

EFFECTS OF FOREST FRAGMENTATION ON BROOD PARASITISM AND NEST PREDATION IN EASTERN AND WESTERN LANDSCAPES

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Abstract. The fragmentation of North American forests by agriculture and other human activities may negatively impact the demographic processes of birds through increases in nest predation and brood parasitism. In fact, the effects of fragmentation on demographic processes are thought to be a major underlying cause of long-term population declines of many bird species. However, much of our understanding of the demographic consequences of fragmentation has come from research conducted in North America east of the Rocky Mountains. Thus, results obtained from these studies may not be applicable to western landscapes, where habitats are often naturally heterogeneous due to topographic variation and periodic fire. We utilized data from a large database of nest records (>10,000) collected at sites both east and west of the Rocky Mountains to determine if the effects of fragmentation are consistent across broad geographic regions. We found that forest fragmentation tended to increase the frequency of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) east of the Rockies but we were unable to detect a significant difference in the West. Within the eastern United States, nest predation rates were consistently higher within fragmented sites relative to unfragmented sites. Yet, in the West, fragmentation resulted in a decrease in nest predation relative to unfragmented sites. This is perhaps accounted for by differential responses of the local predator community to fragmentation. Our results suggest that the effects of fragmentation may not be consistent across broad geographic regions and that the effects of fragmentation may depend on dynamics within local landscapes.

Key Words: brood parasitism; forest fragmentation; nest predation; Western North America.

Forest fragmentation occurs when large, continuous, forested tracts are converted to other vegetation types or land uses so that only a few scattered fragments remain (Faaborg et al. 1995). Fragmentation is a characteristic feature of most human dominated landscapes (Burgess and Sharpe 1981) and is particularly evident in portions of northern Europe and eastern North America (east of the Rocky Mountains) where agricultural production and urban development have reduced once contiguous forests into small, and often isolated patches (Andr n 1992, Donovan et al. 1995b, Robinson et al. 1995a).

For the past several decades considerable attention has been given to the effects of forest fragmentation on avian populations within North America because of widespread population declines (Gates and Gysel 1978, Ambuel and Temple 1983, Wilcove 1985, Askins et al. 1990, Robinson et al. 1995a). The fragmentation of once continuous forests may result in both a quantitative and qualitative loss of habitat for species (Faaborg et al. 1995). Fragmentation can negatively influence avian populations by reducing the total area of native vegetation resulting in the extinction of some species. In addition, as an area is fragmented into increasingly smaller patches, the amount of edge relative to interior area increases. This exposes populations to the conditions of a different surrounding ecosystem and consequently to what are known as "edge effects" (Murcia 1995). Research conducted to date suggests several characteristics of forest

fragments that may negatively affect avian populations. Small forest patches with a high edge to interior ratio have: (1) High rates of nest predation. The abundance of avian and mammalian nest predators (avian and mammalian) often are higher along forest edges than within the forest interior (e.g., Gates and Gysel 1978, Chasko and Gates 1982, Hanski et al. 1996). (2) High rates and intensities of brood parasitism. The Brown-headed Cowbird (*Molothrus ater*) is often more abundant along forest edges, and nests adjacent to edges typically have higher rates of parasitism (Donovan et al. 1995b, Robinson et al. 1995a, Young and Hutto 1999). (3) Reductions in pairing success. Several species within forest fragments and near forest edges have a reduced chance of attracting mates than when in large continuous forests and within the forest interior (Wander 1985, Gibbs and Faaborg 1990, Villard et al. 1993, Burke and Nol 1998). (4) Lower food availability for breeding birds. Burke and Nol (1998) demonstrated that invertebrate biomass was lower within forest fragments than large continuous forests.

These fragmentation effects are thought to be a major underlying influence of long term population declines of many birds, particularly forest-interior species within eastern North America (Whitcomb et al. 1981, Robbins et al. 1989b, Sauer and Droege 1992, Ball et al. 1994). Consequently, many small forest fragments in eastern North America support few if any forest-

interior species (Robbins et al. 1989b, Freemark and Collins 1992).

Concern over avian population declines and the potential demographic consequences to fragmentation have led to numerous studies designed to examine the potential effects of forest fragmentation on avian productivity. Previous studies have suffered from two major problems. First, studies of fragmentation effects have often depended on data from artificial nests, which often do not reflect rates or patterns of predation on real nests (e.g., Major and Kendal 1996). Studies using artificial nests also cannot provide information on the rates and patterns of cowbird parasitism. Second, much of our current understanding of the demographic consequences of fragmentation has come from research conducted east of the Rocky Mountains (George and Dobkin *this volume*). Because most fragmentation studies are conducted over a relatively small geographical area (but see Donovan et al. 1995b, Robinson et al. 1995a), often with no replication, the results cannot be generalized to other locations or regions. The effects of forest fragmentation within eastern North America may not automatically be applied to the West for several reasons. Unlike once contiguous eastern forests, forests west of the Rocky Mountains have a naturally heterogeneous pattern due to topographic variation, periodic fire, flooding and other climatic events (Franklin et al. *this volume*, Hejl et al. *this volume*). Thus, human induced fragmentation in the West (e.g., logging) may not have yet created sufficiently different landscape patterns to affect avian populations (Hejl 1992, Freemark et al. 1995, Hejl et al. *this volume*). Unlike fragmentation in eastern North America, fragmentation in the West is a relatively recent phenomenon and thus there may not have been sufficient time for birds to respond (Rosenberg and Raphael 1986). Additionally, the pattern of nest predation may not be comparable between regions because local predator communities likely differ. Large predators found in western North America, but largely absent in the East, may keep mesopredator populations in check (Soulé 1988, Rogers and Caro 1998). Thus, the effects of fragmentation on avian demographic processes in the East may not apply to western North America.

In this paper, we utilized data from 20 replicated study sites to examine the effects of forest fragmentation on the reproductive success and nest predation rates of a suite of forest nesting species breeding at sites east and west of the Rocky Mountains. We also examined if forest fragmentation affects the frequency (number of nests parasitized) and intensity (number of parasite eggs laid per nest) of brood parasitism dif-

ferently in eastern versus western sites. Finally, we review the available literature on the effects of fragmentation on nest predation by geographic region (east vs. west).

METHODS

We used nesting data from 10,446 nests (103,855 days of exposure) of 23 species of open nesting passerines (Table 1). The data used in these analyses come from the Breeding Biology Research and Monitoring Database, a collaborative effort in which researchers monitor avian breeding productivity and habitat conditions using standardized sampling protocols (Martin et al. 1997) at sites located throughout the continental U.S. Data were utilized from 20 study sites located east and west of the Rocky Mountains (Fig. 1). Examination of Figure 1 illustrates that sites were not evenly distributed across North America and include a grouping centered along the Mississippi River and a grouping along the western side of the Rocky Mountains. For simplicity we refer to sites east of the Rocky Mountains as eastern sites and those along the western side of the Rockies as western sites. Each site utilized was replicated and composed of 4 to 30 separate study plots. Sites were chosen from the database for this analysis if the principal investigator designated them as either largely fragmented by human activities (agriculture or logging), or unfragmented. Because our classification of sites is subjective, we also calculated the proportion of forest within a 10-km radius of each study plot from a GIS layer produced by the USDA Forest Service covering the entire United States. A 10-km radius was chosen because this area relates well to distances most cowbirds commute between breeding and feeding areas (Thompson 1994, Thompson and Dijak 2000), and previous studies have used this area as a simple measure of forest fragmentation (Robinson et al. 1995a, Donovan et al. 1995b, Hochachka et al. 1999, Thompson et al. *this volume*). Forest coverage was calculated using FRAGSTATS (McGarigal and Marks 1995).

Three unfragmented sites in the east and three in the west were paired with a nearby fragmented site to examine local landscape-level effects of fragmentation on daily mortality rates (Table 2). Species were chosen for the analysis if they satisfied all three of the following criteria: (1) they are open nesting passerines that primarily nest in forest habitats, (2) the total number of nests available for each species was greater than 50, and (3) the species were recorded breeding at more than one site. All statistical analyses were conducted using PC-SAS (SAS Institute 1998). Tests were parametric unless transformations of the data could not meet assumptions of normality and homogeneous variances. Results from statistical tests are referred to as significant when $P \leq 0.05$. Values reported in the RESULTS section are means \pm SE.

REPRODUCTIVE SUCCESS

We examined the effects of fragmentation on components of reproductive success by performing paired t-tests on mean clutch size and mean number of offspring fledged per nest, blocking by species and testing for habitat differences. Because cowbirds often remove host eggs before parasitizing nests (Nolan 1978), we

TABLE 1. FOCAL SPECIES USED IN ANALYSES

Common name	Scientific name	Nest placement	Number of nests
Eastern Wood-pewee	<i>Contopus virens</i>	Tree	169
Western Wood-pewee	<i>Contopus sordidulus</i>	Tree	264
Acadian Flycatcher	<i>Empidonax virescens</i>	Tree	1624
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Shrub	210
Wood Thrush	<i>Hylocichla mustelina</i>	Shrub	814
Swainson's Thrush	<i>Catharus ustulatus</i>	Shrub	162
Veery	<i>Catharus fuscescens</i>	Shrub	100
American Robin	<i>Turdus migratorius</i>	Shrub	1461
Cedar Waxwing	<i>Bombycilla cedrorum</i>	Tree	163
Warbling Vireo	<i>Vireo gilvus</i>	Tree	468
Red-eyed Vireo	<i>Vireo olivaceus</i>	Shrub	673
Yellow Warbler	<i>Dendroica petechia</i>	Tree	1276
Kentucky Warbler	<i>Oporornis formosus</i>	Ground	115
Hooded Warbler	<i>Wilsonia citrina</i>	Shrub	363
Worm-eating Warbler	<i>Helmitheros vermivorus</i>	Ground	286
Ovenbird	<i>Seiurus aurocapillus</i>	Ground	411
American Redstart	<i>Setophaga ruticilla</i>	Tree	335
Northern Cardinal	<i>Cardinalis cardinalis</i>	Shrub	307
Indigo Bunting	<i>Passerina cyanea</i>	Shrub	492
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Tree	180
Song Sparrow	<i>Melospiza melodia</i>	Shrub	218
Northern Oriole	<i>Icterus galbula</i>	Tree	65
Western Tanager	<i>Piranga ludoviciana</i>	Tree	291

included only unparasitized nests in the analysis of clutch size.

BROOD PARASITISM

The frequency of brood parasitism was calculated by determining the number of nests containing cowbird eggs or young for a species within each study site. We calculated parasitism frequency for a species only when evidence of cowbird parasitism could be found within the database. The intensity of cowbird parasitism was calculated by determining the mean number of cowbird eggs laid within each species' nest, within each study site. Each species was classified according to nest placement as either a ground, shrub, or tree nester (Table 1) to determine if nest placement affected a species' response to forest fragmentation. The classification of nest placement was based on Ehrlich et al. (1988) and Baicich and Harrison (1997). Differences in the frequency of cowbird parasitism between fragmented and unfragmented sites were examined using Friedman's nonparametric analysis of variance (ANOVA) for randomized blocks (Sokal and Rohlf 1981) and differences in intensity of cowbird parasitism were examined by using parametric ANOVAs. For each analysis we blocked by species and tested for habitat affects. Nonparametric Wilcoxon 2-sample tests (Sokal and Rohlf 1981) were performed on the arcsine transformed proportion of nests parasitized for each nesting classification to determine if nest placement affected a species' response to fragmentation.

NEST PREDATION

The daily mortality rate of nests and their associated standard errors were estimated using the Mayfield (1961, 1975) method as modified by Johnson (1979) and Hensler and Nichols (1981). We calculated the dai-

ly mortality rate for nests of each species as the total number of failures divided by the total number of days nests were observed, pooled across all nests within each study site. Differences in daily mortality rates between fragmented and unfragmented sites were examined using analysis of variance blocking by species and testing for habitat affects. We also partitioned daily mortality rates into cause-specific components (predation and parasitism) to determine the mechanisms that may influence reproductive success in fragmented versus contiguous sites. As in the parasitism analyses, we classified each species according to its nest placement. Differences in predation rates between paired fragmented and unfragmented sites were examined using the program CONTRAST (Hines and Sauer 1989). This program uses chi-square statistics to test for homogeneity of mortality rates by creating a linear contrast of the rate estimate (Sauer and Williams 1989).

LITERATURE REVIEW

We also reviewed the available literature to summarize the effects of forest fragmentation and edge effects on nest predation rates between sites east and west of the Rocky Mountains. We limited our review to studies conducted in forested systems and to those that examined the effects of anthropogenic fragmentation (e.g., agriculture and forestry practices). Because most nest predation studies have used artificial nests, we have included them in our review, but recognize that there are inherent weaknesses in their use (Haskell 1995a, Ortega et al. 1998).

RESULTS

Sites classified by investigators as fragmented had significantly lower proportion of forest cov-

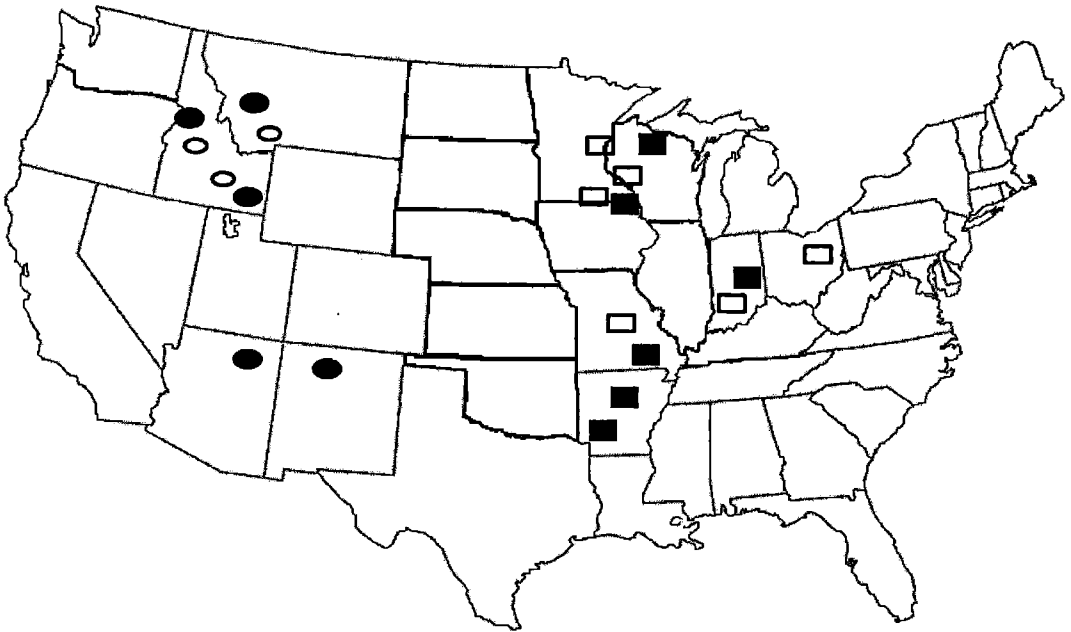


FIGURE 1. Locations of study sites used in analyses. Squares indicate sites designated as "eastern" and circles as "western." Open symbols indicate fragmented sites and closed unfragmented. Each site plotted on the map is composed of several independent study plots.

er within a 10 km radius (0.45 ± 0.10) relative to unfragmented sites (0.90 ± 0.04 , $t = -4.199$, $df = 6.2$, $P = 0.005$).

REPRODUCTIVE SUCCESS

We found no difference in clutch size of unparasitized nests between fragmented and unfragmented sites (East -0.01 ± 0.10 , $t = -0.091$, $df = 1$, $P = 0.930$; West 0.10 ± 0.07 , $t = 1.46$, $df = 1$, $P = 0.194$). Yet, the mean number of offspring fledged per nest attempted was significantly greater in unfragmented relative to fragmented sites in the east (-0.23 ± 0.08 , $t = -2.72$, $df = 1$, $P = 0.02$), but we found

no difference between fragmented and unfragmented sites west of the Rocky Mountains (0.09 ± 0.08 , $t = 1.06$, $df = 1$, $P = 0.314$).

BROOD PARASITISM

The frequency of parasitism by Brown-headed Cowbirds was significantly higher in eastern fragmented sites relative to unfragmented sites ($\chi^2 = 317.34$, $df = 1$, $P < 0.001$) but there were no significant differences among western sites ($\chi^2 = 2.29$, $df = 1$, $P > 0.1$; Fig. 2). In addition, fragmentation resulted in a significantly higher frequency of brood parasitism for all eastern

TABLE 2. LOCATIONS OF PAIRED FRAGMENTED AND UNFRAGMENTED SITES

Site	Landscape	Latitude-longitude	Location
Columbia	Frag	38.95-92.11	Columbia, MO
Mofep	Unfrag	37.04-91.12	Ozarks, MO
SE Forest 1	Frag	43.61-91.25	Southeastern MN
SE Forest 2	Unfrag	43.61-91.25	Southeastern MN
St. Croix	Frag	45.36-82.72	Eastern MN, Western WI
Cheque. NF	Unfrag	46.06-91.11	Chequamegon NF, WI
Bitterroot 1	Frag	46.10-114.23	Bitterroot Valley, MT
Bitterroot 2	Unfrag	46.10-114.23	Bitterroot Valley, MT
South Fork 1	Frag	43.62-111.63	South Fork of Snake River, ID
South Fork 2	Unfrag	43.62-111.63	South Fork of Snake River, ID
PNFF	Frag	44.67-116.20	Payette National Forest, ID
PNFU	Unfrag	44.67-116.20	Payette National Forest, ID

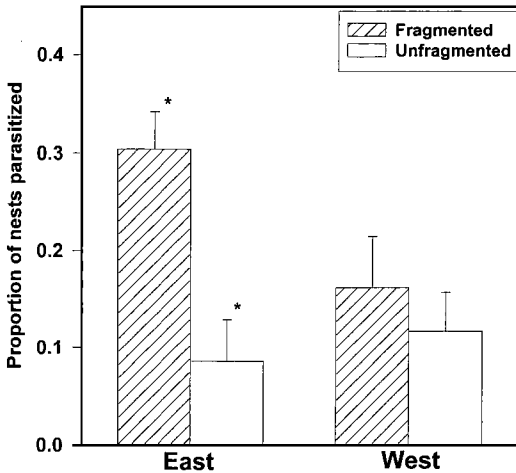


FIGURE 2. Mean frequency of brood parasitism (\pm SE) by Brown-headed Cowbirds in fragmented and unfragmented eastern and western sites. A * indicates $P < 0.05$.

nest placement classifications, but no differences were found among western sites (Table 3).

The intensity of brood parasitism was not affected by forest fragmentation east ($F = 0.07$, $df = 1, 10$, $P = 0.80$) or west ($F = 0.14$, $df = 1, 2$, $P = 0.75$) of the Rockies. Within nest place-

ment classifications, shrub nesters at fragmented western sites had a significantly higher intensity of cowbird parasitism relative to unfragmented sites (Table 3). There were no other differences in parasitism intensity by nest placement classification (Table 3).

DAILY MORTALITY

Eastern fragmented sites tended to have higher daily mortality rates than unfragmented sites ($F = 3.03$, $df = 1, 47$, $P = 0.08$) but the difference was not significant (Fig. 3). However, western unfragmented sites had significantly higher daily mortality rates relative to fragmented sites ($F = 3.87$, $df = 1, 30$, $P = 0.05$; Fig. 3). Eastern shrub nesting birds suffered significantly higher daily mortality rates on fragmented than on unfragmented sites, but no other differences by nest placement classification were observed (Table 3).

The daily mortality rate due to nest predation was not significantly different between eastern fragmented (0.031 ± 0.002) and unfragmented sites (0.030 ± 0.003 ; $F = 0.10$, $df = 1, 31$, $P = 0.76$), but was significantly higher in western unfragmented sites (0.038 ± 0.003 ; $F = 4.04$, $df = 1, 30$, $P = 0.05$) relative to fragmented locations (0.029 ± 0.003). The daily mortality rate due to parasitism was significantly greater in

TABLE 3. EFFECTS OF HABITAT FRAGMENTATION ON THE FREQUENCY (PERCENTAGE OF NESTS) AND INTENSITY (NUMBER OF EGGS) OF BROWN-HEADED COWBIRD PARASITISM AND DAILY MORTALITY RATES WITHIN NEST PLACEMENT CLASSIFICATIONS FOR SITES EAST AND WEST OF THE ROCKY MOUNTAINS

	Region	Nest placement	Statistics	Fragmented	Unfragmented
				Median, Upper-Lower Quartiles	Median, Upper-Lower Quartiles
Frequency of Cowbird Parasitism					
			Z, df, P		
	East	Ground	2.33, 1, 0.02	28.5, 50.0–20.2	2.0, 13.3–0.9
		Shrub	2.01, 1, 0.05	30.1, 62.7–26.5	6.4, 34.8–0.0
		Tree	1.94, 1, 0.05	9.6, 17.0–8.0	1.6, 5.6–0.07
	West	Shrub	0.44, 1, 0.66	35.3, 52.6–0.0	3.1, 19.0–1.4
		Tree	0.0, 1, 1.00	8.6, 21.1–0.0	1.8, 32.0–0.0
Intensity of Cowbird Parasitism					
			F, $df_{\text{model error}}$, P	Mean \pm SE	Mean \pm SE
	East	Ground	1.16, 1, 1, 0.48	1.7 \pm 0.4	1.0 \pm 0.5
		Shrub	1.25, 1, 6, 0.31	1.7 \pm 0.2	1.4 \pm 0.3
		Tree	1.07, 1, 2, 0.41	1.1 \pm 0.05	1.0 \pm 0.1
	West	Shrub	21.36, 1, 2, 0.04	1.6 \pm 0.06	1.2 \pm 0.06
		Tree	2.2, 1, 2, 0.27	1.2 \pm 0.08	1.4 \pm 0.08
Daily Mortality Rate					
			Z, df, P	Median, Upper-Lower Quartiles	Median, Upper-Lower Quartiles
	East	Ground	1.3, 1, 0.20	0.4, 0.06–0.04	0.03, 0.05–0.03
		Shrub	–2.1, 1, 0.04	0.043, 0.05–0.04	0.037, 0.04–0.03
		Tree	0.14, 1, 0.89	0.039, 0.04–0.03	0.034, 0.04–0.03
	West	Shrub	0, 1, 1.0	0.041, 0.04–0.03	0.04, 0.06–0.03
		Tree	–0.3, 1, 0.77	0.031, 0.04–0.03	0.037, 0.06–0.03

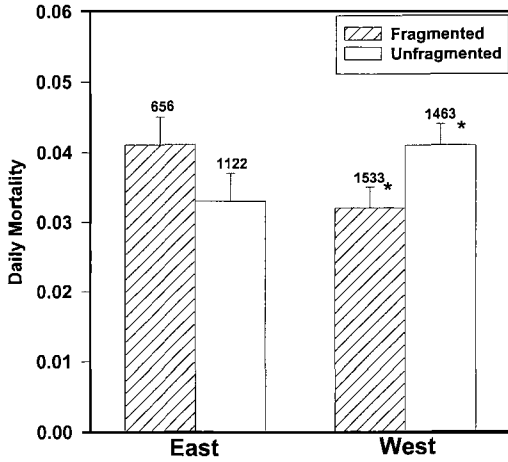


FIGURE 3. Mean daily mortality rate (\pm SE) of nests in fragmented and unfragmented eastern and western sites. The total number of nests used in analyses are given above each bar. A * indicates $P < 0.05$.

eastern fragmented sites ($\chi^2 = 29.04$, $df = 1$, $P < 0.001$; median, upper–lower quartiles of fragmented sites 0.005, 0.01–0; unfragmented sites 0, 0.003–0) but not among western sites ($\chi^2 = 0.278$, $df = 1$, $P > 0.5$).

In two of the three paired eastern sites, daily mortality rates were significantly higher on fragmented relative to unfragmented plots (Fig. 4). This pattern was reversed in the west where two of the three paired sites had significantly higher daily mortality rates on unfragmented plots relative to fragmented ones.

LITERATURE REVIEW

Our review consisted of 39 studies; the vast majority (33) were located east of the Rockies, with only six studies in the West (Table 4). The results of eastern studies were based on 53 field seasons with a mean duration of 1.6 field seasons per study. Western studies were based on only 11 field seasons with a mean of 1.8 field seasons per study. Of the studies that have tested for edge effects, 56% of 16 studies detected an effect in the East, whereas only one of four studies observed an edge effect in the West. Eastern studies that examined the effect of fragmentation on nest predation rates typically found negative relationships. A negative relationship between fragmentation and nest predation was found in 68% of 19 studies, no relationship in 21%, and two studies (~10%) reported a positive relationship. Only three western studies reviewed tested for fragmentation effects; two of three studies found a positive relationship between nest predation rates and fragment size with the third demonstrating no relationship.

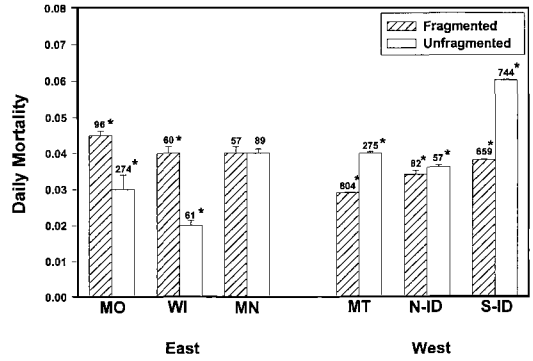


FIGURE 4. Comparison of fragmentation effects on the daily mortality rates (\pm SE) of paired local sites east and west of the Rocky Mountains. The number of nest records utilized in each comparison is indicated above each bar. A * indicates $P < 0.001$; other comparison $P > 0.05$.

It has been suggested that forest fragments embedded in different matrices may differentially affect patterns of nest predation (Andr n 1995, Bayne and Hobson 1997). According to the “Eastern Paradigm,” birds nesting in forest patches imbedded in an agriculture or urban/suburban matrix are expected to have lower reproductive success relative to those nesting in more natural settings (Thompson et al. *this volume*). Thus, we classified studies according to the matrix of the surrounding landscape (e.g., agriculture and forest dominated). Six studies in the East tested for edge effects within an agriculturally dominated matrix and nine within a forested matrix. Five of the six forest-agricultural edge studies demonstrated an increase in nest predation, whereas only four of eight found edge effects within a forested matrix. We were unable to review any western studies that tested for edge effects within an agricultural matrix. Brand and George (2000), however, compared predation rates on artificial nests between sites with different types of adjoining habitat. In contrast to predictions of the “Eastern Paradigm,” Brand and George (2000) found predation rates were lower in patches adjacent to urban/suburban areas than those adjacent to natural grasslands. Three of four western studies within forest-dominated landscapes failed to demonstrate an edge effect.

Ten of the eastern studies reviewed tested for fragmentation effects within an agricultural matrix. Two of ten found no relationship between forest area and nest predation rates but the remaining eight reported significant and negative relationships. The results of eastern studies conducted within a logging matrix are not as apparent; of the nine studies reviewed, five report-

TABLE 4. SUMMARY OF STUDIES EXAMINING THE EFFECTS OF EDGE AND FOREST FRAGMENTATION ON NEST PREDATION RATES EAST AND WEST OF THE ROCKY MOUNTAINS

Reference	Location	Nest type ^a	Matrix	Duration of study ^b	Edge effect	Fragmentation effect ^c
Eastern Studies						
Bayne and Hobson 1997	SK	A	Agriculture	2	no	
Burger 1988	MO	A	Agriculture	1	yes	
Donovan et al. 1995	Midwest	R	Agriculture	3		–
Donovan et al. 1997	Midwest	A	Agriculture	1		–
Fauth 2000	IN	R	Agriculture	3	no	0
Gates and Gysel 1978	MI	R	Agriculture	2	yes	
Haskell 1995	NY	A	Agriculture	1		0
Hobson and Baynes 2000	SK	R	Agriculture	4		–
Hoover et al. 1995	PA	R	Agriculture	2		–
Linder and Bollinger 1995	IL	A	Agriculture	1	yes	
Marini et al. 1995	IL	A	Agriculture	1	yes	
Robinson et al. 1995	Midwest	R	Agriculture	5		–
Saracco and Callazo 1999	NC	A	Agriculture	1	yes	
Sargent et al. 1998	SC	A	Agriculture	1		–
Seitz and Zegers 1993	PA	A	Agriculture	1		–
Weinberg and Roth 1998	DE	R	Agriculture	2		–
Wilcove 1985	MD, TN	A	Agriculture	1		–
Bayne and Hobson 1997	SK	A	Forested	2	no	
DeGraaf and Angelstam 1993	NH	A	Forested	1		0
Fenske-Crawford and Niemi 1999	MN	A	Forested	1	no	
Gale et al. 1997	CT	R	Forested	2		0
Hanski et al. 1996	MN	R	Forested	1	no	
King et al. 1996	NH	R	Forested	2	yes	
King et al. 1998	NH	A	Forested	1	yes	
Niemuth and Boyce 1997	WI	A	Forested	2	yes	
Rudnicki and Hunter 1993	ME	A	Forested	2	no	0, +
Small and Hunter 1988	ME	A	Forested	1	no	–
Vander Haegen and DeGraaf 1996	ME	A	Forested	1	yes	–
Vander Haegen and DeGraaf 1996	ME	A	Forested	1		+
Yahner and Mahan 1996	PA	A	Forested	1		–
Yahner and Scott 1988	PA	A	Forested	1		–
Yahner and Wright 1985	PA	A	Forested	1	no	
Keyser et al. 1998	AL	A	Residential	1		–
Western Studies						
Hannon and Cotterill 1998	AB	A	Agriculture	2		0, +
Tewksbury et al. 1998	MT	R	Agriculture	2		+
Brand and George 2000	CA	A	Forested	1	yes	
Cotterill and Hannon 1999	AB	A	Forested	3	no	0
Ratti and Reese 1988	ID	A	Forested	1	no	
Song and Hannon 1999	AB	A	Forested	2	no	

^a R = study monitoring the effect on real nests, A = study monitoring effect on artificial nests.

^b Number of field seasons on which results are based.

^c This column indicates the direction of the relationship between forest area and nest predation rates. A "0" indicates no relationship, a "–" indicates a negative relationship and a "+" indicates a positive relationship. Studies with more than one symbol represent annual variation in response.

ed negative relationships between forest area and nest predation rate, two reported a positive relationship, and two reported no relationship. Only two western studies reviewed tested for fragmentation effects within an agricultural matrix, and both of these studies found a positive relationship between nest predation rates and fragment size.

DISCUSSION

We found that the patterns of brood parasitism were not consistent between sites east and west

of the Rocky Mountains. The frequency of brood parasitism was significantly higher in eastern fragmented sites relative to unfragmented sites, but not in the West. In addition, all nest placement classifications within fragmented eastern sites had a higher frequency of parasitism relative to unfragmented sites, but we were unable to detect a difference in the West. It appears this differential response may, in part, be due to greater variation in the frequency of parasitism among western sites. For example, some fragmented western sites reported no cowbird

parasitism for shrub and tree nesting species and others reported rates as high as 52%, a rate comparable to the most severely affected eastern fragmented sites. This higher variability among western sites in their response to brood parasitism may be attributed to lower cowbird abundance in the West as compared to the East (Sauer et al. 2000). Morrison and Hahn (*this volume*), in an extensive review of the literature, did not find evidence to suggest that cowbird parasitism varied by region. Rather, they suggest that the major factors determining the impacts of cowbirds on their hosts operate continent-wide. The frequency and intensity of cowbird parasitism may be difficult to predict across large geographic regions and may depend primarily on local factors such as the presence of agriculture and patch size (Hahn and Hatfield 1995, Hochachka et al. 1999, Morrison and Hahn *this volume*).

It is clear from this study that the effects of forest fragmentation on nest predation rates are not necessarily consistent across the continent. We found that eastern fragmented sites had fewer offspring fledged per nest attempted, and tended to have higher daily mortality rates relative to unfragmented sites. These results are in agreement with the "Eastern Paradigm" (e.g., Thompson et al. *this volume*). In contrast, western unfragmented sites had significantly higher daily mortality rates due to nest predation relative to fragmented ones. Paired sites east and west of the Rockies also tended to follow this same general pattern, higher daily mortality rates in fragmented eastern sites and unfragmented western sites (see Fig. 4).

Studies reviewed for this paper also suggest that forest fragmentation may not be generalized between sites east and west of the Rockies. Eastern studies typically reported a negative relationship between forest area and nest predation rates (68%). This generality is improved when only studies conducted within an agricultural matrix are examined (80%). Unfortunately, only two western studies could be located, and thus any conclusions regarding the effects of fragmentation on nest predation in the West are speculative. However, both of these studies reported a positive relationship between forest area and nest predation rates and both studies explained their results on the basis of a differential response of nest predators. Tewksbury et al. (1998) demonstrated that nest predation was higher on unfragmented sites relative to sites fragmented by agriculture and human development within the Bitterroot Valley of Montana. They suggested this pattern was due to the re-

sponse of nest predators to fragmentation. Red squirrels (*Tamiasciurus hudsonicus*), important nest predators in their system, were more abundant in forested landscapes and declined with increasing forest cover (but see Bayne and Hobson 2000). Similarly, an artificial nest study conducted in woodlots surrounding agricultural land in Alberta, Canada, found higher rates of nest predation within larger woodlots during one breeding season and no difference during another (Hannon and Cotterill 1998). They suggested that forest interior predators, such as small mammals, were important in driving this response.

Any attempt to uncover patterns associated with nest predation is difficult because predation is an inherently complex phenomenon. Each study site will have a particular suite of reptilian, mammalian, and avian predators (e.g., Miller and Knight 1993, Fenske-Crawford and Niemi 1997, Thompson et al. 1999; Cavitt 1999, 2000) and these predators will either take nests incidentally (Vickery et al. 1992) or deliberately forage for nests (Sonerud and Fjeld 1987). Furthermore, this suite of nest predators will vary from site to site across North America and will likely respond to fragmentation differently (Bayne and Hobson 1998, 2000).

Unfortunately, few studies have been conducted within the western U.S. that examine the effects of forest fragmentation on nest predation rates. Our analyses and literature review are based on only a handful of western sites in comparison to the numerous studies conducted in the East. Consequently, we are not certain of the generality of our results throughout the West. However, these results do suggest that (1) sufficient evidence exists to question the application of patterns observed in the eastern U.S. across broad geographic regions, (2) more studies on the effects of fragmentation are needed throughout the western U.S., particularly studies that simultaneously monitor both the fates of real nests and the response of the predator communities, and (3) long-term studies are needed to separate real effects from stochastic processes.

ACKNOWLEDGMENTS

The results presented here are the products of an extensive list of investigators and their field assistants. Without their collective efforts and generous contributions of data to the BBIRD (Breeding Biology Research and Monitoring Database) project this research would not have been possible. We also wish to thank T. L. George, D. Dobkin, and an anonymous reviewer for comments and suggestions on drafts of this manuscript, and N. Summers for editorial assistance. This research was supported by the BBIRD program under the Global Change Research Program of the USGS Biological Resources Division.