

Wood Thrush *Hylocichla mustelina*

Draft: 29 May 2003

EXECUTIVE SUMMARY

Preferred breeding habitat: A wide variety of deciduous and mixed deciduous/coniferous forests, especially mid-successional, upland, mesic ones, typically with a tall canopy, well-shaded and well-developed understory shrub layer, and a fairly open forest floor with moist, decaying leaf litter

Nest placement: In a crotch or saddled over the fork of a horizontal branch of a tree or shrub, at an average height of 2.5-4.0 m.

Mean clutch size and fledging brood size (\pm SD):

- Non-parasitized nests: clutch 3.38 ± 0.72 ; brood 3.08 ± 0.91
- Cowbird parasitized nests: clutch 3.04 ± 0.96 ; brood 1.81 ± 1.28

Number of broods per season: Two, rarely three.

Annual adult survival rates: Male 66%, female 65%

Requirements for population stability ($\lambda \geq 1$):

- Fledge at least 2.2 own young per female per year
- Daily nest mortality $\leq 5.5\%$ ($\geq 22\%$ nest success) assuming zero parasitism
- Daily nest mortality $\leq 4.3\%$ ($\geq 31\%$ nest success) with 20% nest parasitism
- Daily nest mortality $\leq 3.5\%$ ($\geq 38\%$ nest success) with 40% nest parasitism
- Generally $\leq 35\%$ nest parasitism across BBIRD sites
- Percent forest cover $\geq 80\%$ within a 10 km radius

Nest mortality and parasitism rates in relation to landscape context:

- Daily nest predation rate 0.6-2.4% in contiguous forest, but 2.2-5.9% in forests fragmented by agriculture or logging.
- Daily nest predation rate 1-5% in large (generally >100 ha) forest fragments, but 3-6.2% in small (generally <100 ha) forest fragments.
- Nest parasitism rate 0-20% when percent forest cover within a 10 km radius $>60\%$, but 20-80% when forest cover within 10 km radius $<60\%$.

The importance of spatial scale to the relationship between nesting success and landscape context:

- Nest predation rate is most strongly correlated with the degree of forest fragmentation at local landscape scales (within 1-10 km radii), with patch-scale edge effects being less important.
- Nest parasitism rate is little influenced by local edge effects, but is strongly correlated with local and broader landscape-level fragmentation indices (within 5-100 km radii), suggesting that local edge effects are strongly constrained by landscape-level effects of fragmentation, within a 100 km radius especially.

General conclusions:

- Nest parasitism has a severe effect on breeding productivity, reducing host fledging success by an average of 41% among parasitized nests.
- Nest parasitism rate is most strongly determined by the degree of forest fragmentation at landscape scales (within 5-100 km radii).

- Nest predation rate is most strongly determined by the degree of forest fragmentation at local landscape scales (within 1-10 km radii).
- Lambda is negatively correlated with degree of forest fragmentation across multiple scales, but particularly local landscape scales of within a 5-10 km radius.

Management guidelines:

- Wood Thrush breeding densities and nest predation rates are generally unaffected by group and single-tree selective logging, and small patch clear cuts. Although densities are reduced in large clear-cuts in the short term, they generally recover within ten years. Given the Wood Thrush's preference for mid-successional habitats over much of its range, or at least a mosaic of mature and early- to mid-successional habitats, these types of silviculture could enhance habitat quality for this species. Further research is, however, necessary to determine whether such silvicultural practices will facilitate the penetration of forest by cowbirds, and thus elevate nest parasitism rates. In some areas, such as the central Appalachians, where the Wood Thrush exhibits a dependence on closed-canopy cover conditions, single-tree selection and thinning understory trees that compete for root space would create favorable conditions for this species, but any intermediate or harvest cutting that opens the canopy would probably decrease populations (Crawford et al. 1981). Prescribed burning has little effect on breeding densities, but heavy understory cutting and border-edge cutting may reduce densities substantially.
- In large tracts of mature, deciduous forest, a mosaic of early and mid-successional forest stands, along with the protection of mature riparian forest, will become necessary to accommodate both the breeding and post-dispersal habitat requirements of Wood Thrushes, given that such habitats may be important for the survival of juveniles during the critical early period of independence (Anders et al. 1998, Vega-Rivera et al. 1998), and for adults during their molting phase (Vega-Rivera et al. 1999). Furthermore, the creation of a dynamic habitat mosaic that includes mid-successional habitats may be necessary to prevent substantial Wood Thrush population declines as forest matures to old-growth forest (Holmes & Sherry 2001). Although natural disturbances, such as fire and wind, have the potential to create such a mosaic, the process should be facilitated by silvicultural practices that create a mosaic of mature and early- to mid-successional habitats, such as selective logging and small clear-cuts. However, such management decisions should take into account the tradeoffs between creating early successional habitats, on the one hand, and reducing the extent of undisturbed, mature-forest habitat for forest-interior specialists, and possibly increasing parasitism risks, on the other hand.
- Given the severe effect of cowbird parasitism on Wood Thrush breeding productivity, any management efforts that reduce cowbird abundance both locally and in the broader landscape (within up to a 15 km radius) will benefit thrush populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Wood Thrush breeding habitat by minimizing (1) the extent of agriculture and development (particularly human dwellings) within or adjoining forests (not always feasible); (2) the extent of short grass openings, such as along road verges, utility corridors and around

- human dwellings; and (3) the presence of livestock within or adjoining forests. Where possible, logging roads should be narrow enough that they do not break the canopy, or closed and re-vegetated as soon as possible. Campgrounds should be managed to minimize extensive areas of grass, and garbage should be removed quickly to avoid attracting and subsidizing potential nest predators such as raccoons, opossums and corvids (Robinson & Wilcove 1994).
- In regions where the Wood Thrush is a conservation concern, a broad-scale planning objective should be to maintain or improve the integrity (by minimizing the amount of agricultural land, particularly livestock grazing lands, within forested areas) of the larger forest tracts within the region to ensure that percent forest cover within a 10 km radius of focal forest tracts is maintained above 80%. Where possible, forest preserves should be at least 10,000 ha in extent, to reduce the impact of cowbird parasitism (Robinson & Wilcove 1994), particularly in landscapes with a high degree of fragmentation at the broad scale (within 50-100 km radius), such as the Midwest.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

A Neotropical migrant, the Wood Thrush occupies breeding grounds throughout most of the eastern United States and extreme south-eastern Canada, and wintering grounds from south-eastern Mexico to Panama (Roth et al. 1996).

Within their breeding range, Wood Thrushes inhabit the interior and edges of a wide variety of deciduous and mixed deciduous/coniferous forests, especially mid-successional, upland, mesic ones (Bond 1957; James et al. 1984; Roth et al. 1996). Forest occupied typically have a tall canopy, a well-shaded and well-developed understory shrub layer that contains at least a few small trees with low, exposed branches for nesting in, and a fairly open forest floor with moist, decaying leaf litter for foraging in. Higher densities tend to be associated with greater canopy height and fewer small trees (James et al. 1984). A strong association with mid-successional forests is given as an explanation for the dramatic decrease in annual breeding densities from 5-10 adults/10 ha to 0-2 adults/10 ha over a 40-year period in a New Hampshire forest maturing from mature second-growth to old-growth forest (Holmes & Sherry 2001).

The habitat requirements of juveniles, which disperse from their natal territory sites to nearby refuge sites until they later leave on migration, appear to differ from those of adults that breed in mature forests. In a study in the Missouri Ozarks, juveniles raised within mature oak-hickory forest dispersed a mean distance of 2.08 km (SD = 1.48 km) to occupy refuge sites that included early successional oak-hickory and pine forests, mid-successional pine forest, mature riparian forest, and forest/field edges (Anders et al. 1998). In northern Virginia, juveniles dispersed an average distance of 1.5 km to occupy second-growth scrub/deciduous sapling sites along forest borders and abandoned farms, gypsy moth damaged deciduous forest, and Virginia pine forest with a heavy deciduous understory (Vega-Rivera et al. 1998). These refuge habitats were characterized by a dense understory and thick ground cover, which may serve to reduce the risk of predation by small forest raptors, the principal predators of juveniles (Anders et al. 1997).

Alternatively, these habitats contain more of the fruiting trees and shrubs used as food sources by juveniles at this time (Anders et al. 1997, Vega-Rivera et al. 1998). Radio-telemetry has also shown that adults may disperse up to 7 km post-breeding, to settle and moult in habitats with a greater density of the understory and in the number of deciduous saplings than breeding sites, where protection from predators is hypothesized to be greater (Vega-Rivera et al. 1999).

Breeding density averaged 2.9 adults/10 ha in mature New Hampshire forest (Holmes & Sherry 2001), averaged 6.1 pairs/10 ha in mature, mixed-oak woodland of southern Ohio (Artman et al. 2001), ranged from 0.15-1.30 pairs/10 ha in Georgia (Powell et al. 2000b), and ranged between 17-30 pairs annually in an isolated, 15 ha forest fragment in suburban Delaware (Roth & Johnson 1993). Although more likely to occur in larger-area forests, the Wood Thrush may often nest in 1 ha fragments and semi-wooded residential areas and parks (Roth et al. 1996). Breeding density was slightly reduced (1.0-1.5 females/ha) in very small fragments (0.2-2.1 ha) compared to a small, 15 ha fragment (1.7-1.8 females/ha; Weinberg & Roth 1998).

Nest site characteristics

In a crotch of the main stem, or saddled over the fork of a horizontal branch of a tree or shrub, with some concealment. The nest is usually sited on a lower limb, occasionally in the leafy parts of the tree or shrub canopy, with the mean nest height 2.2 m (range 1.0-6.5 m) in Pennsylvania (Hoover & Brittingham 1998), 2.5 m in New York state (Hahn & Hatfield 2000), 3.0 m in Smoky Mountains (Simons & Farnsworth 1996), 3.9 m in Arkansas Ozarks (Li 1994), 3.1 m (range 1.2-6.4 m) in southern Ontario (Friesen et al. 1999a) and 4.0 m (range 0.6-22.3 m, but 80% <6 m) in Delaware (Roth et al. 1996). Behavioral rules for nest-site selection are primarily: 1) the site must provide some concealment for the nest; 2) the site should preferably be against or near the main stem; and 3) build the nest in tall (>2 m) shrubs if they are available (Hoover & Brittingham 1998).

BREEDING PRODUCTIVITY

Laying seasons

Earliest and latest nests in the BBIRD database were initiated on 28 April and 23 July respectively. These are in agreement with a laying season of 29 April to 20 July in Georgia (Powell et al. 1999), and 26 April to 1 August in southern Illinois (Trine 2000). Most BBIRD data are derived from latitudes 35-40°N and 40-45°N, with the peak laying season occurring two weeks later at latitudes 40-50°N than at latitudes 30-40°N (Figure 1). The length of the laying season differed little between latitudes (Figure 1), with an average laying season length of 68 days.

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (Brackbill 1958; Roth et al. 1996). The mean clutch size of unparasitised nests is 3.6 in Virginia (Dececco et al. 2000), 3.5 (n = 40) in Arkansas (Li

1994), and 3.3 in Maryland (n = 16; Brackbill 1958), Pennsylvania (n = 111; J. Hoover cited in Trine 2000), Delaware (n = 74; Longcore & Jones 1969) and among nests laid in May in Delaware (n = 327; Roth et al. 1996). BBIRD data indicate a mean clutch size in unparasitised nests of 3.38 (SD = 0.72, n = 1,448). Clutch size decreases markedly with succeeding nest attempts through the season (Brackbill 1958; Longcore & Jones 1969; Roth et al. 1996), averaging 3.7 (n = 150) for first nests, 3.0 (n = 116) for second nests (inclusion of parasitised nests reduces means of first and second nests slightly), 2.8 (n = 48) for third nests, and 2.6 (n = 10) for fourth nests (Roth et al. 1996). The mean incubation period has been reported as 12.7 days (n = 59) in Delaware (Roth et al. 1996), 12.8 days in Maryland (n = 8; Brackbill 1958), 12.9 days (n = 23) in Arkansas (Li 1994) and 13.0 days (SD = 1.4) in Virginia (Dececco et al. 2000), and the nestling period as 11.9 days (n = 34) in Arkansas (Li 1994) and 12.0 days in Virginia (Dececco et al. 2000). BBIRD data indicate a mean incubation period of 12.8 days (range 11-16 days; n = 78) and a mean nestling period of 11.6 days (range 9-14 days; n = 98). Re-nesting intervals are reported as 7 days after nest loss (n = 1; Brackbill 1958), and averaging 10.3 days (n = 4, range 9-12 days; Brackbill 1958), 13.4 days (n = 35, range 7-31 days; Friesen et al. 2000), and 16 days (n = 58; Roth et al. 1996) after successful fledging of first broods. In the calculations of seasonal productivity, we used a 68-day laying season, 27-day nesting period (2-day laying, 13-day incubation, 12-day nestling), and re-nesting intervals of 7 days and 15 days following nest failure and successful fledging respectively.

The estimated annual breeding productivity among BBIRD sites ranged between 1.6 (at a site with 83% parasitism and 60% nest failure) and 3.9 fledglings per female (Table 1). Annual breeding productivity ranged from 1.7-3.8 fledglings/female, averaging 2.6 fledglings/female, over the period 1974-1990 in a 15 ha Delaware forest fragment (Roth & Johnson 1993). At a site in southern Illinois suffering 75-95% parasitism and 50-80% nest failure, seasonal productivity was 0.3-2.1 fledglings/female (n = 60 breeding pairs: Trine 1998). At a site in northern Indiana with 90% parasitism and 58% nest predation, seasonal productivity averaged 1.8 fledglings/female (n = 17 females: Fauth 2000). Our modeled estimates are thus within the range of field estimates of seasonal productivity, suggesting the model exhibits adequate performance.

Assumptions in calculations of finite rate of population increase (λ)

Reported adult survival rates vary widely, partly as a consequence of differences in the rate of breeding dispersal between years. The most detailed data on adult survival rates are derived from a 22-year study of color-banded birds occupying a 15-ha Delaware forest fragment (Roth & Johnson 1993, Roth et al. 1996, Brown & Roth 2002), but the interpretation of even these data vary between publications. Roth & Johnson (1993) report that the site fidelity of breeding adult Wood Thrushes is strongly related to breeding success. Females whose nests fail when breeding in small forest fragments frequently disappear, presumably dispersing to re-nest elsewhere (Roth & Johnson 1993, Friesen et al. 2000). Furthermore, inter-annual return rates are strongly correlated with breeding success the previous season (Roth & Johnson 1993). Among experienced breeders, return rates were 66% (n = 113) and 65% (n = 83) for males and females respectively if they bred successfully the previous season, but 44% (n = 29) and 32% (n = 22) if their breeding was unsuccessful. A similar pattern was noted for first-time

breeders, with return rates of 54% ($n = 69$) and 36% ($n = 93$) for males and females respectively if they bred successfully, but 50% ($n = 36$) and 18% ($n = 34$) if their breeding was unsuccessful (Roth & Johnson 1993). Roth et al. (1996) report that 64% of 3-year resident males ($n = 39$), 71% of 4-year resident males ($n = 28$), 64% of 4-year resident females ($n = 14$), and 75% ($n = 12$) of 5-year resident females returned the next year, although return rates decline after these ages. They suggest that the strong site fidelity by older breeders (on site for 3-5 years) makes their return rate a reasonable estimate of annual survival, suggesting probable annual survival rates of about 70% for males and 75% for females (Roth et al. 1996). Brown & Roth (2002), on the other hand, found that although producing at least one fledgling during the breeding season positively influenced the probability of return for second-year females, the probability of return for other age and sex classes was not influenced by annual success. Furthermore, they suggested that, because only three individuals (of the 794 studied) that disappeared in one year returned to breed in subsequent years, return and survival could be viewed as equivalent, with negligible known error. In this study (Brown & Roth 2002), the average annual return rate was 46.7% for second-year males ($n = 180$), 56.9% for after-second-year males ($n = 195$), 36.0% for second-year females ($n = 225$), and 58.2% for after-second-year females ($n = 194$).

A combined mark-recapture and radio-telemetry study estimated weekly adult survival during the breeding season at 0.989 (Powell et al. 2000a), which extrapolates to 56.3% annual survival. Using radio-telemetry, weekly survival was 1 for males ($n = 68$) and 0.981 for females ($n = 63$), which extrapolates to 61% survival of females through a 6-month breeding season, but 100% survival of males (Powell et al. 2000b). Given that most mortality among Neotropical migrants may occur during migration, with relatively low mortality on the breeding and wintering grounds, the influence of the radio transmitter in these studies may be substantial. Conway et al. (1995) estimated monthly survival of Wood Thrushes on the wintering grounds as 0.9 (SE = 0.027), which extrapolates to annual survival of 28%, but this estimate is likely heavily biased low by the problem of accounting for dispersal in a mark-recapture study.

Most juvenile mortality appears to occur within 5 days of fledging (Powell et al. 2000b; Vega-Rivera et al. 1998), and again immediately after long-distance dispersal from the natal territory to refuge sites around 20 days post-fledging (Powell et al. 2000b). Three studies using radio-telemetry estimated survival as: 1) 0.752 during the first 100 days post-fledging (Powell et al. 2000b); 2) 0.423 ($n = 49$) during the first 56 days post fledging, with all mortality occurring within the first 3 weeks (Anders et al. (1997); and 3) 0.674 ($n = 29$) during the first 81 days post-fledging (Vega- Rivera et al. 1998). Given that predation is responsible for the great majority of post-fledging mortality (Anders et al. 1997), the influence of the radio-transmitter in elevating the risk of mortality in these studies cannot be discounted. There are no juvenile survival estimates through the first year.

We decided that the evidence for a correlation between return rate and breeding success is strong, and that the return rates of older, successful breeders are probably the most reasonable estimates of annual survival. We therefore assume an annual adult female survival rate of 65%. We further assume a juvenile survival rate estimate of 32.5% (50% of the adult survival rate estimate, following the hypothesis of Greenberg

(1980) and Temple & Cary (1988) that juvenile survival is approximately 50% of adult survival among small, north-temperate passerines).

Effects of nest micro-habitat on probability of nest predation and parasitism

One of the only consistent differences in the nest-site characteristics of successful versus failed nests is a positive relationship between nest concealment and nest survival (Johnson 1997, Hoover & Brittingham 1998, Farnsworth & Simons 1999).

Effects of Brown-headed Cowbird nest parasitism on host reproductive success

As a preferred host species of the Brown-headed Cowbird, the Wood Thrush incurs severe costs to its own breeding success as a consequence of parasitism. BBIRD data indicate that the mean clutch size in parasitized nests (3.04, SD = 0.93, n = 257) was 10% lower than that of non-parasitized nests (3.38, SD = 0.72, n = 1,448). Mean fledging success was 41% lower from successful parasitized nests (1.81, SD = 1.28, n = 143) than from non-parasitized nests (3.08, SD = 0.91, n = 726). The mean number of Brown-headed Cowbird eggs laid per parasitized Wood Thrush nest increased significantly ($F = 78.4$; $P < 0.001$), and the mean number of host young fledged per successful nest decreased significantly ($F = 48.0$; $P < 0.001$) as the site-specific parasitism rate increased (Figure 2). In a heavily parasitized Wood Thrush population, where nests received up to 7 cowbird eggs, each cowbird egg was associated with the removal of 0.4 Wood Thrush eggs, a 4% reduction in hatching success of host eggs, and a 5% decrease in the survival of host nestlings per cowbird nest-mate, resulting in a cumulative cost of 18-24% reduced breeding success per cowbird egg (Trine 2000).

Effects of landscape-level habitat variables on nest parasitism

Among both plots and sites, nest parasitism rate was strongly correlated with the degree of forest fragmentation across all spatial scales (Table 2, Figures 3-4). At the local patch scale, nest parasitism was not significantly correlated with distance to the nearest developed land cover edge, but strongly correlated with local and broader landscape-level fragmentation indices, suggesting that local edge effects are strongly constrained by landscape-level effects of fragmentation. Although the sample of sites from the southern Midwest is small, there is the suggestion that, at the patch and local landscape scale (within 1-10 km radii), nest parasitism in this region may be greater than in the northern Midwest and the East (Figure 4). Such regional differences have been noted before (e.g. Hoover & Brittingham 1993). However, in keeping with the hypothesis of broad-scale constraints on local-scale effects of fragmentation, this potential regional difference disappears at the broad-landscape scale of within a 50-100 km radius, suggesting that differences in the degree of forest fragmentation at these broader scales explains the differences in parasitism rate at more local scales.

Parasitism rate has been found to vary little within the first 150 m from forest edges (Dowell et al. 2000). Parasitism rates were similarly little different (42% and 50% respectively) between very small (3-14 ha) and small (26-140 ha) forest fragments in a heavily fragmented, agricultural landscape in Ontario (Friesen et al. 1999b), although size

of forest tract had the greatest influence on nest survival in Pennsylvania (Hoover & Brittingham 1998). In the Midwest, parasitism rates were 44-81% in fragmented forests as opposed to 0-2% in the interiors of contiguous forests (Li 1994; Donovan et al. 1995), but averaged 91% in large (1,000-3,000 ha) forest fragments in southern Illinois (Trine 2000). At one heavily parasitized site, nest parasitism increased steadily at greater distances from the forest edge, from approximately 80% within 100 m of forest edges, to 100% within 400-800 m of the nearest edge, suggesting greater parasitism in interior forest embedded in highly fragmented landscapes (Robinson & Wilcove 1994), possibly as a result of greater host density in interior forest. Nest parasitism rate increased significantly with reduced forest cover within a 10 km radius of nine sites across the Midwest (Robinson et al. 1995). However, in a forest-edge site in New York state, where several species suffered >50% brood parasitism, parasitism levels on Wood Thrush, the most abundant species, was only 10% (Hahn & Hatfield 2000).

Table 1. Summary of Wood Thrush breeding productivity and estimated finite rate of population increase (λ) across BBIRD sites.

Site	No. of nests	Clutch size ¹	Parasitism rate (%) ²	Daily predation rate (%) ³	Nest success (%) ⁴	Fledglings/nest ⁵	Annual fecundity ⁶	Lambda
Finger Lakes Natl Forest, NY	5	3.25	0	2.53	24.59	2.25	1.58	0.91
Central Missouri	40	2.80	82.50	2.62	39.69	1.71	1.65	0.92
St Croix R. Valley, MN	15	3.00	46.67	3.25	41.02	1.89	1.85	0.95
Northern Ohio	370	3.33	32.16	3.55	34.00	2.22	1.93	0.96
Western Maryland	127	3.17	27.56	4.54	27.98	2.54	1.94	0.97
Wayne Natl Forest, OH	864	3.38	3.47	5.49	20.11	3.19	1.94	0.97
Mississippi R., MN/WI	38	3.50	50.00	3.23	41.20	2.06	2.02	0.98
NW Monongahela Natl Forest, WV	161	3.20	0.62	4.08	30.66	2.94	2.39	1.04
Hoosier Natl Forest, IN	371	3.47	24.80	4.29	29.62	3.07	2.44	1.05
SE Monongahela Natl Forest, WV	147	3.59	2.72	3.06	40.72	3.08	3.00	1.14
Nantahala Natl Forest, NC	7	3.29	0	2.65	37.79	3.33	3.10	1.15
Ozarks, Missouri	68	3.30	0	2.66	46.74	3.05	3.24	1.18
Chippewa Natl Forest, MN	85	3.50	0	1.90	56.61	3.00	3.57	1.23
Chequamegon Natl Forest, WI	6	3.33	0	1.54	65.80	3.00	3.89	1.28

¹Number of host eggs incubated in non-parasitized nests

²Percentage of nests that received 1 or more cowbird eggs

³Percentage of nests lost to predators per day

⁴Percentage of nests that produced at least 1 host fledgling or cowbird

⁵Number of host young fledged per successful nest

⁶Average number of host young fledged per female per year

Table 2. Summary of the best predictor variables (fragmentation indices) for the relationship between each of nest parasitism rate and lambda (assuming double-brooded) across plots (all plots with ≥ 5 nests) and sites (plot averages for scales of patch and 1-10 km radii) using multiple regression analysis. Spatial scales included: the patch of forest within which the study plot was embedded; 1-10 km radii of study plot centers; and 50-100 km radii of study site centers. Non-significant results included for comparison across scales. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Scale	Plots				Sites		
	Dependent variables	Independent variables	Adj. R2	Slope	Independent variables	Adj. R2	Slope
Patch	Parasitism	Forest edge density	0.25***	0.65	Patch core area	0.61***	-0.17
	Predation	Forest area	0.04*	0.004	To nearest edge	-0.02	
	Lambda	Forest edge density	0.11**	-0.17	Patch forest edge density	0.45**	-0.26
1 km	Parasitism	Core forest area	0.18***	-0.47	Fractal index	0.59***	2.71
	Predation	Avg forest patch size >10 ha	0.1**	0.019	Contagion	0.07	
	Lambda	Core forest area	0.03		% grassland	0.40**	-0.6
5 km	Parasitism	Shannon-Weaver diversity	0.34***	0.6	Shannon-Weaver diversity	0.78***	0.78
	Predation	Avg forest patch size >10 ha	0.08**	0.005	Fractal dimension	0.22*	0.072
	Lambda	Fractal dimension	0.24***	-1.27	% grassland	0.68***	-0.59
10 km	Parasitism	Shannon-Weaver diversity	0.4***	0.68	Total edge density	0.72***	6.32
	Predation	% developed	0.06*	-0.025	Fractal dimension	0.25*	0.15
	Lambda	Fractal dimension	0.22***	-2.15	% grassland	0.65***	-0.55
50 km	Parasitism				Total edge density	0.76***	7.77
	Predation				Fractal dimension	0.09	
	Lambda				Avg forest patch size	0.48**	0.072
100 km	Parasitism				Total edge density	0.76***	10.53
	Predation				Fractal dimension	0.04	
	Lambda				Total edge density	0.48**	-2.75

Effects of landscape-level habitat variables on nest predation rate

Among sites, daily nest predation rate was most significantly positively related to landscape fractal dimension within a 10 km radius ($F = 5.4$, $P = 0.039$, $R^2 = 0.25$). A multiple regression entering two independent variables, fractal dimension within a 10 km radius and distance to the nearest forest edge, is also significant ($F = 7.5$, $P = 0.009$, $R^2 = 0.50$). Thus, daily predation rate increases as the degree of landscape-level forest fragmentation within a 10 km radius (represented by fractal dimension) increases ($r_p = 0.74$, $P = 0.004$), and predation rate also increases with increasing distance from the nearest forest edge once the influence of landscape-level fragmentation is controlled for ($r_p = 0.62$, $P = 0.023$). At six sites with sufficient data, correlations between nest predation rate and distance to nearest edge among plots were positive at five sites, and negative at one site, although never significantly so.

Daily nest predation was 2.2-3.1% in fragmented forests compared with 1.2-2.2% in contiguous forest in the Midwest (Donovan et al. 1995), and daily nest mortality (largely from predation) 2.1% in contiguous forest in Arkansas Ozarks (Li 1994). Robinson et al. (1995) found that daily nest predation rate increased significantly with reduced forest cover within a 10 km radius of nine sites across the Midwest. In Pennsylvania, the nest success of Wood Thrushes was found to be strongly correlated with forest patch size, with 86% of nests successful in contiguous forest, 72% successful in large fragments (>100 ha) and 43% successful in small fragments (<100 ha; Hoover et al. 1995). A similar pattern of survival in relation to woodlot size was observed among artificial nests set to resemble Wood Thrush nests (Wilson et al. 1998). This effect of forest area on nesting success was largely due to edge-mediated differences in nest predation, resulting in 46% nest success within 50 m of forest edges, 67% success 50-100 m from edges, and 79% at distances greater than 100 m from edges. Both mammalian (mainly Raccoon and Feral Cat) and avian (mainly Blue Jay and American Crow) predators were more abundant in smaller forest patches, whereas nest parasitism was inconsequential, and did not vary in relation to forest size (Hoover et al. 1995). In a southern Ontario agricultural landscape, daily nest predation was significantly higher in small woodlots (mostly less than 100 ha) than in larger woodlots (mostly 100-2,300 ha), with 6.2% and 2.7% mortality respectively, although nest predation was not significantly related to distance from the nearest edge (Burke & Nol 2000). Similarly, in a collection of relatively large (<2,500 ha) forest fragments embedded in a heavily fragmented landscape in southern Illinois, nest predation was not correlated with distance from the nearest forest edge, with predation uniformly high (55-75%) up to 800 m from the nearest edge (Robinson & Wilcove 1994). Nest predation rates (58% average predation) were also unrelated to forest area and distance to nearest forest edge among 14 forest fragments (7-500 ha in size) in northern Indiana (Fauth 2000). In a highly fragmented, agricultural landscape in southwestern Ontario with 51% nest success overall, neither forest patch size nor distance to the nearest forest edge significantly affected nest success among patches ranging in size from 3-140 ha (Friesen et al. 1999b).

In summary, the dominant factor influencing nest predation rates of the Wood Thrush appears to be the degree of forest fragmentation within the local landscape, with patch-scale edge effects playing a lesser role. In general, nest predation increases with

increasing forest fragmentation, as a consequence of the greater abundance of edge-adapted predators associated with agricultural landscapes in more fragmented landscapes.

Effects of landscape-level habitat variables on the finite rate of population increase

Among both plots and sites, λ was strongly negatively correlated with the degree of forest fragmentation across multiple spatial scales, particularly at the local landscape scale of within a 5-10 km radius (Table 2, Figures 8-9).

Effects of silviculture on nest predation and nest parasitism

Selective logging added little to existing fragmentation effects in southern Illinois forests in which levels of both nest parasitism and nest predation were chronically high – nest parasitism (72-92%) and daily nest predation rate (2.78-5.93%) did not differ between selectively logged and uncut forest compartments (Robinson & Robinson 2001). However, nest parasitism tended to be greater in forest adjoining large clear-cuts (21% parasitism, $n = 29$ nests), exterior forest edges (16%, $n = 37$), and in forest adjoining small, managed wildlife openings (50%, $n = 4$), than in interior forest (8%, $n = 52$) in southern Indiana forests saturated with cowbirds (Winslow et al. 2000), suggesting that fragmentation associated with logging could facilitate the penetration of forest by cowbirds.

No consistent differences in daily nest mortality rates were found within and adjoining 15-year-old two-age (2.3% and 5.9% respectively) and 15-year-old clearcut logging plots (2.6% and 4.1% respectively), and mature, unharvested forest (2.4%) in an extensive West Virginia forest (Duguay et al. 2001), but sample sizes ($n = 15-30$) were not particularly large. In a study with larger samples, there was no difference in nest success for birds breeding within 300 m of forest clearcut edges (56% success) versus birds breeding at distances of 301-950 m from clearcut edges (50%) in a forested landscape in northeastern Wisconsin (Flaspohler et al. 2001). Thus, the limited data available do not indicate an effect of silviculture on nest predation rates.

Breeding densities were not significantly different between forest subjected to recent (1-5 years previously) and older (10-15 years) group and single-tree selection logging that created openings of 0.02-0.4 ha, than in uncut forest, on both ridges (0.66-1.58 and 0.43-0.49 detections per ten 50-m radius point counts in cut and uncut forest respectively) and in ravines (2.83-3.91 and 3.06-3.81 detections in cut and uncut forest respectively), in a 2,000 ha southern Illinois forest (Robinson & Robinson 1999). Densities (detections per 50-m radius point count) did not differ between forest plots 15 years after two-age timber harvest (1.2 detections), mature (75-80 year old) forest adjoining two-age plots (0.6 detections), within or adjoining 15-year-old clearcuts (1.1 and 0.7 detections respectively), and mature forest not adjoining logging plots (0.6 detections) in an extensively forested area of West Virginia (Duguay et al. 2001). Wood Thrush abundance was not markedly different between mixed-oak and aspen forest plots with 50-75% of their area constituting regenerating (2-10 years old) clear-cuts (1.7-4.1 individuals/10 ha) than uncut forest (2.3 individuals /10 ha) in Pennsylvania (Yahner 1993). However, in the central Appalachians, the Wood Thrush exhibited a dependence on closed-canopy cover conditions, suggesting that single-tree selection and thinning

understory trees that compete for root space would create favorable conditions for this species, but any intermediate or harvest cutting that opens the canopy would probably decrease populations (Crawford et al. 1981). Breeding densities in mature, uncut forest were significantly higher than in forest subjected to group-selection (2-5 openings of 0.2-0.4 ha every 8 ha), shelterwood, and clearcut-logging 4-5 years post harvest, but not significantly different in plots subjected to single-tree selective logging in southeastern Missouri (Annand & Thompson 1997). However, densities were not significantly affected by retention shelterwood silviculture in Georgia pine woodlands (Powell et al. 2000b). Breeding densities (detections per 50-m radius point count) in an Arkansas oak-hickory forest were substantially reduced in plots subjected to either a heavy understory cutting (all unmerchantable species taller than 1.4 m and <14 cm diameter) or both the understory treatment and overstory thinning to a basal area of 15 m²/ha (0.00-0.01 detections) than in unharvested control plots (0.13 detections: Rodewald & Smith 1998). Densities were lower in selectively (single tree and group selection) harvested Mississippi bottomland hardwood forest (0.8 territories/10 ha), and in intensively managed, 6-9-year-old cottonwood plantations (0-0.7 territories/10 ha), than in unharvested forest (3.1 territories/10 ha: Twedt et al. 1999). Border-edge cutting of woodlot edges to create a shrub transitional zone 15-40 m wide resulted in the loss of Wood Thrushes from the affected areas (Fleming & Guiliano 1998). Wood Thrushes were similarly virtually absent from heavily logged areas in a northern hardwood forest, but densities began to return to pre-logging levels after ten years (Webb et al. 1977).

Effects of burning on nest success

No data on nest success, but repeated prescribed burning (1-4 years of annual burning) of a mixed-oak forest in southern Ohio, which resulted in incremental, but temporary, reductions in the availability of leaf litter, and understory shrubs and saplings, had no significant effect on Wood Thrush breeding densities (Artman et al. 2001). Similarly, breeding densities were not significantly affected by winter prescribed burning in Georgia (White et al. 1999, Powell et al. 2000b).

Effects of grazing/browsing on nest success

No data.

Overview of landscape-level habitat effects on breeding productivity and population growth rate

Nest parasitism rate increased as the degree of fragmentation at any scale increased. The relative magnitude of patch-scale edge effects on nest parasitism rate were, however, constrained by the degree of forest fragmentation at landscape scales, particularly within 5-100 km radii of sites. The risk of parasitism, and the distance to which Brown-headed Cowbirds will penetrate forest interiors are correlated with the local population size of cowbirds in suitable habitat surrounding the forest (Donovan et al. 1997). The local abundance of cowbirds is, to a large extent, limited by the availability of suitable feeding areas, an area effect. Thus, local cowbird abundance increases as the relative area of

human-transformed, usually agricultural habitats surrounding or perforating the forest increases. In turn, edge effects at the patch scale are expected to be strongly constrained by variation in local cowbird abundance associated with these area effects at local landscape scales within as much as a 10 km radius (Thompson et al. 2002, Lloyd et al. in review). Furthermore, land cover at a broad landscape scale appears to act as an important constraint on cowbird parasitism rate, and by inference on cowbird density, at local landscape scales, although the mechanism behind this process remains uncertain (Lloyd et al. in review).

The dominant factor influencing nest predation rates of the Wood Thrush appears to be the degree of forest fragmentation within the local landscape, with patch-scale edge effects playing a lesser role. This again suggests that the relative abundance of edge-adapted predators (associated with agricultural landscapes) within forest edges is constrained by the extent of forest fragmentation at local landscape scales. Evidence of scale-dependence in nest predation rates, with landscape-level effects overwhelming patch-level edge effects, has been reported elsewhere (Donovan et al. 1997, Lloyd et al. in review).

With both nest parasitism rate and nest predation rate correlated with the degree of forest fragmentation at landscape scales, it is not surprising that λ is strongly influenced by the degree of forest fragmentation at local and broad landscape scales, particularly within a 5-10 km radius, with $\lambda \geq 1$ generally only when forest cover within a 10 km radius is $\geq 80\%$.

Area or edge sensitivity can counteract the negative effects of forest fragmentation on reproductive success (Donovan & Lamberson 2001). Within a 23 ha old-growth forest fragment in suburban Maryland, the breeding density of Wood Thrushes increased steadily from around 4.5 nests/ha within 25 m of forest edges to 20 nests/ha within 100-160 m of forest edges, suggesting strong edge sensitivity (Dowell et al. 2000). Breeding density was slightly reduced (1.0-1.5 females/ha in very small forest fragments (0.2-2.1 ha) compared to a small, 15 ha fragment (1.7-1.8 females/ha; Weinberg & Roth 1998). Although the Wood Thrush does generally display some localized edge and area sensitivity, and is more likely to occur in larger-area forests, it often nests in fragments as small as 1 ha in semi-wooded residential areas and parks (Roth et al. 1996). Furthermore, forest fragmentation appears to have little effect on male pairing success, with high pairing success in forest fragments of 0.2-2.1 ha (Roth & Johnson 1993; Weinberg & Roth 1998) and 3-12 ha (Friesen et al. 1999a). This suggests that patch-scale edge and area sensitivity may not counteract the effects of reduced reproductive success to any great extent, particularly given the stronger correlation between reproductive success and landscape level fragmentation rather than with patch-scale edge effects.

Mapping predicted source and sink habitat

A simplistic source/sink map will be presented, using the simple decision rule that forest habitat with $<80\%$ forest cover within a 10 km radius is sink, and forest habitat with $>80\%$ forest cover within a 10 km radius is source.

MANAGEMENT GUIDELINES

Wood Thrush breeding densities and nest predation rates are generally unaffected by group and single-tree selective logging, and small patch clear cuts. Although densities are reduced in large clear-cuts in the short term, they generally recover within ten years. Given the Wood Thrush's preference for mid-successional habitats over much of its range, or at least a mosaic of mature and early- to mid-successional habitats, these types of silviculture could enhance habitat quality for this species. Further research is, however, necessary to determine whether such silvicultural practices will facilitate the penetration of forest by cowbirds, and thus elevate nest parasitism rates. In some areas, such as the central Appalachians, where the Wood Thrush exhibits a dependence on closed-canopy cover conditions, single-tree selection and thinning understory trees that compete for root space would create favorable conditions for this species, but any intermediate or harvest cutting that opens the canopy would probably decrease populations (Crawford et al. 1981). Prescribed burning has little effect on breeding densities, but heavy understory cutting and border-edge cutting may reduce densities substantially.

In large tracts of mature, deciduous forest, a mosaic of early and mid-successional forest stands, along with the protection of mature riparian forest, will become necessary to accommodate both the breeding and post-dispersal habitat requirements of Wood Thrushes, given that such habitats may be important for the survival of juveniles during the critical early period of independence (Anders et al. 1998, Vega-Rivera et al. 1998), and for adults during their molting phase (Vega-Rivera et al. 1999). Furthermore, the creation of a dynamic habitat mosaic that includes mid-successional habitats may be necessary to prevent substantial Wood Thrush population declines as forest matures to old-growth forest (Holmes & Sherry 2001). Although natural disturbances, such as fire and wind, have the potential to create such a mosaic, the process should be facilitated by silvicultural practices that create a mosaic of mature and early- to mid-successional habitats, such as selective logging and small clear-cuts. However, such management decisions should take into account the tradeoffs between creating early successional habitats, on the one hand, and reducing the extent of undisturbed, mature-forest habitat for forest-interior specialists, and possibly increasing parasitism risks, on the other hand.

Given the severe effect of cowbird parasitism on Wood Thrush breeding productivity, any management efforts that reduce cowbird abundance both locally and in the broader landscape (within up to a 15 km radius) will benefit thrush populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Wood Thrush breeding habitat by minimizing (1) the extent of agriculture and development (particularly human dwellings) within or adjoining forests (not always feasible); (2) the extent of short grass openings, such as along road verges, utility corridors and around human dwellings; and (3) the presence of livestock within or adjoining forests. Where possible, logging roads should be narrow enough that they do not break the canopy, or closed and re-vegetated as soon as possible. Campgrounds should be managed to minimize extensive areas of grass, and garbage should be removed quickly to avoid attracting and subsidizing potential nest predators such as raccoons, opossums and corvids (Robinson & Wilcove 1994).

In regions where the Wood Thrush is a conservation concern, a broad-scale planning objective should be to maintain or improve the integrity (by minimizing the

amount of agricultural land, particularly livestock grazing lands, within forested areas) of the larger forest tracts within the region to ensure that percent forest cover within a 10 km radius of focal forest tracts is maintained above 80%. Where possible, forest preserves should be at least 10,000 ha in extent, to reduce the impact of cowbird parasitism (Robinson & Wilcove 1994), particularly in landscapes with a high degree of fragmentation at the broad scale (within 50-100 km radius), such as the Midwest.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

Several lines of evidence suggest that Wood Thrushes reach peak densities in, and have specific requirements for, mid-successional forest habitats, with population density substantially reduced in old-growth forest. Management of old-growth forest for Wood Thrushes, would therefore suggest that carefully planned logging to create a mosaic of habitats would benefit this species. The optimal configuration, extent and duration of rotation cycles for such logging needs to be explored, and the trade-offs with habitat management for old-growth specialist species carefully examined before adaptive management decisions of this nature are taken.

The limited data available suggests that forest openings created by logging will not compromise Wood Thrush nesting success in extensively-forested regions (with high forest cover at broad landscape scales), and perhaps not add significantly to the effects of fragmentation in landscapes heavily fragmented by agriculture, where forests may be already saturated with predators and cowbirds. However, the extent to which logging may facilitate cowbird parasitism of Wood Thrush nests in moderately-fragmented landscapes remains unknown.

REFERENCES

- Anders, A.D., Dearborn, D.C., Faaborg, J. & Thompson, F.R., III. 1997. Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* 11: 698-707.
- Anders, A.D., Faaborg, J. & Thompson, F.R., III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115: 349-358.
- Annand, E.M. & Thompson, F.R. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61: 159-171.
- Artman, V.L., Sutherland, E.K. & Downhower, J.F. 2001. Prescribed burning to restore mixed-oak communities in southern Ohio: effects on breeding-bird populations. *Conservation Biology* 15: 1423-1434.
- Brackbill, H. 1958. Nesting behavior of the Wood Thrush. *Wilson Bulletin* 70: 70-89.
- Brown, W.P. & Roth, R.R. 2002. Temporal patterns of fitness and survival in the Wood Thrush. *Ecology* 83: 958-969.
- Burke, D.M. & Nol, E. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* 10: 1749-1761.
- Conway, C.J., Powell, G.V.N & Nichols, J.D. 1995. Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. *Conservation Biology* 9: 855-864.

- Crawford, H.S., Hooper, R.G. & Titterington, R.W. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *Journal of Wildlife Management* 45: 680-692.
- Dececco, J.A., Marshall, M.R., Williams, A.B. & Cooper, R.J. 2000. Comparative seasonal fecundity of four Neotropical migrants in middle Appalachia. *Condor* 102: 653-663.
- Donovan, T.M., Jones, P.W., Annand, E.M. & Thompson, F.R. III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064-2075.
- Donovan, T.M. & Lamberson, R.H. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. *Ecology* 82: 1170-1179.
- Duguay, J.P., Bohall Wood, P. & Nichols, J.V. 2001. Songbird abundance and avian nest survival rates in forests fragmented by different silvicultural treatments. *Conservation Biology* 15: 1405-1415.
- Fauth, P.T. 2000. Reproductive success of Wood Thrushes in forest fragments in northern Indiana. *Auk* 117: 194-204.
- Fleming, K.K. & Giuliano W.M. 1998. Effect of border-edge cuts on birds at woodlot edges in southwestern Pennsylvania. *Journal of Wildlife Management* 62: 1430-1437.
- Friesen, L.E., Wyatt, V.E. & Cadman, M.D. 1999a. Pairing success of Wood Thrushes in a fragmented agricultural landscape. *Wilson Bulletin* 111: 279-281.
- Friesen, L.E., Cadman, M.D. & Mackay, R.J. 1999b. Nesting success of Neotropical migrant songbirds in a highly fragmented landscape. *Conservation Biology* 13: 338-346.
- Friesen, L.E., Wyatt, V.E., Cadman, M.D., Mackay, R.J., Cheskey, E.D., Allen, M.L. & Ramsay, D. 2000. Extent of double-brooding and seasonal movement of nesting females in a northern population of Wood Thrushes. *Wilson Bulletin* 112: 505-509.
- Greenberg, R. 1980. Demographic aspects of long distance migration. *In Migrant Birds in the Neotropics: Ecology, Behaviour, Distribution, and Conservation* (A. Keast and E.S. Morton, Eds), pp. 493-504. Smithsonian Institution Press, Washington, D.C.
- Hoover, J.P. & Brittingham, M.C. 1993. Regional variation in cowbird parasitism of Wood Thrushes. *Wilson Bulletin* 105: 228-238.
- Hoover, J.P., Brittingham, M.C. & Goodrich, L.J. 1995. Effects of forest patch size on nesting success of Wood Thrushes. *Auk* 112: 146-155.
- Hoover, J.P. & Brittingham, M.C. 1998. Nest-site selection and nesting success of Wood Thrushes. *Wilson Bulletin* 110: 375-383.
- Johnson, M.S. 1997. The effect of age on nest concealment and its complementary effect on production. *Wilson Bulletin* 109: 68-73.
- Lloyd, P., Martin, T.E., Redmond, R.L., Hart, M.M., Langner, U. & Bassar, R.D. in review. Assessing the influence of spatial scale on the relationship between avian nesting success and forest fragmentation: a case study for the Ovenbird (*Seiurus aurocapillus*). *In Scaling and Uncertainty Analysis in Ecology* (J.B. Wu, B. Jones, H. Li and O.L. Loucks, Eds). Columbia University Press.

- Powell, L.A., Conroy, M.J., Hines, J.E., Nichols, J.D. & Kremenetz, D.G. 2000a. Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* 64: 302-313.
- Powell, L.A., Lang, J.D., Conroy, M.J., & Kremenetz, D.G. 2000b. Effects of forest management on density, survival, and population growth of Wood Thrushes. *Journal of Wildlife Management* 64: 11-23.
- Robinson, W.D. & Robinson, S.K. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology* 13: 58-66.
- Robinson, S.K. & Robinson, W.D. 2001. Avian nesting success in a selectively harvested north temperate deciduous forest. *Conservation Biology* 15: 1763-1771.
- Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Robinson, S.K. & Wilcove, D.S. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. *Bird Conservation International* 4: 233-249.
- Rodewald, P.G. & Smith, K.G. 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. *Journal of Wildlife Management* 62: 1411-1417.
- Roth, R.R. & Johnson, M.S. 1993. Long-term dynamics of a Wood Thrush population breeding in a forest fragment. *Auk* 110: 37-48.
- Roth, R.R., Johnson, M.S. & Underwood, T.J. 1996. Wood Thrush (*Hylocichla mustelina*). In *The Birds of North America*, no. 246 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Temple, S.A. & Cary, J.R. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2: 340-347.
- Thompson, F.R. III, Donovan, T.M., DeGraaf, R.M., Faaborg, J. & Robinson, S.K. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Studies in Avian Biology* 25: 8-19.
- Trine, C.L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. *Conservation Biology* 12: 576-585.
- Trine, C.L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. In *Ecology and Management of Cowbirds and their Hosts* (J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson & S.G. Sealy, Eds.) pp. 135-144. University of Texas Press, Austin.
- Twedt, D.J., Wilson, R.R., Henne-Kerr, J.L. & Hamilton, R.B. 1999. Impact of forest type and management strategy on avian densities in the Mississippi Alluvial Valley, USA. *Forest Ecology and Management* 123: 261-274.
- Vega-Rivera, J.H., Rappole, J.H., McShea, W.J. & Haas, C.A. 1998. Wood Thrush post-fledging movements and habitat use in northern Virginia. *Condor* 100: 69-78.
- Vega-Rivera, J.H., McShea, W.J., Rappole, J.H. & Haas, C.A. 1999. Post-breeding movements and habitat use of adult Wood Thrushes in northern Virginia. *Auk* 116: 458-466.
- Webb, W.L., Behrend, D.F. & Saisorn, B. 1977. Effects of logging on songbird populations in a northern hardwoods forest. *Wildlife Monographs* 55: 1-35.

- Weinberg, H.J. & Roth, R.R. 1998. Forest area and habitat quality for nesting Wood Thrushes. *Auk* 115: 879-889.
- White, D.H., Chapman, B.R., Brunjes, J.H., Raftovich, R.V. Jr. & Seginak, J.T. 1999. Abundance and reproduction of songbirds in burned and unburned pine forests of the Georgia Piedmont. *Journal of Field Ornithology* 70: 414-424.
- Wilson, G.R., Brittingham, M.C. & Goodrich, L.J. 1998. How well do artificial nests estimate nest success of real nests? *Condor* 100: 357-364.
- Winslow, D.E., Whitehead, D.R., Whyte, C.F., Koukal, M.A., Greenberg, G.M. & Ford, T.B. 2000. Within-landscape variation in patterns of cowbird parasitism in the forests of south-central Indiana. *In Ecology and Management of Cowbirds and their Hosts* (J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson & S.G. Sealy, Eds.) pp. 298-310. University of Texas Press, Austin.

Figure 1. Wood Thrush laying season (number of new nests initiated each week) in relation to latitude. Laying season length estimated using the MacArthur index (Ricklefs 1966).

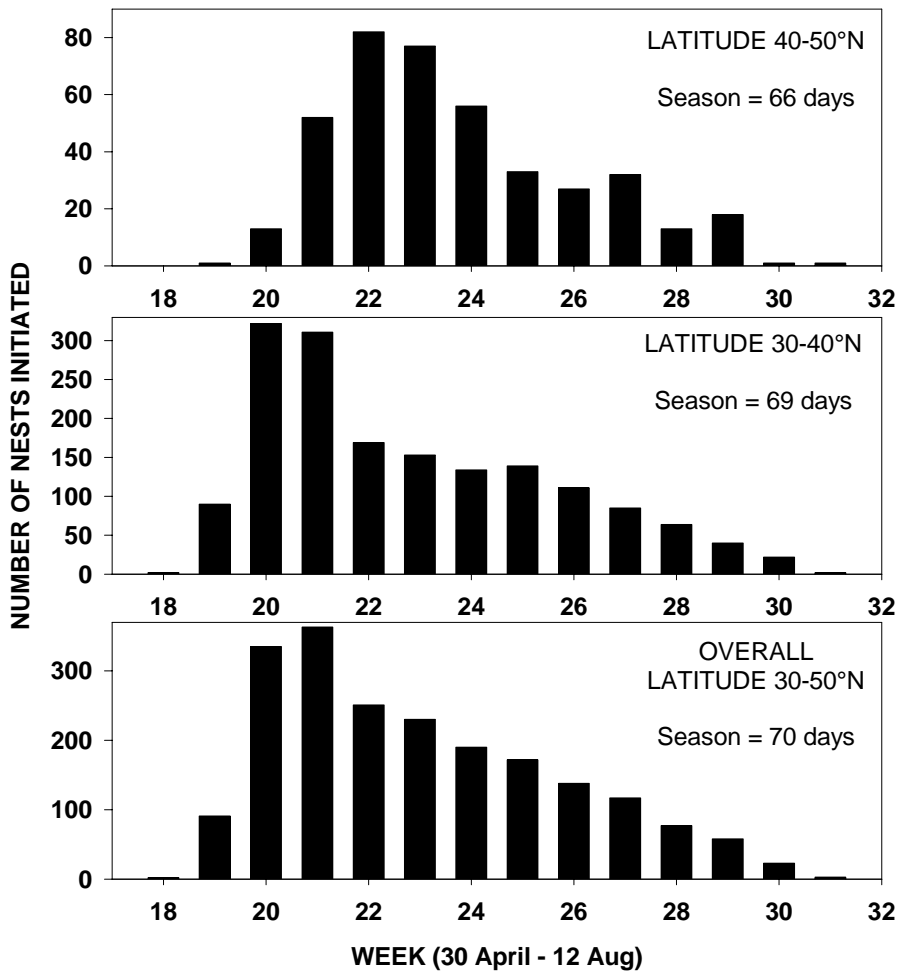


Figure 2. The mean number of Brown-headed Cowbird eggs laid per parasitized Wood Thrush nest (top) increases significantly ($F = 78.4$; $P < 0.001$), and the mean number of host young fledged per successful nest (bottom) decreases significantly ($F = 48.0$; $P < 0.001$) as the site-specific parasitism rate increases. Data on cowbird eggs include published data from three additional sites with 89-100% nest parasitism (Robinson & Wilcove 1994, Fauth 2000).

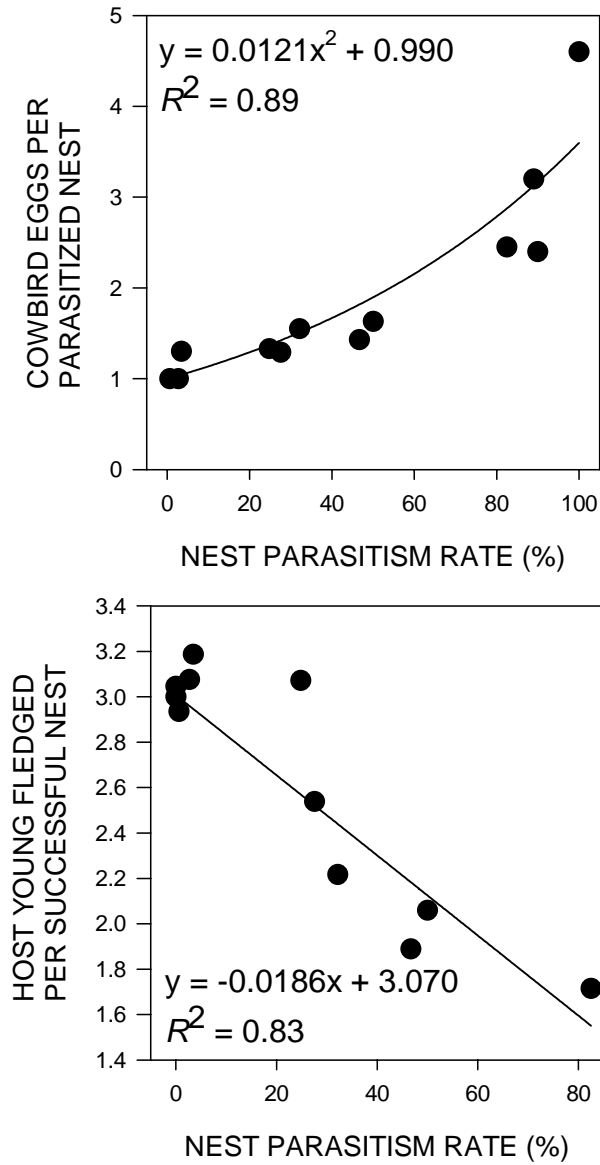


Figure 3. Relationship between nest parasitism rate (arcsine transformed) and various indices of forest fragmentation at spatial scales from the forest patch to within 1-10 km radii of plot centers, for all plots with ≥ 5 nests. Plots are grouped into three classes on the basis of relative percent forest cover at the 100 km radius scale (low, medium and high forest cover respectively).

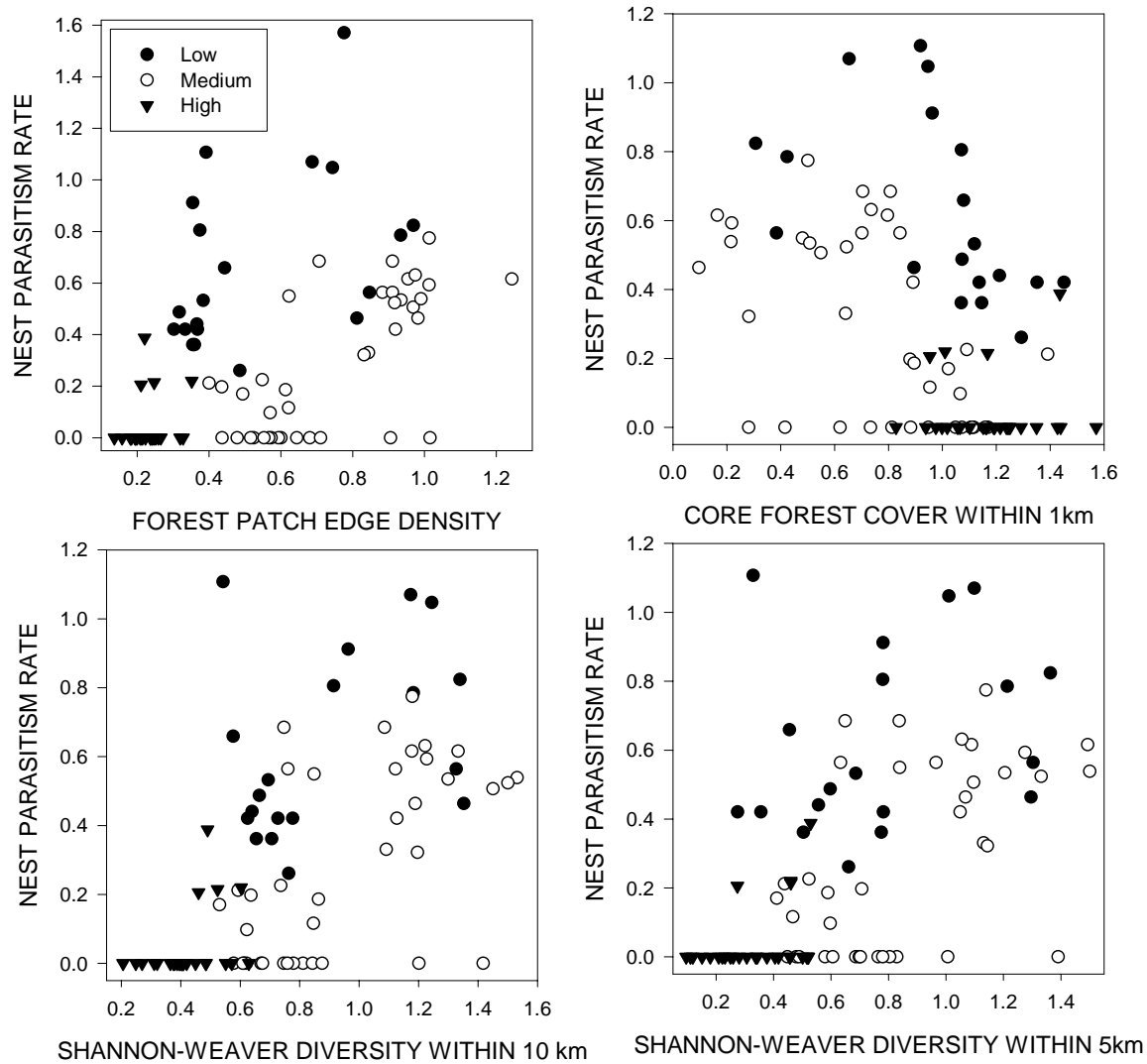


Figure 4. Relationship between nest parasitism rate (arcsine transformed) and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers. Sites are classified according to region: East; Northern MidWest; and Southern MidWest.

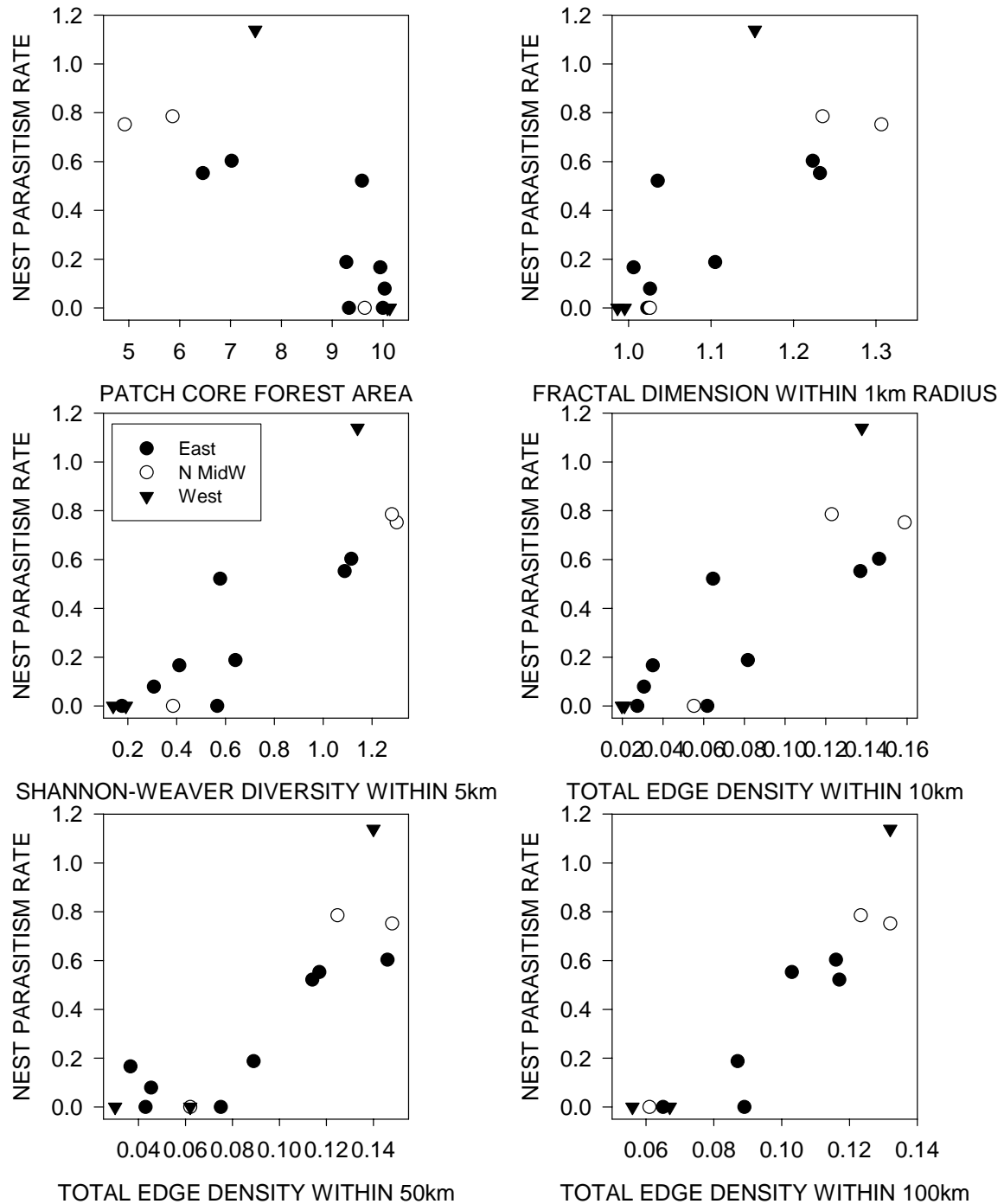


Figure 5. Relationship between daily nest predation rate and various indices of forest fragmentation at spatial scales from the forest patch to within 1-10 km radii of plot centers, for all plots with ≥ 5 nests. Plots are grouped into three classes on the basis of relative percent forest cover at the 100 km radius scale (low, medium and high forest cover respectively).

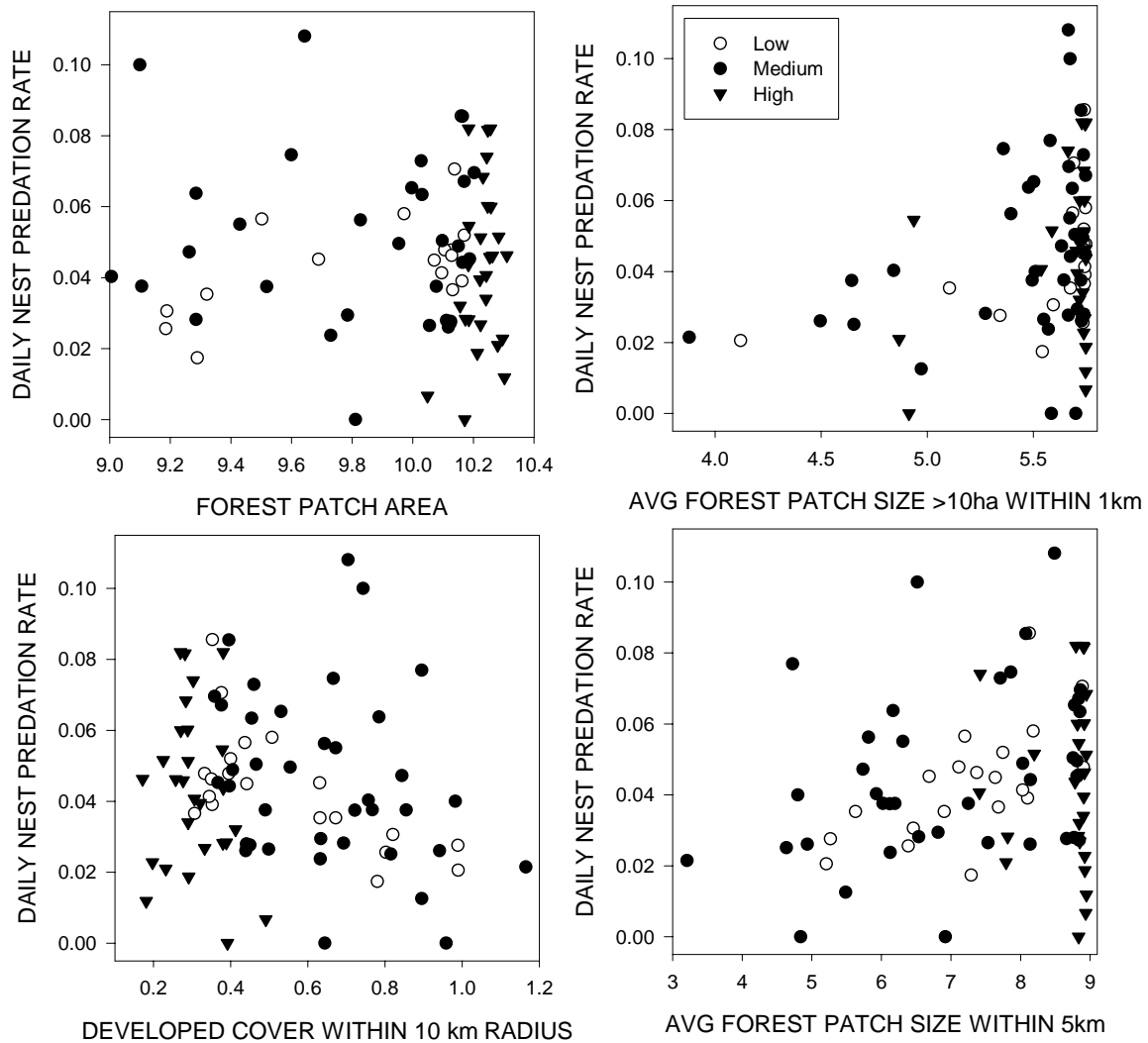


Figure 6. Relationship between daily nest predation rate and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers. Sites are classified according to region: East; Northern MidWest; and Southern MidWest.

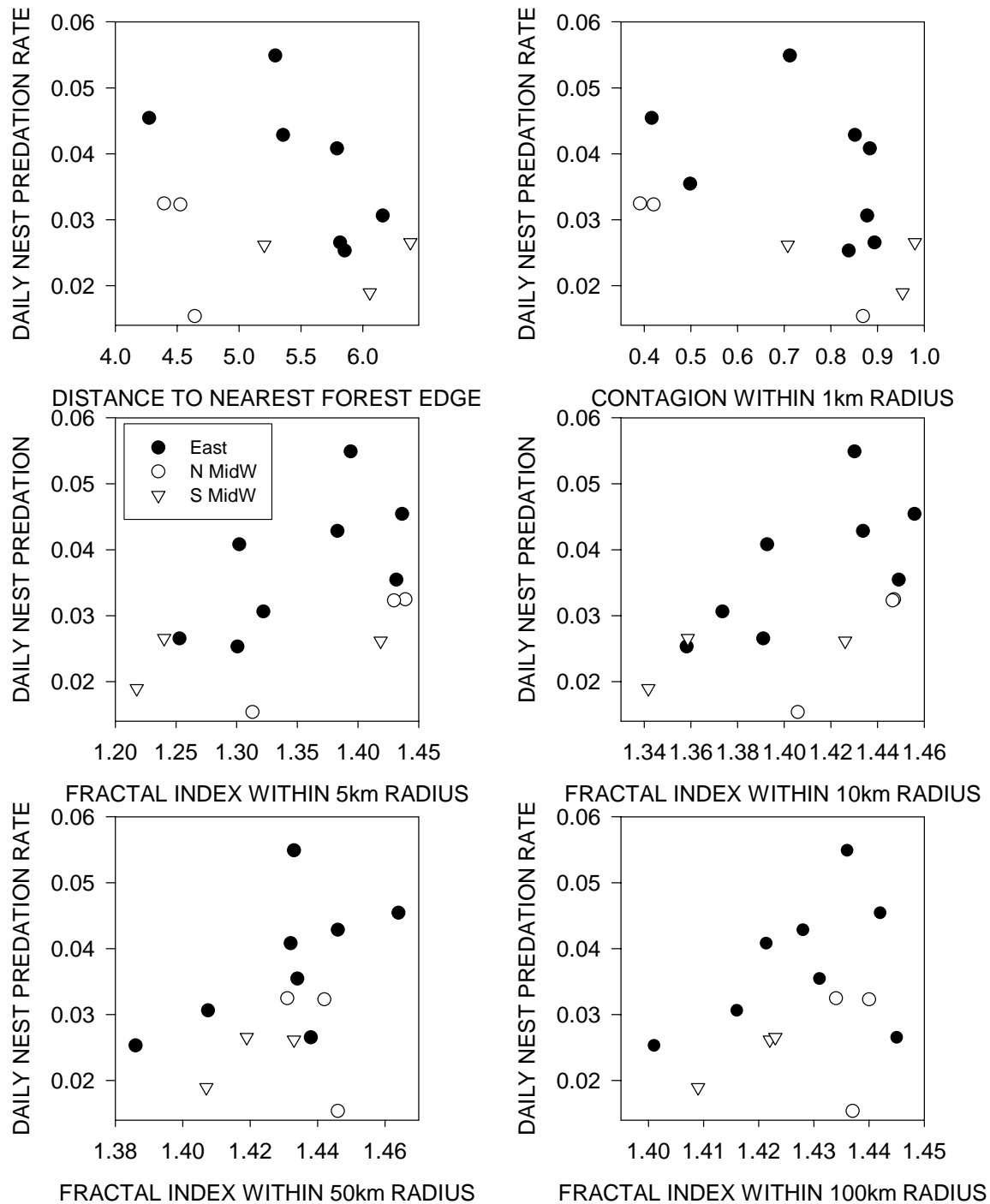


Figure 7. Daily predation rate increases as the degree of landscape-level forest fragmentation within a 10 km radius (represented by fractal dimension) increases ($r_p = 0.74$, $P = 0.004$), and predation rate also increases with increasing distance from the nearest forest edge once the influence of landscape-level fragmentation is controlled for ($r_p = 0.62$, $P = 0.023$).

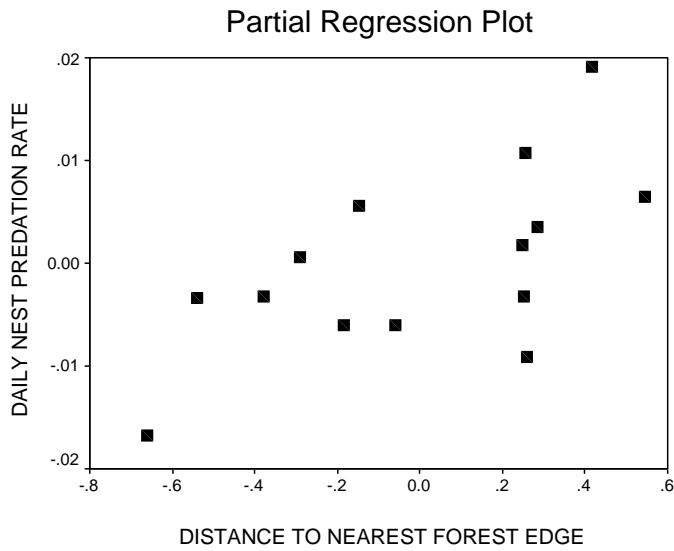
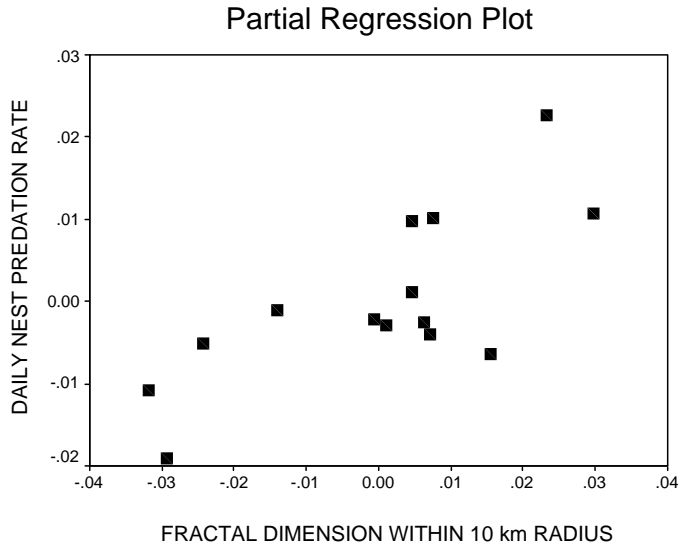


Figure 8. Relationship between lambda and various indices of forest fragmentation at spatial scales from the forest patch to within 1-10 km radii of plot centers, for all plots with ≥ 5 nests. Plots are grouped into three classes on the basis of relative percent forest cover at the 100 km radius scale (low, medium and high forest cover respectively).

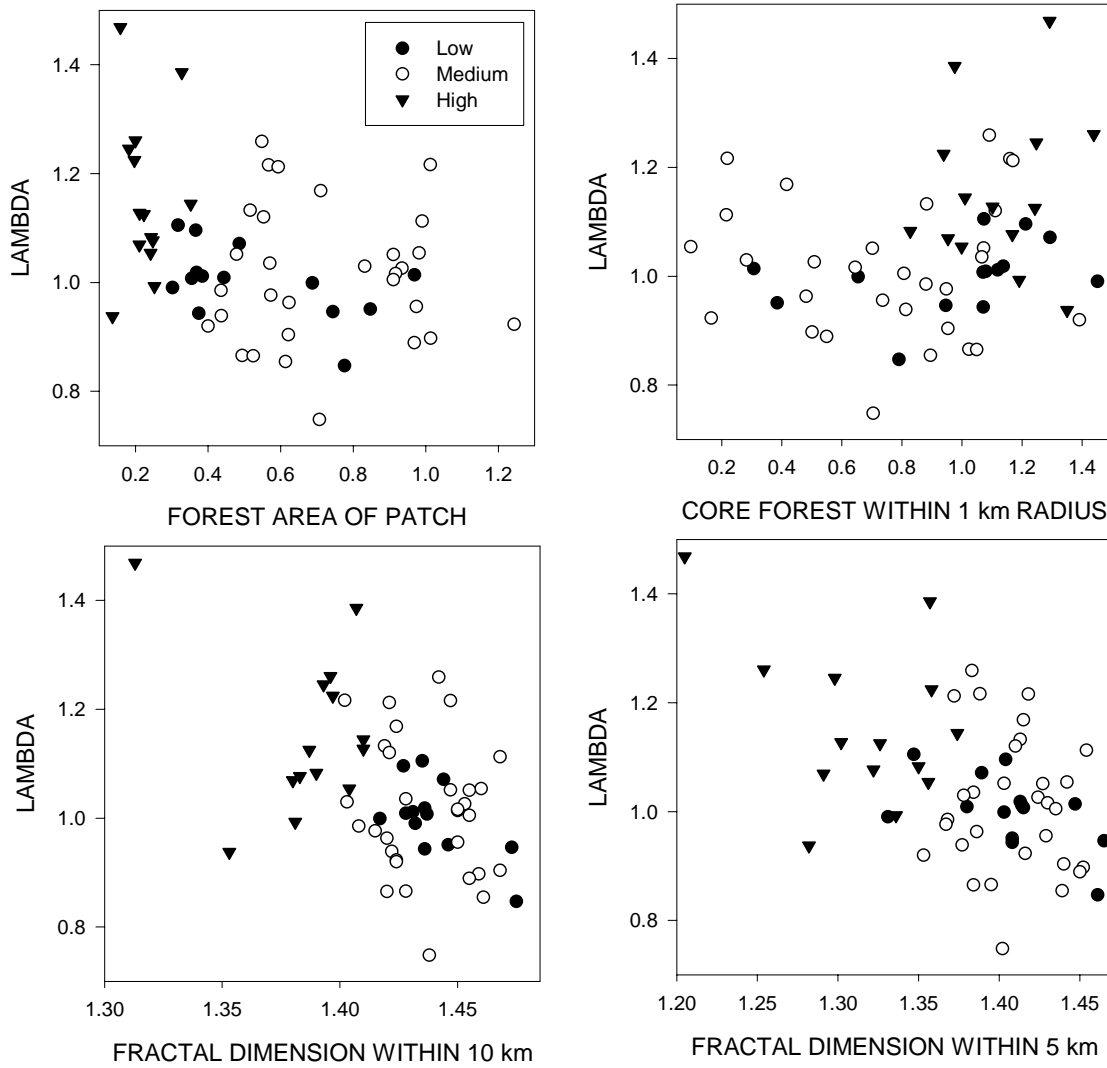


Figure 9. Relationship between lambda and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers. Sites are classified according to region: East; Northern MidWest; and Southern MidWest.

