. An example of one such cited hypothesis is that "nest predators are more abundant in small habitat patches." A functional response refers to differences in predator behavior (typically stated as "activity"). A numerical response refers to differences in predator abundance.

In many cases, one paper mentioned several individual hypotheses about nest predators. If the authors referred to specific predator species or groups, we considered each hypothesis individually. If the authors used a broader term such as "nest predators," followed by a list of species as examples, the citation was recorded as a reference to nest predators in general. We recorded whether authors referred to a specific habitat or landscape type. We also recorded whether authors suggested potential mechanisms underlying predator hypotheses—for example, if an author stated that nest predators were more abundant in edges and attributed this to increased food availability in edges.

For a study to be included in our analyses of tested predator effects, researchers had to have (1) directly measured the response—numerical, functional, or species richness—of one or more nest-predator species in relation to edge, patch, or landscape and (2) used a statistical test to evaluate predator response. Predator measurements, moreover, needed to have taken place at least partially during the local avian nesting period. Studies that only measured rates of predation on nests were not considered direct tests of predator response. Studies need not have explicitly referred to their study animals as nest predators, as long as they were a documented nest-predator species, and papers were not restricted to the avian nest-predation literature.

Studies that pooled non-nest-predator species with nest-predator species in statistical tests (e.g., Bennett 1987; Estrada et al. 1994) were excluded because we could not be sure to what extent the non-nest-predator data affected the analyses. Similarly, studies in which habitat effects could not be separated from fragmentation effects (e.g., Andr en 1992) were not included. Studies conducted on oceanic islands were omitted from the review so as not to confound fragmentation with island effects. A few studies were difficult to classify with respect to response type (e.g., Heske 1995; Pedlar et al. 1997) because the terms predator *activity* and *abundance* were used in reference to the same tests. In those cases, we interpreted predator measurements taken at the local (edge or patch) scale to be tests of a functional response and those taken at the landscape scale to be tests of a numerical response.

We documented the habitat(s) and/or landscape type(s) within which data collection for each predator test occurred. Landscapes were classified as one of four types: agricultural, predominantly forested (including areas managed for timber production), urban/suburban, and grassland. We also noted whether authors suggested mechanisms for predator effects based on retrodiction from tested effects in their studies, because this can be an effective way to generate hypotheses for future research.

Meta-Analysis

We conducted a meta-analysis of selected data from papers that had one or more tested effects on predators. Meta-analysis is used to elucidate general trends from numerous individual statistical tests (Fernandez-Duque & Valeggia 1994). Ideally, we would have calculated effect sizes for each comparison to standardize the effect among studies, but few studies provided the information necessary to do so (i.e., means, standard deviations, and sample size). Furthermore, many studies in our review tested similar effects with different methods and for different taxonomic groups. Thus, we opted for a type of vote-counting strategy in which we calculated the fre-

quency of significant versus nonsignificant results (Gurevitch & Hedges 1993). We considered p values of <0.05 to be significant or relied on the interpretation of the author(s). Vote counting has received criticism for being biased because studies with small sample sizes are less likely to have statistically significant results than those with large sample sizes (Gurevitch & Hedges 1993). Thus, the results cannot be used to determine the magnitude of an effect. Another caveat is that there may be a publishing bias toward papers with significant results. Despite the limitations, we believe that the vote-counting method is an effective way to determine the generality of results and to identify any existing patterns.

Predator species were grouped into one of four categories: birds, rodents, medium/large mammals, and snakes. We defined a predator effect as one in which predators were shown to be more abundant, more active, or more species-rich in edges, small patches, or certain landscapes. We used two-way likelihood-ratio chi-square tests to determine whether the percentage of tests with predator effects was independent of (1) scale (edge, patch, landscape), (2) landscape type (agricultural, forested, urban/suburban, grassland), (3) geographic region (Australia, Canada, Scandinavia, eastern United States, mid-western United States, western United States), and (4) predator group (birds, rodents, medium/large mammals, snakes). We also tested whether predator response to local-scale features (edge, patch size) was independent of (1) land-cover type (e.g., agricultural, land forest, grassland, logged forest) surrounding patches and (2) landscape type.

Results

Summary of Cited Hypotheses

The number of publications that cited hypotheses about nest predators and fragmentation ($n = 120$) greatly exceeded the number that actually tested them ($n = 31$) (Table 1). Papers typically mentioned two or more predator hypotheses. We documented 136 citations referring to nest predators and edges, 48 relating predators to patch size, and 78 about predators and landscape type. Cited hypotheses were most commonly in reference to predator abundance ($n = 164$), followed by activity ($n = 85$) and richness ($n = 13$).

Over half (53%) of cited hypotheses were in reference to nest predators in general, while another 16% used the term “generalist predators.” A smaller percentage of hypotheses (19%) focused on single species. This resulted in a taxonomic discrepancy in cited versus tested effects. Publications tended to generalize across broad nest-predator groups when mentioning predator hypotheses, whereas the majority of tested effects were on individual species (Table 2). Of the 50 citations focusing

Table 1. Frequency of citations and tests of nest-predator hypotheses at three spatial scales of fragmentation.

Predator hypothesis		Cited*		Tested*	
response type	scale	no. of papers	no. of citations	no. of studies	no. of tests
Functional	edge	64	78	6	10
	patch	6	6	1	1
	landscape	1	1	0	0
Numerical	edge	46	50	14	54
	patch	31	41	8	23
	landscape	63	73	14	36
Richness	edge	8	8	1	2
	patch	1	1	0	0
	landscape	4	4	0	0
Total		120	262	31	126

*A single paper could contain multiple citations and/or multiple tests.

on single species, 32 (64%) referred to mammals, 16 (32%) to birds (Corvidae), and 2 (4%) to a snake (black rat snake). (Scientific names are provided in Table 2.) Individual species most commonly implicated in fragmentation hypotheses included the American Crow ($n = 7$), Blue Jay ($n = 5$), and raccoon ($n = 12$).

Approximately 63% ($n = 166$) of cited hypotheses referred to specific habitat types. Of these, 164 referred to forest, 1 to grassland (Pasitschniak-Arts & Messier 1995), and 1 to chaparral (Langen et al. 1991). Sixty-five percent ($n = 170$) of cited hypotheses were in reference to one or more specific landscape types. Of these, 80 referred to agricultural land, 80 to predominantly forested land, and 30 to urban or suburban landscapes (some papers alluded to more than one landscape type).

Proposed mechanisms to explain predator responses for either cited or tested hypotheses fell into one of five major categories: (1) increased food availability, (2) mesopredator release (for explanation, see Crooks & Soulé 1999), (3) predator influx into habitat patches from the external matrix, (4) predator use of edges as travel or forage lanes, and (5) structural differences in vegetation. A greater percentage of studies with cited predator hypotheses suggested mechanisms for effects than did studies with tested predator effects (Tables 3 & 4). The most common mechanisms proposed to explain increased activity of predators in edges were increased food availability and predator use of edges as travel or forage lanes. An increased number of nest predators in edges was usually attributed to increased food in edges or an influx of predators from surrounding areas. Increased predator abundance in small patches was usually attributed to increased food availability, mesopredator release, and predator influx from surrounding areas. An increased number of predators in fragmented landscapes was generally attributed to increased food availability and mesopredator release.

Summary of Tested Effects

Thirty-one papers contained tests ($n = 126$) of nest predators in relation to fragmentation that met our criteria (Table 1). There were 66 tests examining predators in relation to edges, 24 in relation to patch size, and 36 in relation to landscape type. There were 11 tests of functional responses of predators, 113 of numerical responses, and 2 of species-richness responses. The majority of studies tested effects for a single predator species or taxon, at a single scale, and for a single response type (Table 5). There were 20 tests (18%) on individual avian species, 55 (49%) on individual rodent species, 33 (29%) on individual medium or large mammals, and 4 (4%) on an individual snake species (black rat snake) (Table 2). There were five species—the dingo (*Canis familiaris dingo*), coyote (*C. latrans*), Grackle (*Quiscalus quiscula*), eastern gray squirrel (*Sciurus carolinensis*), and fox squirrel (*S. niger*)—specifically mentioned in fragmentation hypotheses for which we found no relevant tests. Several studies pooled two or more species in tests of predator abundance (avian predators: Rich et al. 1994; Hoover et al. 1995; Marini et al. 1995; Bayne & Hobson 1997a; Gardner 1998; Major et al. 1999; small mammals: Heske 1995; Bayne & Hobson 1998; Yahner 1992; medium-sized mammals: Heske 1995; Marini et al. 1995).

No relevant tests were found for three scale/response combinations: patch/richness, landscape/functional, and landscape/richness. The most widely cited hypothesis, that predators are more active in edges, was tested in only 6 studies. Of these, tests were performed on only four different species, with the exception of one test that pooled medium and large mammals (Heske 1995). Moreover, although 31 studies contained applicable tests of predators, 55% of these tests were performed in only 4 studies (Rosenberg & Raphael 1986, 36 tests; Bayne & Hobson 1997a, 11 tests; Bayne & Hobson 1998, 12 tests; Dijak & Thompson 2000, 10 tests).

The majority of studies with tested predator effects took place in North America (87%), although 3 studies took place in Australia and one in Denmark (Table 5). Most studies ($n = 29$) were conducted in forest habitat, with the exception of those by Weatherhead and Charland (1985), Durner and Gates (1993), and Bowers et al. (1996), whose studies took place at least partially in grassland habitat, and that of Oehler and Litvaitis (1996), whose study took place in a range of habitats. Nine studies took place entirely within agricultural landscapes, 15 within predominantly forested landscapes, 1 within a grassland landscape, and 6 within two or more landscape types. Common methods employed to investigate predator response include live-trapping (11 studies), kill-trapping (5 studies), scent-station surveys (6 studies), and various counts (14 studies) for abundance comparisons. Radiotelemetry (3 studies) and scent-station surveys (2 studies) were used for activity analyses.

Table 2. Number of tests of hypotheses concerning nest predators and fragmentation at the edge, patch, or landscape scale listed by individual predator species.^a

<i>Nest predator</i>		<i>No. of studies^b</i>	<i>No. of tests</i>	<i>References</i>
<i>scientific name</i>	<i>common name</i>			
<i>Corvus brachyrhynchos</i>	American Crow	3	3	Yahner & Scott 1988; Thompson et al. 1992; Bayne & Hobson 1997a
<i>C. corax</i>	Common Raven	2	4	Rosenberg & Raphael 1986; Bayne & Hobson 1997a
<i>C. corone cornix</i>	Hooded Crow	1	1	Møller 1989
<i>Cyanocitta cristata</i>	Blue Jay	5	5	Kroodsma 1984; Yahner & Scott 1988; Thompson et al. 1992; Marini et al. 1995; Robinson & Robinson 1999
<i>C. stelleri</i>	Stellar's Jay	1	3	Rosenberg & Raphael 1986
<i>Didelphis virginiana</i>	opossum	2	6	Heske 1995; Dijak & Thompson 2000
<i>Elaphe obsoleta</i>	black rat snake	2	4	Weatherhead & Charland 1985; Durner & Gates 1993
<i>Garrulus glandarius</i>	European Jay	1	1	Møller 1989
<i>Glaucomys sabrinus</i>	northern flying squirrel	2	7	Rosenberg & Raphael 1986; Bayne & Hobson 1998
<i>Martes americana</i>	American marten	2	3	Chapin et al. 1998; Hargis et al. 1999
<i>M. pennanti</i>	fisher	1	3	Rosenberg & Raphael 1986
<i>Mephitis mephitis</i>	striped skunk	1	3	Rosenberg & Raphael 1986
<i>Microtus pinetorum</i>	woodland vole	2	3	Heske 1995; Menzel et al. 1999
<i>Perisoreus canadensis</i>	Gray Jay	1	1	Bayne & Hobson 1997a
<i>Peromyscus leucopus</i>	white-footed mouse	8	10	Gottfried 1979; Linzey 1989; Yahner 1992; Heske 1995; Bowers et al. 1996; Nupp & Swihart 1996; DeGraaf et al. 1999; Menzel et al. 1999
<i>P. maniculatus</i>	deer mouse	4	12	Rosenberg & Raphael 1986; Bayne & Hobson 1997a, 1998; Menzel et al. 1999
<i>Pica pica</i>	Magpie	2	2	Møller 1989; Bayne & Hobson 1997a
<i>Procyon lotor</i>	raccoon	4	9	Heske 1995; Oehler & Litvaitis 1996; Pedlar et al. 1997; Dijak & Thompson 2000
<i>Rattus fuscipes</i>	bush rat	1	1	Dunstan & Fox 1996
<i>R. rattus</i>	black rat	1	1	Dunstan & Fox 1996
<i>S. griseus</i>	western gray squirrel	1	3	Rosenberg & Raphael 1986
<i>Spilogale gracilis</i>	western spotted skunk	1	3	Rosenberg & Raphael 1986
<i>Tamias senex</i>	Allen's chipmunk	1	3	Rosenberg & Raphael 1986
<i>T. striatus</i>	eastern chipmunk	3	3	Yahner 1992; Heske 1995; DeGraaf et al. 1999
<i>Tamiasciurus douglasii</i>	Douglas squirrel	1	3	Rosenberg & Raphael 1986
<i>T. hudsonicus</i>	red squirrel	4	9	Hagan et al. 1996; Bayne & Hobson 1997a, 1998; Tewksbury et al. 1998

^a Studies that contained tests with two or more species pooled are not listed here but can be found in Table 5.

^b A single study could contain multiple tests.

Four of 10 tests of predator activity suggest that nest predators utilized edge more than would be expected by chance. Three of these tests were on black rat snakes (Weatherhead & Charland 1985; Durner & Gates 1993) and one was on raccoons in Ontario, Canada (Pedlar et al. 1997). In contrast, American martens, raccoons in New Hampshire (Oehler & Litvaitis 1996), and raccoons, opossums, and furbearers in Illinois (Heske 1995) were not more active in edges (Chapin et al. 1998).

In 76% of tests on predator abundance in relation to edge, no significant effect was found. There were 12 tests of avian predators, 28 tests of rodents, and 14 of medium and large mammals. Avian predators were more abundant in edges in 25% of tests (Møller 1989; Rich et

al. 1994; Gardner 1998), rodents in 7% of tests (Rosenberg & Raphael 1986; Bayne & Hobson 1998), and medium and large mammals in 14% of tests (Dijak & Thompson 2000). A few studies documented a higher abundance of some predator species away from edges, including the European Jay (Møller 1989), white-footed mouse (Linzey 1989), and gray fox, fisher, and striped skunk (Rosenberg & Raphael 1986).

Only one study (Marini et al. 1995) examined predator species richness in relation to edge. There were significantly more species of avian nest predators in forest edges, whereas medium-sized mammalian predator species richness did not differ between forest edge and interior. Only one test of predator activity with respect to

Table 3. Frequency of suggested mechanisms for hypothesized fragmentation effects on nest predators in scientific publications.

Hypothesis		Mechanisms*					
scale	response	IF	MR	PI	TL	S	none
Edge	functional	15		2	44	3	27 (34)
	numerical	5		9			39 (78)
	richness			1			7 (88)
Patch	functional			2	1		3 (50)
	numerical	9	11	15		2	13 (32)
Landscape	functional						1 (100)
	numerical	26	8				44 (60)
	richness	1					3 (75)
Total		56	19	28	45	5	138 (53)

*Mechanisms: IF, increased food or resource availability; MR, mesopredator release; PI, predator influx from surrounding areas; TL, travel- or forage-lane hypothesis; S, structural differences in vegetation; none, no mechanisms suggested (percent of all citations).

patch size was conducted (Chapin et al. 1998). American martens, an area-sensitive, forest-dependent species (Chapin et al. 1998), utilized larger forest patches significantly more than smaller patches.

In 57% of tests of predator abundance with respect to patch size, no significant difference was found. In 26% of tests, nest predators were more abundant in smaller patches, and in 17% predators were less abundant in smaller patches ($n = 23$ tests). There were 4 tests of avian predators, 13 tests of rodents, and 6 tests of medium-sized mammals. Species more abundant in smaller patches included avian predators (Hoover et al. 1995; Dunstan & Fox 1996), arboreal rodents (Hoover et al. 1995), white-footed mice (Nupp & Swihart 1996), black rats (Dunstan & Fox 1996), and medium-sized mammals (Hoover et al. 1995). But several of the aforementioned species displayed different patterns in different studies. For example, two other studies found that arboreal mammal species were equally or less abundant in small

Table 4. Frequency of suggested mechanisms for edge, patch, and landscape effects on nest predators determined by retrodiction from tested effects in published studies.

Hypothesis		Mechanisms*					
scale	response	IF	MR	PI	TL	S	none
Edge	functional	3			1		2 (33)
	numerical	2			2	1	59 (95)
	richness						2 (100)
Patch	functional						1 (100)
	numerical	3	3	4		2	17 (71)
Landscape	numerical	6	2			2	44 (60)
Total		14	5	4	3	5	109 (83)

*Mechanisms: IF, increased food and resource availability; MR, mesopredator release; PI, predator influx from surrounding areas; TL, travel- and forage-lane hypothesis; S, structural differences in vegetation; none, no mechanisms suggested (percent of all citations).

forest patches (Rosenberg & Raphael 1986; Bayne & Hobson 1998). Three studies examining *Peromyscus* spp., moreover, found no differences in abundance with respect to forest patch size in either agricultural (Gottfried 1979; Bayne & Hobson 1998) or predominantly forested (Rosenberg & Raphael 1986) landscapes, contrary to the findings of Nupp and Swihart (1996). All tests with significant patch effects were conducted within agricultural landscapes and with agricultural land as the surrounding habitat type.

A higher percentage of tests examining predator abundance at the landscape scale were significant (55%). Landscape effects were typically tested in one of two ways: (1) two or more landscape types were compared (e.g., Bayne & Hobson 1997a, 1998; Tewksbury et al. 1998; Dijak & Thompson 2000) or (2) within a similar matrix, landscapes of different extents of fragmentation were compared (Rosenberg & Raphael 1986; Yahner & Scott 1988; Thompson et al. 1992; Yahner 1992; Bowers et al. 1996; Hagan et al. 1996; Hargis et al. 1999; Robinson & Robinson 1999). There were 14 tests in which two or more landscape types were compared. Nest predators were often significantly more abundant in agricultural landscapes (9 of 14 tests; 64%) than in forested landscapes. All but one of these tests were on single species. There were 5 tests of avian predators, all corvids. American Crows and Magpies were both more abundant in an agricultural landscape, whereas Gray Jays were more abundant in a forested landscape (Bayne & Hobson 1997a). There were no significant landscape effects for the Common Raven or all corvids combined (Bayne & Hobson 1997a). Six tests were performed on rodent species. Red squirrels and northern flying squirrels were more abundant in an agricultural landscape, whereas deer mice displayed no obvious abundance pattern (Bayne & Hobson 1997a, 1998). Two studies examined medium-sized mammal species (3 tests). Both raccoons and opossums were significantly more abundant in landscapes with greater amounts of agriculture (Oehler & Litvaitis 1996; Dijak & Thompson 2000).

There were seven studies (22 tests) in which different extents of fragmentation were compared, all but 1 of which took place within predominantly forested landscapes. Nest predators were significantly more abundant in areas with increasing fragmentation in only 4 (18%) tests. Three were tests on corvids (Yahner & Scott 1988; Robinson & Robinson 1999), and 1 was a test on deer mice (Rosenberg & Raphael 1986). Four species were significantly less abundant in more fragmented landscapes, including the white-footed mouse (Bowers et al. 1996), western gray squirrel, gray fox, fisher (Rosenberg & Raphael 1986), and American marten (Hargis et al. 1999).

Meta-Analysis

Predator response was not independent of spatial scale ($\chi^2 = 8.96$, $df = 4$, $p = 0.06$; Fig. 1). With all predator-

Table 5. Studies investigating functional, numerical, or species-richness responses of nest predators in relation to habitat fragmentation at the edge, patch, or landscape scale.^a

Reference	Location	Taxa studied ^b	Scale ^c	Response type ^d	No. of tests	No. of significant tests
Bayne & Hobson 1997a	Saskatchewan	B,R	E,L	N	11	5
Bayne & Hobson 1998	Saskatchewan	R	E,P,L	N	12	4
Bowers et al. 1996	Virginia	R	L	N	1	1
Chapin et al. 1998	Maine	M	E,P	F	2	1
DeGraaf et al. 1999	Massachusetts	R	E	N	2	0
Dijak & Thompson 2000	Missouri	M	E,L	N	9	4
Dunstan & Fox 1996	Australia	R	P	N	2	2
Durner & Gates 1993	Maryland	S	E	F	2	1
Gardner 1998	Australia	B	E	N	1	1
Gottfried 1979	Iowa	R	P	N	1	0
Hagan et al. 1996	Maine	R	L	N	1	0
Hargis et al. 1999	Utah	M	L	N	1	1
Heske 1995	Illinois	M,R	E	F,N	6	0
Hoover et al. 1995	Pennsylvania	B,M	P	N	3	3
Kroodsma 1984	Tennessee	B	E	N	1	0
Linzey 1989	Pennsylvania	R	E	N	2	2
Major et al. 1999	Australia	B	P	N	1	1
Marini et al. 1995	Illinois	B,M	E	N,R	5	1
Menzel et al. 1999	North Carolina	R	E	N	6	0
Møller 1989	Denmark	B	E	N	3	2
Nupp & Swihart 1996	Indiana	R	P	N	1	1
Oehler & Litvaitis 1996	New Hampshire	M	E,L	N,F	2	1
Pedlar et al. 1997	Ontario	M	E	F	1	1
Rich et al. 1994	New Jersey	B	E	N	3	1
Robinson & Robinson 1999	Illinois	B	L	N	1	1
Rosenberg & Raphael 1986	California	B,M,R	E,P,L	N	36	11
Tewksbury et al. 1998	Montana	R	L	N	1	1
Thompson et al. 1992	Missouri	B	L	N	2	0
Weatherhead & Charland 1985	Ontario	S	E	F	2	2
Yahner 1992	Pennsylvania	R	L	N	2	0
Yahner & Scott 1988	Pennsylvania	B	L	N	2	2

^a Only statistical tests relevant to this review were included in the table.

^b B, birds; R, rodents; M, medium and large mammals; S, snakes.

^c E, edge; P, patch; L, landscape.

^d N, numerical; F, Functional; R, species richness.

response types (functional, numerical, species richness) combined, positive predator effects were obtained at a frequency of 18.2% for edge tests, 25.0% for patch tests, and 36.1% for landscape tests. The same basic pattern obtained when only numerical response tests were examined ($\chi^2 = 10.392$, $df = 4$, $p = 0.03$). Positive predator-abundance effects were obtained in 12.3% of edge tests, 26.1% of patch tests, and 36.1% of landscape tests.

Predator response varied according to landscape type ($\chi^2 = 18.758$, $df = 6$, $p = 0.005$) (Fig. 2). With all response types combined, positive effects were obtained at a frequency of 41.2% in agricultural landscapes, 12.9% in predominantly forested landscapes, 0% in grassland landscapes (only 1 test), and 25.0% when a range of landscape types were compared.

Predator response was not consistent across geographic regions ($\chi^2 = 17.513$, $df = 5$, $p = 0.004$). Positive effects were obtained at a frequency of 75% in Australia (although only 4 total tests), 38.5% in Canada, 33.3% in Scandinavia (although only 3 total tests), 27.6%

in the eastern United States, 26.92% in the midwestern United States, and 5.3% in the western United States.

Predator response varied according to predator group ($\chi^2 = 12.951$, $df = 6$, $p = 0.04$). For all response types and spatial scales combined, positive results were obtained at a frequency of 37.9% for avian predators, 18.9% for medium and large mammals, 17.9% for rodents, and 75.0% for snakes. Significant negative results (i.e., higher abundance, activity, and richness away from edges, in larger patches, and in less fragmented landscapes) were obtained at a frequency of 6.9%, 24.3%, 12.5%, and 0% for these taxon groups, respectively.

Predator response to local-scale attributes (edge or patch size) was not independent of external habitat type ($\chi^2 = 15.999$, $df = 5$, $p = 0.007$). Positive local-scale effects were obtained at a frequency of 66.7% when the adjacent land use was agricultural, 5.6% when the surrounding habitat was forested, 16.7% when grassland, 5.6% when clearcut forest, and 5.6% for other uses. Predator response to edge and patch size was also not

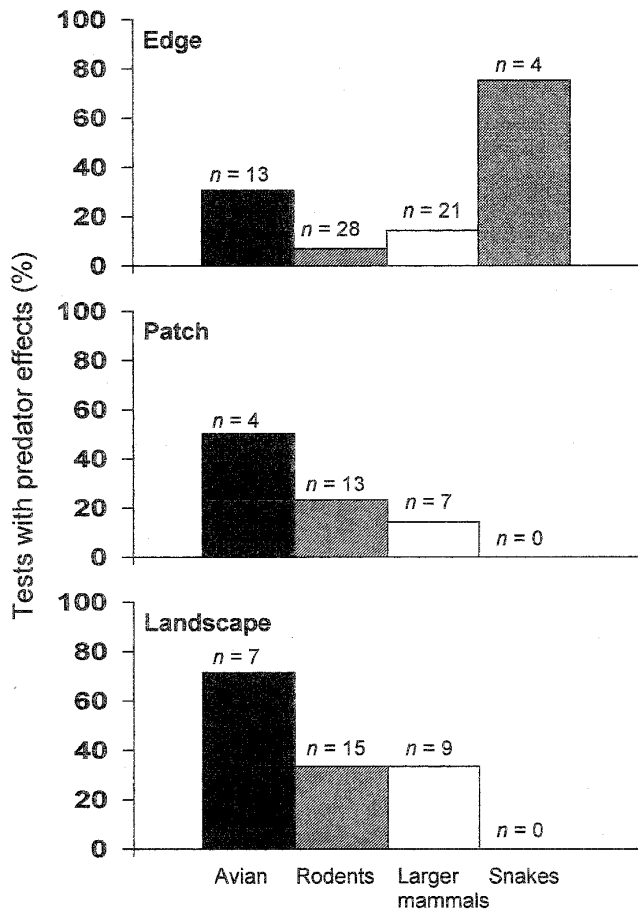


Figure 1. Percentage of tests in which nest-predator taxa (avian, rodents, medium and large mammals, and snakes) were more abundant, more active, or more species-rich in edges (edge), small patches (patch), or certain landscapes (landscape). Sample sizes (number of tests) are shown above columns.

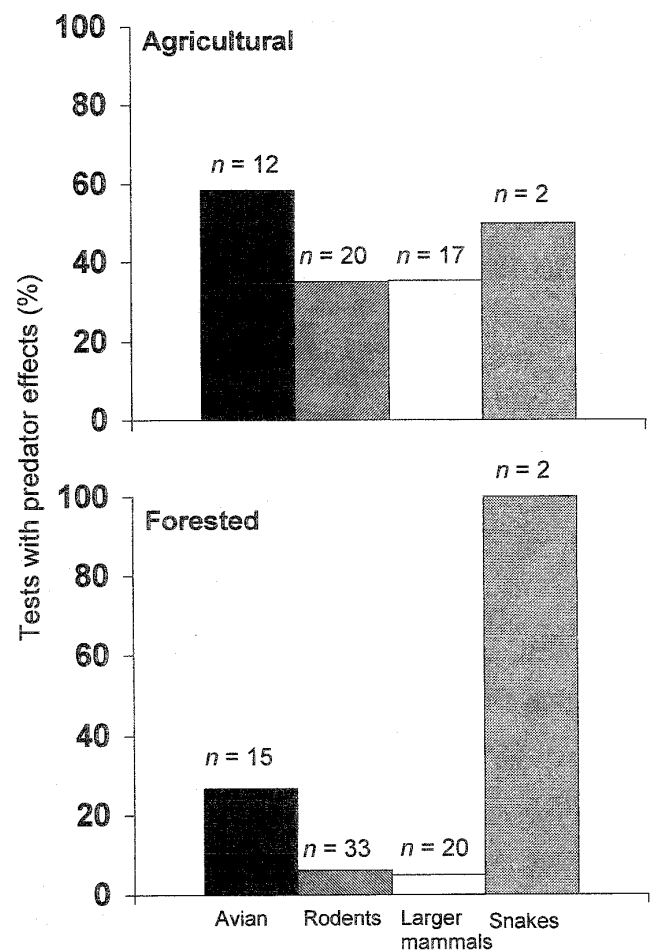


Figure 2. Percentage of tests in which nest-predator taxa (avian, rodents, medium and large mammals and snakes) were more abundant, more active, or more species-rich in edges, small patches, or certain landscapes within agricultural versus predominantly forested landscapes. Sample sizes (number of tests) are shown above columns.

independent of landscape type ($\chi^2 = 9.069$, $df = 1$, $p = 0.003$). Local-scale effects were measured in only two landscape types, agricultural and forested. Positive local-scale effects occurred at a frequency of 33.3% when studies took place in an agricultural landscape but at only 8.3% when studies were conducted in mostly forested landscapes.

Discussion

Our current understanding of the effects of fragmentation on nest predators is limited. Despite numerous cited hypotheses about nest predators and fragmentation in the literature, most remain poorly tested. We found many instances in which authors discussed predator hypotheses and cited studies (e.g., Bider 1968) that lacked direct tests on predators, lacked replication, and/or did not report results of statistical tests (but we did not enumerate these).

Results of tests on predators and fragmentation have been inconsistent. For example, many predator species exhibited contrasting responses to fragmentation across different tests and studies. Moreover, predator tests have been biased toward North America, forested habitats, avian and mammalian species, and numerical responses. Few studies have examined snake response to fragmentation, even though snakes are an important or dominant component of nest-predator assemblages (Thompson et al. 1999). We found no tests of snake abundance or species richness in relation to edge, patch, or landscape. At each spatial scale, tests of rodent species were the most numerous, possibly because small mammals are comparatively easy to capture. We also found no applicable tests of nest predators in urban or suburban landscapes, despite the common perception that human-

inhabited areas may support greater numbers of predators partly because of additional food sources (e.g., Marzluff et al. 1998). In addition, we found no tests of nest-predator species richness in relation to patch size or landscape type.

There were also few studies of predator foraging activity and dispersal with respect to spatial features such as edges. The idea that predators use edges as travel or forage lanes is one of the most commonly cited hypotheses in the literature on avian nest predation versus success, yet few tests have been performed. Moreover, the term "predator activity" is not clearly defined. It may refer, for example, to the amount of physical movement a predator exhibits within an area, and/or the amount of time a predator spends within that area. Many tests of predator activity, moreover, have been confounded. Studies should identify individual animals in order to distinguish a functional response from a numerical one. Of the papers we reviewed, only those using radiotelemetry satisfied this criterion.

Despite the relative dearth of information available on the effects of fragmentation on nest predators, our meta-analysis revealed some interesting patterns. We suggest that predator response varies according to (1) the spatial scale at which measurements are taken, (2) landscape context, (3) geographic region, and (4) predator taxon. Predator effects were most frequently detected in tests at the landscape scale, followed by patch and edge scales, respectively. Our determination that local-scale effects were more variable than landscape effects and that these local effects differed according to the surrounding land-cover type supports the hypothesis by Thompson et al. (2002) that edge and patch effects are constrained by factors at the landscape scale. Our findings also parallel the results of studies examining avian nest-predation rates in relation to edge, which have been inconsistent (Paton 1994) but most prevalent in more fragmented landscapes (Donovan et al. 1997; Hartley & Hunter 1998) and in landscapes fragmented by agriculture (Bayne & Hobson 1997a). Elevated rates of avian nest predation in landscapes fragmented by agriculture (Andr n 1995; Marzluff & Restani 1999) may thus be a direct consequence of increased predator abundance, activity, and/or species richness. Agriculture likely enhances predator populations by providing additional food sources (Andr n 1995; Marzluff et al. 1998; Dijkstra & Thompson 2000). This would explain why predator effects were most prevalent within landscapes fragmented by agriculture, and why local-scale effects specifically were most common when the land surrounding habitat patches was agricultural.

Biogeographic differences in predator response were also evident. In the United States, for example, predator effects were more prevalent in tests conducted in the eastern and midwestern portions of the country than in the western United States. This finding is likely a func-

tion of regional differences in predator communities and land-use practices. Tewksbury et al. (1998) suggest that fragmentation of western forests, for example, may lead to declines of nest-predator species, whereas fragmentation of midwestern forests may conversely augment populations of nest predators (Thompson et al. 2002). The causes behind increased or decreased predator abundance in different landscapes, however, have yet to be quantitatively assessed.

Not all nest predators respond similarly to fragmentation, which might explain much of the variability in nest predation rates across studies (Paton 1994). Avian predators were consistently more likely than mammalian predators to respond in a positive way to fragmentation parameters. Unfortunately, because of the scarcity of tests on snakes, we cannot yet make informed inferences regarding snake responses. Another caveat is that most studies examined only one predator species or guild and extrapolated the results to nest predators in general, which may be misleading because we have shown that the nature of a predator response to fragmentation is taxon-specific.

In addition, several interactions probably occur between different spatial scales, patterns of land cover and use, biogeographic regions, habitat types, and predator species which cumulatively act to make predator response to fragmentation more complex than is commonly portrayed. Regardless of these complexities, however, we suggest that efforts to mitigate nest predation would be most successful if they focused on minimizing (1) the overall extent of fragmentation of habitat at a landscape scale and (2) the interspersed of habitat with land uses that provide additional sustenance for predators.

Because nest predation is an important process affecting the local demography of nesting birds and potentially of avian populations, it is important to understand the factors affecting predation rates. To understand which scenarios pose the greatest risk to nesting birds and to develop conservation strategies to mitigate these, additional studies are needed of the response of nest predators to fragmentation and the relationships among predator abundance, activity, and species richness and rates of nest predation.

In summary, the response of nest-predator species to habitat fragmentation appears to be taxon-specific, and context-dependent. Management efforts geared toward the conservation of declining avian species may therefore need to be customized to the predators primarily responsible for local nest mortality and the nature of the landscape mosaic.

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