

Red-eyed Vireo *Vireo olivaceus*

Preferred breeding habitat: Deciduous and mixed deciduous-coniferous forest, generally preferring mesic and bottomland habitats to drier habitats. In pine-dominated landscapes, frequents riparian areas where deciduous trees more abundant. Although a bird of mature forest interiors, it is generally absent from sites where understory shrubs are sparse or lacking, and tolerates smaller canopy openings.

Nest placement: In a terminal or sub-terminal fork of a leafy branch, commonly at a height of 3-7 m in a 7-12 m high midstory to understory tree or shrub.

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

- Non-parasitized nests: clutch 3.27 ± 0.72 ; brood 2.76 ± 0.95
- Cowbird parasitized nests: clutch 2.86 ± 0.93 ; brood 1.03 ± 1.13

Number of broods per season: One to two.

Annual adult survival rates: Assumed male and female: 71.4%

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

- Fledge at least 2.3 own young per successful nest
- Daily nest mortality $\leq 4.8\%$ ($\geq 28\%$ nest success) assuming zero parasitism
- Daily nest mortality $\leq 3.7\%$ ($\geq 38\%$ nest success) with 20% nest parasitism
- Daily nest mortality $\leq 2.3\%$ ($\geq 55\%$ nest success) with 40% nest parasitism
- Generally $\leq 20\%$ nest parasitism across BBIRD sites
- Generally $\leq 3.7-4.2\%$ nest predation rate across BBIRD sites
- Percent forest cover $\geq 60\%$ within a 100 km radius

Nest mortality and parasitism rates in relation to landscape context:

- Daily nest predation rate 1.2-3.1%, 1.1-5.3%, and 2.8-7.0% when forest cover within 100 km radius $>80\%$, 60-80%, and $<60\%$ respectively.
- Nest parasitism rate $\geq 20\%$ when percent forest cover $\leq 78\%$ within a 5 km radius
- Nest parasitism rate $\geq 40\%$ when percent forest cover $\leq 57\%$ within a 5 km radius

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

- Nest predation rate increases as the distance to the nearest forest edge increases, but these local-scale edge effects are constrained by the degree of forest fragmentation at the broad landscape scale of within a 100 km radius.
- Nest parasitism rate is also greater within forest edge habitat, but these local-scale edge effects are constrained by the degree of forest fragmentation at the local landscape scale of within a 5-10 km radius.

General conclusions:

- Nest parasitism has a severe effect on Red-eyed Vireo breeding productivity, reducing host fledging success by 63% among parasitized nests.
- Nest parasitism rate is most strongly determined by the degree of forest fragmentation at spatial scales of 5-10 km radii.
- Nest predation rate is most strongly determined by the degree of forest fragmentation within a 100 km radius.
- Lambda is negatively correlated with degree of forest fragmentation at broader landscape scales, particularly within a 100 km radius.

Management guidelines:

- The Red-eyed Vireo's tolerance of a wide range of habitats and variety of smaller canopy openings suggest that it will tolerate a fairly broad range of silvicultural practices, including group selection, small or narrow clearcuts, thinning to remove overmature trees, cutting trees larger than a specified diameter limit, or single-tree selection. Large clearcuts and intensive site preparation will reduce populations (Crawford et al. 1981), but populations may recover within 15 years post harvest.
- Given the severe effect of cowbird parasitism on Red-eyed Vireo 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 vireo populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Red-eyed Vireo 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.
- In regions where the Red-eyed Vireo 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 100 km radius of focal forest tracts is maintained above 60%.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

A Neotropical migrant, the Red-eyed Vireo breeds across an extensive area of Canada, and the eastern half and north-west of the United States as far south as the Gulf Coast, and winters principally in the Amazon basin of South America (Cimprich et al. 2000).

It breeds in deciduous and mixed deciduous-coniferous forest (Cimprich et al. 2000), being twice as abundant on forested ridges than in ravines in the southern Illinois Ozarks (Robinson & Robinson 1999). However, in pine-dominated landscapes it is most abundant in riparian areas, even small streams, where deciduous hardwoods are most abundant (Cimprich et al. 2000). Breeding density is also generally greater on mesic and bottomland sites than drier sites (Cimprich et al. 2000). It is generally absent from sites where understory shrubs are sparse or lacking (Cimprich et al. 2000). In northern areas, it displays a preference for alder (*Alnus*) thickets and aspen (*Populus*) groves (Barlow & Power 1970).

In Central Appalachian hardwoods, the Red-eyed Vireo displays a relatively wide latitude in habitats used, being tolerant of differences in canopy closure, and tolerant of pole or mature stands. It is thus often found where the overstory canopy is closed, but tolerates a moderately open canopy with a low vegetative layer (Crawford et al. 1981). The latitude shown by the Red-eyed Vireo for openings in the canopy suggests that it will tolerate a fairly broad range of silvicultural practices, ranging from group selection, small or narrow clearcuts, thinning to remove overmature trees, or single tree selection (Crawford et al. 1981).

Red-eyed Vireo territory densities in suitable habitat range from 6-15 pairs/10 ha (median = 11: Holmes & Sherry 2001) and 16 pairs/10 ha (Robinson 1981) in New Hampshire forest, 15 pairs/10 ha in mature cove hardwood forests in the southeastern U.S. (Hamel 1992), 12 pairs/10 ha in sugar maple (*Acer saccharum*) forest in southern Quebec (Darveau et al. 1992), 10 pairs/10 ha in oak-maple forest in Illinois (Kendeigh 1982), 12 pairs/10 ha at a mesic site dominated by white and black oaks (*Quercus alba* and *Q. velutina*) in northwestern Arkansas, but only 1 pair/10 ha at a nearby xeric site dominated by post oak (*Q. stellata*: Shugart & James 1973), 9.8 pairs/10 ha in a mixed-oak forest in southern Ohio (Artman et al. 2001), and no more than 0.2 pairs/10 ha in shrub-dominated habitats and pastures with scattered trees (Graber et al. 1985). Over a 50-year period, the breeding density in an upland Illinois forest ranged from 1.8-6.2 pairs/10 ha, while density in a nearby bottomland forest ranged from 1.7-5.9 pairs/10 ha (Kendeigh 1982). Mean territory size 0.69 ha (range 0.86-3.71 ha; n = 45) in Michigan aspen forest (Southern 1958), but 3.0 ha (n = 12) in Illinois elm-maple forest (Twomey 1945).

Nest site characteristics

The nest is built in a terminal or sub-terminal fork of a leafy branch in a midstory to understory tree or shrub, being frequently shaded and concealed by vegetation above (Cimprich et al. 2000). Average nest height ranged from 2.4-8.2 m (most commonly 3-7 m) in shrubs or trees of a mean height that ranged from 6.9-31.2 m (most commonly 7-12 m) across BBIRD sites. The overall mean nest height was 4.4 m and substrate height 9.5 m.

BREEDING PRODUCTIVITY

Laying seasons

Earliest and latest Red-eyed Vireo nests in the BBIRD database were initiated on 30 April and 23 July respectively. At latitudes 35-40°N, most laying occurred during a 6-week period 7 May to 17 June, with a peak in the week of 14-20 May (Figure 2). At latitudes 40-45°N, most laying occurred during a 6-week period 21 May to 1 July, with a peak in the week of 4-10 June, three weeks later than the peak at latitudes 35-40°N. At latitudes 45-50°N, most laying occurred during a 5-week period 28 May to 1 July, with a peak in the week of 11-17 June. This latitudinal variation in the timing of laying is in general agreement with other reported data (reviewed in Cimprich et al. 2000). The average length of the laying season across latitudes was estimated as 47 days. This is somewhat longer than the mean laying season length of 38 days (range 28-43 days over 4 years) at sites in southeastern West Virginia (Dececco et al. 2000).

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (Cimprich et al. 2000). The mean clutch size of unparasitised nests is 4.0 in Illinois (Graber et al. 1985), 3.3 (n = 28) in Ontario (Lawrence 1953) and 3.2 in Virginia (Dececco et al. 2000). BBIRD data indicate a mean clutch size in unparasitised nests of 3.27 (SD = 0.72, n = 503). The mean incubation

period has been reported as 12.8 days (range 11-15 days; n = 11) in Ontario and Michigan (Cimprich et al. 2000), 12.5 days (n = 45) in Arkansas (Li 1994), and 14.0 days (SD = 0.9) in Virginia (Dececco et al. 2000). Young are reported to leave the nest at age 10-12 days (Cimprich et al. 2000), with a mean nestling period of 10.5 days (n = 44) in Arkansas (Li 1994) and 11.5 days (SD = 1.4) in Virginia (Dececco et al. 2000). BBIRD data indicate a mean incubation period of 12.8 days (range 10-15.5; n = 35) and a mean nestling period of 11.1 days (range 9-15 days; n = 22). The mean re-nesting interval following nest loss is 6.5 days (range 4-9 days; n = 4; Lawrence 1953). The Red-eyed Vireo may occasionally attempt 2 broods as far north as central Ontario (Lawrence 1953), and often raises 2 broods in southern Louisiana (Cimprich et al. 2000), yet it is widely regarded as single-brooded at least as far south as southern Virginia (Burke & Nol 2000; Cimprich et al. 2000; Dececco et al. 2000). To calculate breeding productivity, we used a 47-day laying season, a nesting period of 26 days (2-day laying, 13-day incubation, 11-day nestling), and a re-nesting interval of 6 days after nest loss. Given that the Red-eyed Vireo may be double-brooded, we compare the results of two modeling approaches – one assuming it is single-brooded, and one assuming it is double-brooded, with a re-nesting interval of 10 days following successful fledging.

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

Based on recaptures of banded birds, the probability of breeding adults surviving to the following year is 0.53 (Savidge & Davis 1974). A West Virginia study found that 49% (n = 96) of males returned to the study site the following breeding season (R. Cooper cited in Cimprich et al. 2000). Later estimates from this latter study suggest that the annual survival rate of adult males ranges between 51% and 76% (n = 142 males, over 4 years), with a breeding dispersal rate of 27% detected (Marshall et al. 2002). The design of the West Virginia study, using groups of three 30 ha plots separated by 10-20 km, means that even these latter estimates are likely to underestimate survival, due to the problem of accounting for breeding dispersal into unsurveyed habitat. Using a long-term dataset from an extensive color-banded population in southern Arizona, annual survival rate of the related Warbling Vireo (*Vireo gilvus*) was estimated at 71.4% (SE = 1.71%: both sexes included) by Clarke and Martin (unpublished ms). The mean clutch size of Warbling Vireo at the Arizona site (3.3) is the same as that of the Red-eyed Vireo, so we assume a 71.4% annual adult survival rate for the Red-eyed Vireo, given that adult survival rate exhibits a relatively tight inverse relationship with fecundity (Ricklefs 2000). We further assume a juvenile survival rate estimate of 35.7% (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

No data.

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

BBIRD data indicate that the mean clutch size in parasitized nests (2.86, SD = 0.93, n = 180) was 13% lower than that of non-parasitized nests (3.27, SD = 0.72, n = 503). Mean fledging success was 63% lower from successful parasitized nests (1.03, SD = 1.13, n = 103) than from non-parasitized nests (2.76, SD = 0.95, n = 302). Similarly, fledging success in parasitized nests was 52% lower than non-parasitized nests in southern Ontario, fledging 1.6 and 3.3 young per successful nest respectively (Burke & Nol 2000), and 27% lower among nests with a single cowbird egg than non-parasitized nests (fledging 1.85 and 2.53 young respectively) in Virginia (Dececco et al. 2000). Among BBIRD sites, the mean number of Brown-headed Cowbird eggs laid per parasitized Red-eyed Vireo nest increased non-significantly ($F_7 = 2.11$; $P = 0.2$), and the mean number of host young fledged per successful nest decreased significantly ($F_{10} = 13.11$; $P = 0.006$), as the site-specific parasitism rate increased.

Effects of landscape-level habitat variables on nest parasitism

Among all plots, nest parasitism rate was strongly positively related to the degree of forest fragmentation across spatial scales from the forest patch within which plots were embedded, to within 1-10 km radii of plots (Table 2, Figure 3). This relationship was most significant at the 10 km radius scale. At only one site (N Ohio) was there sufficient variation in percent forest cover across plots, and then only at the 1 km radius scale, to test for a relationship between nest parasitism rate and percent forest cover. Although the correlation was negative, it was non-significant ($r = -0.49$; $P = 0.18$).

Among sites, nest parasitism rate was also strongly positively correlated with the degree of forest fragmentation across all spatial scales, from the patch scale to within a 100 km radius of site centers (Table 2, Figure 4). This relationship was most significant at local landscape scales, particularly the 5 km radius scale, with percent developed land cover (Table 2). There was little evidence of regional differences in nest parasitism rate across spatial scales (Figure 5).

These data provide further support to the findings of several other studies that have found strong effects of forest fragmentation at a variety of spatial scales on Red-eyed Vireo nest parasitism rate. In Ontario, cowbird parasitism was recorded at 24% of Red-eyed Vireo nests in small forest fragments (mostly less than 100 ha) surrounded by agriculture, but not at nests in large forest fragments (mostly 100-2,300 ha) or contiguous forest (Burke & Nol 2000). Furthermore, the probability of parasitism was strongly dependent on the proximity of the nest to a forest/agriculture edge – the parasitism rate decreased from 75% within 50 m of a forest edge to around 13% at distances of 101-200 m, and 0% at distances greater than 200 m (Burke & Nol 2000). Similarly, in one Midwest study, nests in forest fragments (180-1,870 ha, with similar edge density) incurred 69% parasitism rates, whereas nests in contiguous forest incurred just 8% parasitism (Donovan et al. 1995). Furthermore, at an extensively forested site in southern Indiana, nest parasitism was significantly higher among nests situated close to an agricultural corridor (77% parasitism) than in interior forest approximately 2 km from the nearest agricultural edge (25% parasitism: Ford et al. 2001). At a broader, local landscape scale, Robinson et al. (1995) found a strong negative correlation between percent forest cover within a 10 km radius and cowbird brood parasitism on Red-eyed Vireo populations across the Midwest.

In summary, nest parasitism rates on the Red-eyed Vireo are strongly influenced by local edge effects - parasitism is reduced at increasing distance from the nearest edge, particularly agricultural edge. However, the local landscape context (especially within a 5-10 km radius) is a more important determinant of nest parasitism rate, suggesting that the degree of fragmentation within the local landscape constrains the overall nest parasitism rate experienced at any site.

Table 1. Summary of Red-eyed Vireo breeding productivity and estimated finite rate of population increase (λ) across BBIRD sites. See Figure 1b for site locations.

Site	No. of nests	Clutch size ¹	Parasitism rate (%) ²	DPR (%) ³	Nest success (%) ⁴	Fledglings/ nest ⁵	Annual fecundity ⁶	Annual fecundity ⁶	Lambda Single brd	Lambda Dbl brd
Western New York	11	3.33	9.09	5.35	13.22					
Western Maryland	15	2.63	46.67	6.98	15.25					
St Croix River Valley, MN	13	3.4	61.54	3.85	31.66					
Bitterroot, MT	11		63.64	1.12	35.24					
Ouachita Natl Forest, AR	9	3.00	0	3.36	41.11					
Northern Ohio	130	3.22	44.62	4.69	21.45	1.65	0.60	0.81	0.82	0.86
Hoosier Natl Forest, IN	272	3.37	38.24	5.8	19.03	2.13	0.71	0.96	0.84	0.88
Upper Mississippi, MN, WI, IL	38	4.00	36.84	2.86	40.28	1.35	0.79	1.02	0.86	0.90
Chippewa Natl Forest, MN	81	3.44	2.47	3.95	31.33	2.18	1.07	1.39	0.90	0.96
Wayne Natl Forest, OH	235	3.3	21.28	4.17	27.95	2.61	1.18	1.55	0.92	0.99
SE Monongahela Natl Forest, WV	101	3.03	12.87	3.14	37.53	2.39	1.34	1.73	0.95	1.02
Ozark Natl Forest, AR	205	3.10	2.44	3.18	38.02	2.60	1.47	1.90	0.98	1.05
NW Monongahela Natl Forest, WV	78	3.28	3.85	2.87	44.43	2.39	1.50	1.93	0.98	1.06
Ozarks, MO	47	3.08	6.38	3.98	31.34	3.11	1.52	1.99	0.99	1.07
Chequamegon Natl Forest, WI	12	3.44	0	1.24	61.42	2.86	2.21	2.82	1.11	1.22
Nicolet Natl Forest, WI	30	3.27	0	1.81	55.95	3.28	2.40	3.06	1.14	1.26

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 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. Independent variables included: forest core area; percent developed land cover (grassland/cropland/other developed); percent cropland; Fractal dimension; the distance between the plot center and nearest forest edge; average patch size; percent forest cover; Aggregation index; and total edge density of all land cover types in the landscape. Lambda1 assumes single-brooded; Lambda2 assumes double-brooded. In all cases, single parameter models were most parsimonious. Non-significant results included for comparison across scales. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Scale	Plots				Sites		
	Independent variables	Dependent variables	Adjusted R2	Slope	Dependent variables	Adjusted R2	Slope
Patch	Parasitism	core area	0.28***	-0.099	core area	0.64***	-0.13
	Predation				Distance to edge		-0.04
	Lambda1				core area		0.13
1 km	Lambda2	Patch area	0.24*	0.23	core area		0.14
	Parasitism	% developed	0.28***	0.81	% developed	0.75***	1.26
	Predation				% cropland		-0.06
5 km	Lambda1				Avg. patch size		0.23
	Lambda2	% core forest		0.13	Avg. patch size		0.24
	Parasitism	% cropland	0.44***	1.98	% developed	0.79***	1.04
10 km	Predation				% developed		0.04
	Lambda1				Avg. patch size	0.42*	0.066
	Lambda2	Avg. patch size	0.43***	0.091	Avg. patch size	0.43*	0.084
50 km	Parasitism	Fractal dim.	0.47***	7.32	% forest	0.75***	-1.07
	Predation				% developed		0.09
	Lambda1				Avg. patch size	0.47*	0.051
100 km	Lambda2	Avg. patch size	0.30**	0.089	Avg. patch size	0.48*	0.064
	Parasitism				Aggregation index	0.66***	-4.59
	Predation				% developed	0.30*	0.037
100 km	Lambda1				Avg. patch size	0.72***	0.052
	Lambda2				Avg. patch size	0.73***	0.065
	Parasitism				Tot. edge density	0.64***	8.91
100 km	Predation				% developed	0.38**	0.047
	Lambda1				Avg. patch size	0.84***	0.069
	Lambda2				Avg. patch size	0.84***	0.087

Table 3. Correlations (r) between site means for landscape variables and each of nest parasitism rate, daily nest predation rate, and finite rate of population increase (lambda) among sites. Landscape variables include percent cover of grassland (planted pasture/hay and semi-natural grassland/herbaceous), forest, and cropland (row crops, small grains, fallow and orchards/vineyards) at 1-150 km radii.

	Parasitism rate vs			Daily predation rate vs			Lambda
	Grass	Forest	Crop	Grass	Forest	Crop	Forest
	r	r	r	r	r	r	r
Patch area		-0.79***			0.33		0.42
1 km	0.83***	-0.80***	0.72**	-0.14	0.03	0.12	0.56
5 km	0.85***	-0.89***	0.74**	0.05	-0.22	0.13	0.71*
10 km	0.80***	-0.88***	0.70**	0.14	-0.29	0.17	0.73*
50 km	0.59*	-0.78***	0.57*	0.45	-0.52*	0.37	0.83**
100 km	0.56*	-0.74***	0.51*	0.63*	-0.60*	0.49	0.84**
150 km		-0.71**			-0.53*		0.80*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Effects of landscape-level habitat variables on nest predation rate

Among all plots, there were no detectable relationships between nest predation rate and any index of forest fragmentation at any of the patch and local landscape scales. Among sites, however, there was firm evidence to suggest that nest predation increased as the degree of forest fragmentation increased (Table 2, Figure 6). Overall, this relationship was significant at only the broad landscape scales (within 50-150 km radii). However, there is evidence that this relationship may be obscured at smaller spatial scales by differences in nest predation rate between regions (see Figure 6). Within the East and Northern Midwest regions, for example, it appears as if nest predation increases with degree of forest fragmentation across all spatial scales. Within the Northern Midwest, this relationship was most significant at the patch scale, with nest predation increasing significantly as the average distance between plot centers and the nearest forest edge (site averages) decreased from 105 m to 75 m ($F = 37.15$, $R^2 = 0.90$, $P = 0.009$), suggesting a strong edge effect on nest predation. Within the East region, this relationship was most significant at the 100 km radius scale, with nest predation increasing as percent developed land cover increased ($F = 8.79$, $R^2 = 0.57$, $P = 0.03$).

These findings are in broad agreement with other published studies. In Ontario, daily nest mortality (due largely to predation) was significantly lower in contiguous forest (3.7%) than in either small (mostly less than 100 ha) or large (mostly 100-2,300 ha) forest fragments surrounded by agriculture (5.8% and 6.8% mortality respectively). However, there was no significant edge effect on nest predation rate (Burke & Nol 2000). Similarly, 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). In the Midwest, where a non-significant trend of increasing nest predation with declining forest cover within a 10 km radius of sites has been found (Robinson et al. 1995), daily nest predation was higher in forest fragments (mean patch size 550-670 ha) surrounded by agriculture (4.54% daily predation) than in contiguous forest (2.96% daily predation: Donovan et al. 1995).

In summary, the evidence supporting a local edge effect on Red-eyed Vireo nest predation is mixed – some studies have demonstrated no edge effect (Burke & Nol 2000, Flaspohler et al. 2001), whereas we found evidence suggestive of an edge effect within the Northern Midwest region. On the other hand, there is strong evidence of broader landscape-scale effects on nest predation rate, particularly at the 100 km radius scale. Such landscape-scale effects could explain the observed higher predation rates in forest fragments of various sizes as opposed to contiguous forest in the absence of evidence of edge effects.

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

Under the assumption of single-broodedness, only two of eleven populations at BBIRD sites were assessed as sources, despite use of the most optimistic estimates of breeding season length and adult and juvenile survival rates available (Table 1). Under the assumption of double-broodedness, six of the eleven populations are assessed as sources, and the remaining five as sinks. Given that the latter is a more likely scenario, we use only the estimates of lambda with the option of double-brooding (as did Donovan et al. 1995) in the analyses of the effects of landscape-level habitat variables on lambda.

Among all plots, lambda was significantly related to the degree of forest fragmentation at the patch scale and within a 5-10 km radius of plot centers (Table 2, Figure 7). This relationship was most significant at the 5 km radius scale, with lambda increasing as the average forest patch size within a 5 km radius increased. Given that all plots from landscapes with relatively low forest cover at the 100 km radius scale are sinks, independent of the degree of forest fragmentation at the smaller patch and 1 km radius scales, it is clear that the relationship between lambda and forest patch size at the patch size is strongly constrained by the degree of forest fragmentation at local and broader landscape scales (Figure 7). Among sites, lambda was significantly related to the degree of forest fragmentation at spatial scales of within 5-100 km radii, with the most significant relationship at the 100 km radius scale (Table 2, Figure 8). This further illustrates the overwhelming influence on lambda of forest fragmentation at broad landscape scales. Although nest parasitism rate has a stronger effect on lambda than nest predation rate ($r_p = 0.75$ and 0.51 respectively), and is most significantly related to the forest fragmentation at the 5 km radius scale, the strong relationship between nest predation rate and forest fragmentation at only the broader landscape scales (50-100 km radii) ensures that lambda is most strongly related to forest fragmentation within a 100 km radius. Such a pattern is expected if overall predator and parasite densities at local scales are constrained by the broader landscape context.

In Ontario, estimated seasonal fecundity was substantially lower for females breeding in forest fragments up to 2,300 ha in size (1.54-1.68 fledglings) than in

contiguous forest (2.82 fledglings). Consequently, forest fragments were assessed as strong population sinks for breeding Red-eyed Vireos at this site (Burke & Nol 2000). Similarly, estimated female seasonal fecundity was lower (1.09 fledglings) in forest fragments (mean patch size 550-670 ha) than in contiguous forest (3.22 fledglings) in the Midwest (Donovan et al. 1995).

Effects of silviculture on nest predation and nest parasitism

There are no data on the effects of silviculture on nest parasitism rates. No significant differences in daily nest mortality rates were found within and adjoining 15-year-old two-age (3.8% and 2.4% respectively) and 15-year-old clearcut logging plots (5.6% and 3.7% respectively), and mature, unharvested forest (4.3%) in an extensive West Virginia forest (Duguay et al. 2001), but sample sizes ($n = 6-12$) were too small to detect differences anyway. 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.

Silvicultural practices have significant effects on breeding densities, however. Breeding densities were significantly reduced on forested ridges 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 (2.83-4.42 and 1.58-3.68 detections per ten 50-m radius point counts respectively), than on uncut ridges (5.69-6.00 detections) in a 2,000 ha southern Illinois forest (Robinson & Robinson 1999). Although densities were similarly lower in ravines subject to similar logging treatments (1.50-2.17 and 0.54-1.81 detections in recent and older treatments respectively) than in uncut ravines (2.62-2.76 detections), these latter differences were non-significant (Robinson & Robinson 1999). However, in southeastern Missouri, densities in forest subjected to single-tree and group-selection (2-5 openings of 0.2-0.4 ha every 8 ha) harvest 4-5 years previously were no different from densities in mature forest, but densities were substantially reduced in shelterwood and clearcut-treated plots 4-5 years post harvest (Annand & Thompson 1997). Similarly, densities were only slightly lower in selectively (single tree and group selection) harvested Mississippi bottomland hardwood forest (2.8 territories/10 ha) than unharvested forest (4.1 territories/10 ha), but negligible in intensively managed, 6-9-year-old cottonwood plantations (Twedt et al. 1999).

Breeding densities were also significantly lower in forests managed by clearcutting (0.75 territories/ha) than in forests with no timber harvest (1.13 territories/ha: Thompson et al. 1992). Similarly, densities were dramatically lower in plots subjected to 50% or 75% clear-cutting, with 0-10-year-old regeneration (2.6-3.5 individuals/10 h), than in uncut forest (12.8 individuals/10 h: Yahner 1993). Breeding densities (detections per 50-m radius point count) in an Arkansas oak-hickory forest were higher, but not significantly so, in unharvested control plots and plots subjected to a heavy understory cutting (all unmerchantable species taller than 1.4 m and <14 cm diameter) (2.28 and 2.35 detections respectively), than in plots subjected to both the understory treatment and overstory thinning to a basal area of 15 m²/ha (1.69 detections: Rodewald & Smith 1998). However, densities (detections per 50-m radius point count) did not differ between forest

plots 15 years after two-age timber harvest (1.75 detections), mature (75-80 year old) forest adjoining two-age plots (1.84 detections), within or adjoining 15-year-old clearcuts (1.95 and 1.87 detections respectively), and mature forest not adjoining logging plots (1.70 detections) in an extensively forested area of West Virginia (Duguay et al. 2001).

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 Red-eyed Vireo breeding densities (Artman et al. 2001).

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 constrained by the degree of forest fragmentation at local landscape scales, particularly within a 5-10 km radius 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).

Limited evidence suggests there can be local edge effects on Red-eyed Vireo nest predation, with predation higher closer to forest edges. On the other hand, there is strong evidence of broader landscape-scale effects on nest predation rate, particularly at the 100 km radius scale. Such landscape-scale effects could explain the observed higher predation rates in forest fragments of various sizes as opposed to contiguous forest in the absence of evidence of edge effects. 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 broader landscape scales, λ is most strongly influenced by the degree of forest fragmentation within a 50-100 km radius, with $\lambda \geq 1$ generally only when forest cover within a 100 km radius is $\geq 60\%$.

A 30-year study in a maturing (from mature second-growth) deciduous forest in New Hampshire found a significant declining trend in Red-eyed Vireo breeding densities, with the number of breeding adults/10 ha decreasing from 20-30 in the period 1969-1976

to 15-25 in the period 1983-1998 (Holmes & Sherry 2001). The percent annual change in abundance at this site during the period 1969-1998 (-0.96%) mirrored a similar decline (-1.33%) on Breeding Bird Survey routes in New Hampshire during the same period (Holmes & Sherry 2001). These results, from a relatively well-forested region, highlight the negative impact of broad-scale forest fragmentation on Red-eyed Vireo populations.

Mapping predicted source and sink habitat

MANAGEMENT GUIDELINES

The tolerance shown by the Red-eyed Vireo for internal openings in the canopy suggests that it will tolerate a fairly broad range of silvicultural practices, ranging from group selection, small or narrow clearcuts, thinning to remove overmature trees, or single tree selection (Crawford et al. 1981). Generally, large clearcuts and intensive site preparation will reduce vireo breeding densities, although populations may recover within 15 years of harvest.

Given the severe effect of cowbird parasitism on Red-eyed Vireo 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 vireo populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Red-eyed Vireo 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.

In regions where the Red-eyed Vireo 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 100 km radius of focal forest tracts is maintained above 60%.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

An accurate estimate of annual adult female survival rate is critical for the estimation of lambda, but is currently lacking for the Red-eyed Vireo. This should be determined with intensive monitoring, over a period of at least five years, of a color-banded population occupying the interior of a large forest tract where reproductive success is high, given that poor reproductive success may result in higher levels of breeding dispersal (e.g. Porneluzi & Faaborg 1999, Bayne & Hobson 2002).

Good estimates of re-nesting intervals following both nest failure and successful fledging are important for any model estimating seasonal productivity. Our estimate of the re-nesting interval following failure is based on a small sample, and no field measurements of the re-nesting interval after successful fledging among double-brooded females have been made. It would therefore be useful to gather additional data by monitoring color-banded individuals throughout a breeding season.

The length of the laying season and the extent of double-brooding by the Red-eyed Vireo appear to differ across latitudes between the north and south of its breeding range. Since these parameters are influential to any model that estimates seasonal productivity, it would be better to incorporate latitudinal variation in these parameters in any model of annual breeding productivity and lambda

Further data on nesting success in both small and large forest patches in landscapes with differing extents of forest fragmentation at broad scales in different regions within the breeding range of the Red-eyed Vireo would be useful for improving resolution in our understanding of the influence of landscape structure on breeding productivity, and thus on the patterns of sources and sinks in the landscape. These data are not difficult to collect, requiring a sample of ideally at least 25 nests (to give a sample of at least 10 successful nests for a reliable estimate of mean number of host young fledged per successful nest) that are monitored frequently enough to accurately determine their fate, and collected from a plot, up to 50 ha in size, of homogenous habitat whose center can be geo-referenced with a precision of approximately 30 meters (to allow plot-specific landscape features to be characterized from a digital land cover map). If any nests are located within 100 m of a habitat edge, measurements of the distance between that nest and the nearest edge would be useful for investigating patch-scale edge effects.

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Figure 1. Red-eyed Vireo laying season (number of new nests initiated each week) in relation to latitude. Laying season length estimated using the MacArthur index.

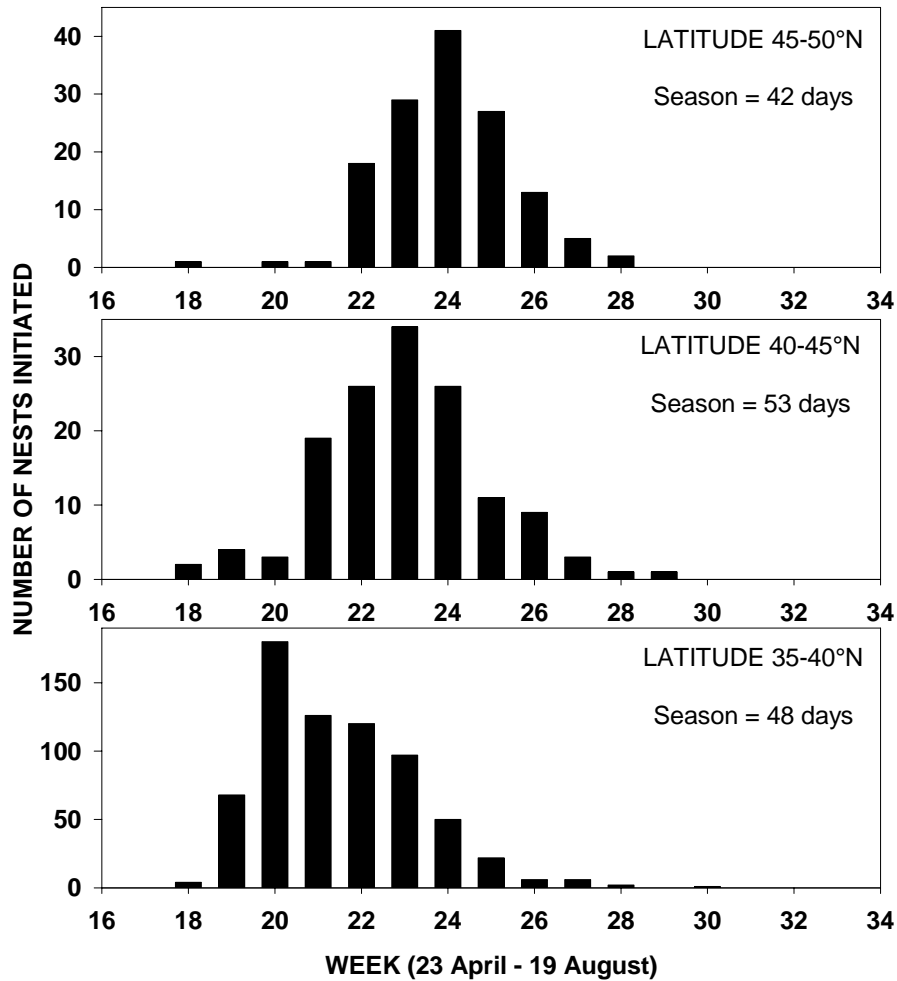


Figure 2. The mean number of Brown-headed Cowbird eggs laid per parasitized Red-eyed Vireo nest (top) increases non-significantly ($F_7 = 2.11$; $P = 0.2$), and the mean number of host young fledged per successful nest (bottom) decreases significantly ($F_{10} = 13.11$; $P = 0.006$) as the site-specific parasitism rate increases.

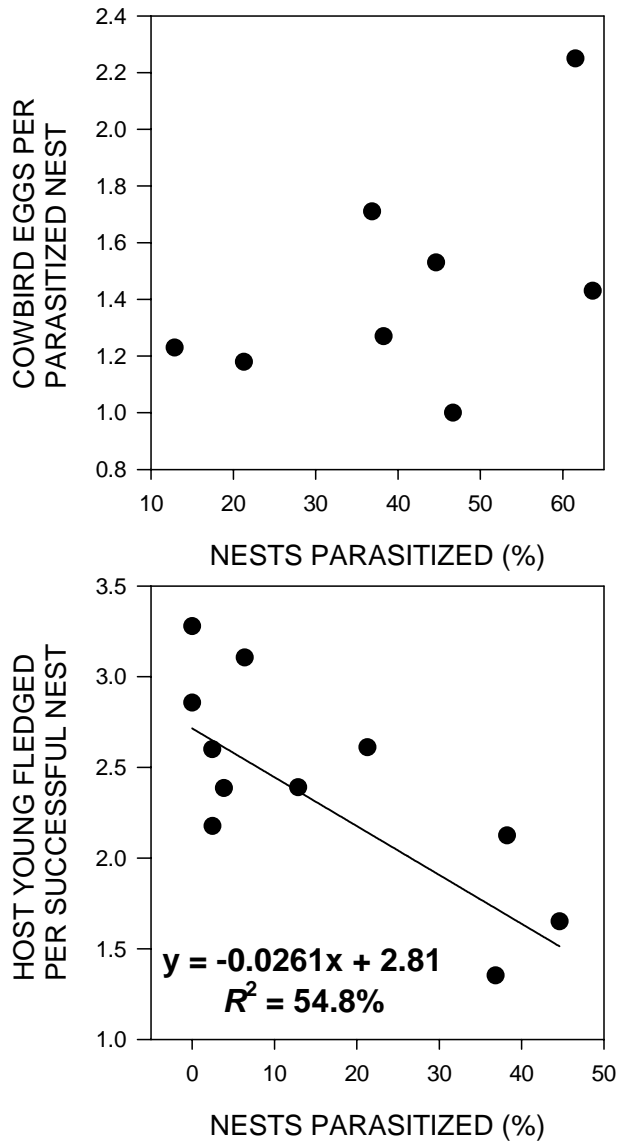


Figure 3. Relationship between Red-eyed Vireo nest parasitism rate (arcsine transformed) and indices of forest fragmentation (ln patch area, arcsine proportion developed and cropland cover, fractal dimension) at spatial scales from the patch to within 1-10 km radii of plot centers for all plots with ≥ 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).

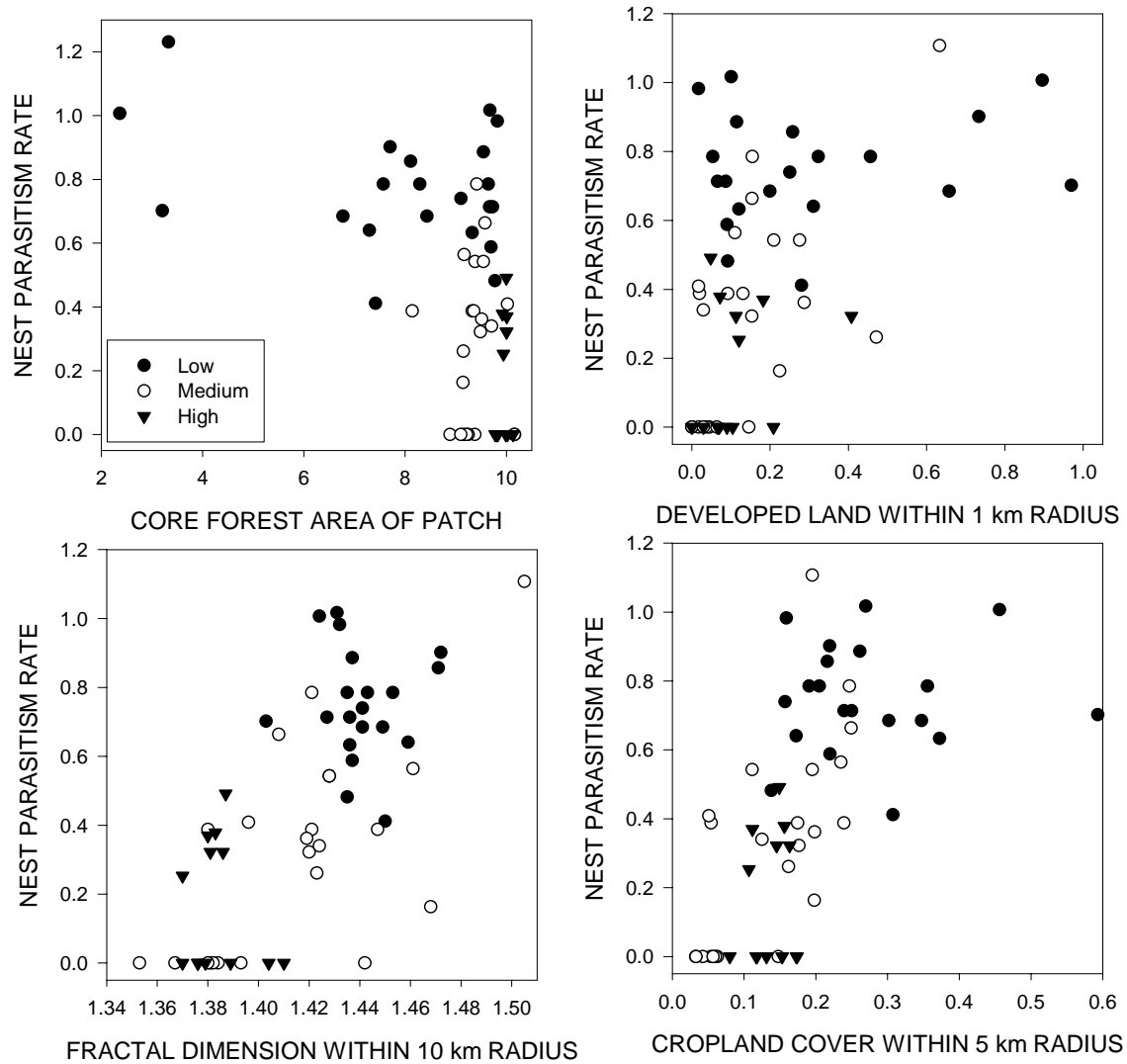


Figure 4. Relationship between nest parasitism rate (arcsine transformed) and indices of forest fragmentation at spatial scales of the patch and within 1-10 km radii of plot centers (site averages), and 50-100 km radii of site centers. Relative percent forest cover at the 100 km radius scale is classified as low, medium, or high.

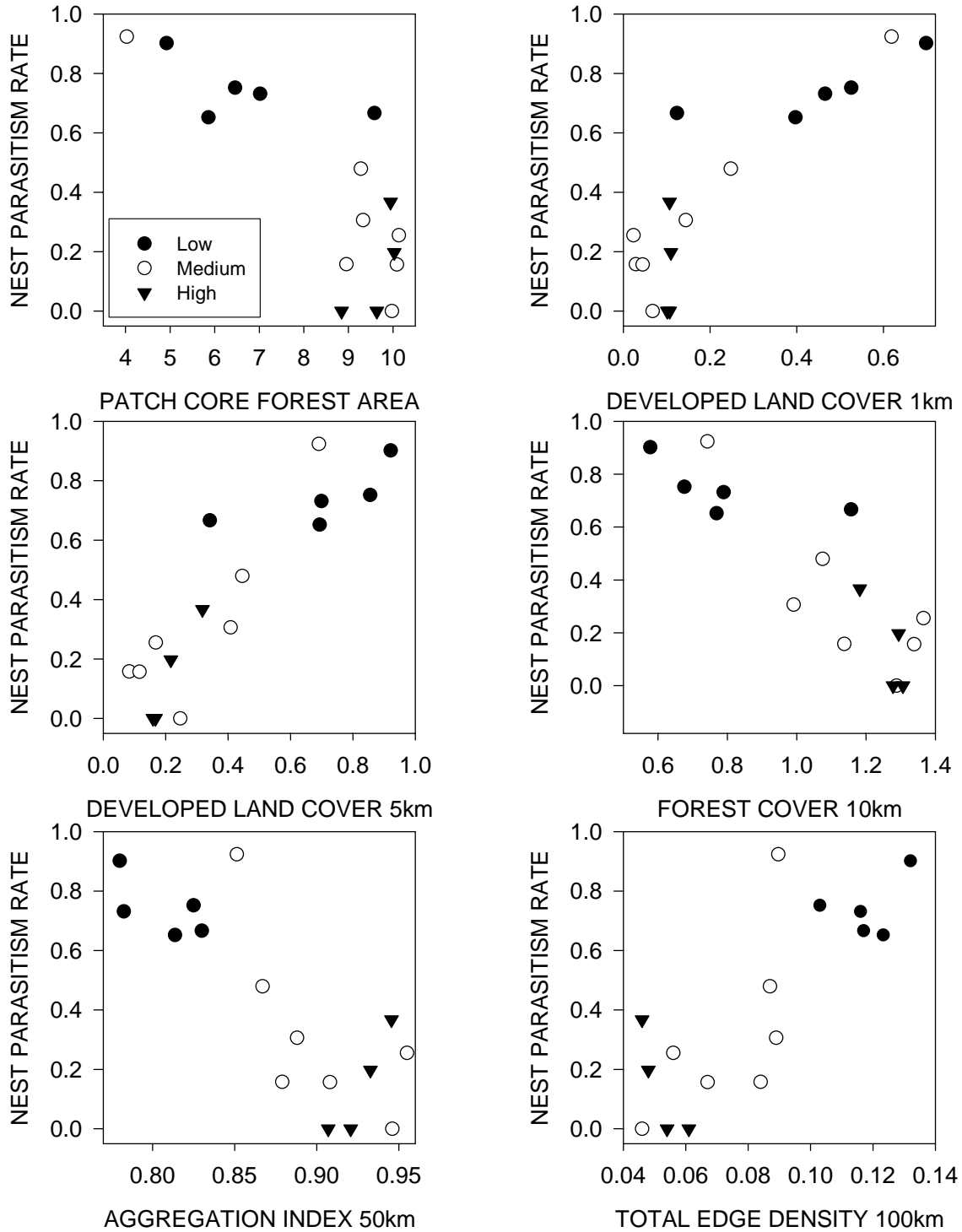


Figure 6. Relationship between daily nest predation rate (arcsine transformed) and distance between plot centre and nearest forest edge (site averages) or percent developed land cover (arcsine transformed) at spatial scales of 1-10 km radii of plot centers (site averages), and 50-100 km radius of site centers. Sites are classified according to region: East; Northern MidWest; Southern MidWest; and West.

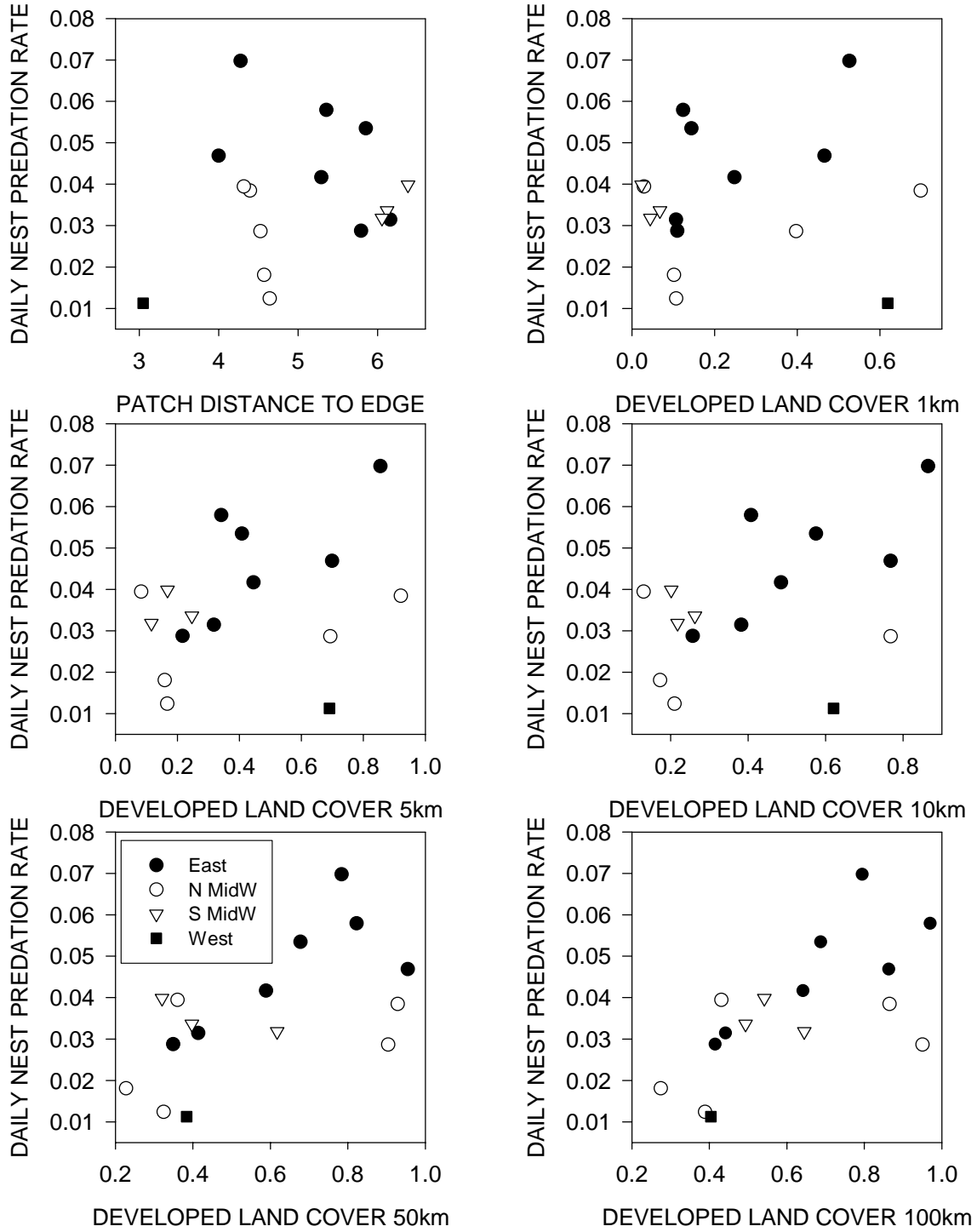


Figure 7. Relationship between Red-eyed Vireo lambda (assuming double-broodedness) and landscape variables at spatial scales of the plot forest patch, and within 1-5 km radii of plot centers for all plots with ≥ 5 nests. Relative forest cover within a 100 km radius of site centers is characterized as low, medium, or high.

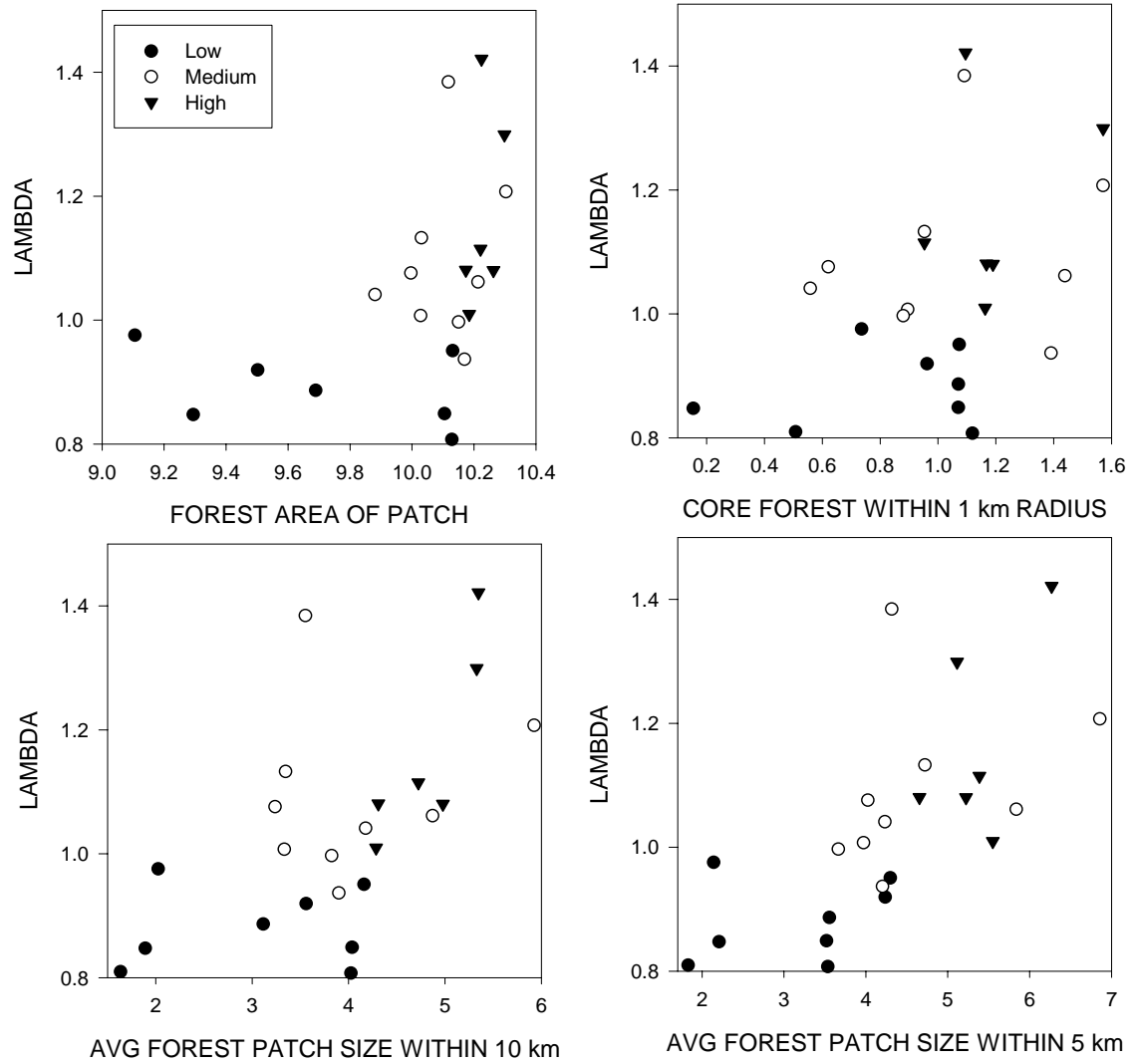


Figure 8. Relationship between Red-eyed Vireo lambda (assuming double-broodedness) and landscape variables at spatial scales of the plot forest patch, within 1-5 km radii of plot centers (site averages), and within radii of 50-100 km of site centers. Relative forest cover within a 100 km radius of site centers is characterized as low, medium, or high.

