

# Worm-eating Warbler *Helmitheros vermivorus*

Draft: 6 April 2003

## EXECUTIVE SUMMARY

**Preferred breeding habitat:** Moderate to steep hillside slopes of large tracts of mature, closed-canopy deciduous or mixed deciduous-coniferous forest with patches of dense shrub cover.

**Nest placement:** On the ground, usually on any available slope, such as hillside, ravine or riparian bank, and well hidden under a drift of dead leaves at the base of a sapling, shrub, root or rock.

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

- Non-parasitized nests: clutch  $4.64 \pm 0.93$ ; brood  $4.31 \pm 1.06$
- Cowbird parasitized nests: clutch  $3.55 \pm 1.23$ ; brood  $2.14 \pm 1.51$

**Number of broods per season:** One

**Annual adult survival rates:** Male: 72.6%; female assumed: 61.7%.

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

- Fledge at least 2.2 young per female per year
- Daily nest mortality  $\leq 4.0\%$  ( $\geq 35\%$  nest success) assuming zero parasitism
- Daily nest mortality  $\leq 3.4\%$  ( $\geq 41\%$  nest success) with 20% nest parasitism
- Daily nest mortality  $\leq 2.9\%$  ( $\geq 47\%$  nest success) with 40% nest parasitism
- Generally  $\leq 40\%$  nest parasitism across BBIRD sites
- Generally  $\leq 2.9$ -4.0% nest predation rate across BBIRD sites
- Percent forest cover  $\geq 50\%$  within a 100 km radius

**Nest mortality and parasitism rates in relation to landscape context:**

- Nest parasitism rate is strongly positively correlated with the degree of forest fragmentation across all spatial scales, but especially at the local landscape scale of within a 5-10 km radius.
- Nest predation rate is positively correlated with the degree of forest fragmentation across multiple spatial scales, including the patch scale and local landscape scale of within a 5-10 km radius.

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

- The relative effect of forest fragmentation on nest predation rate at the patch and local landscape scales is constrained by the degree of fragmentation at the broader landscape scale, such as within a 100 km radius.

**General conclusions:**

- Nest parasitism by the Brown-headed Cowbird has a strong negative effect on breeding productivity.
- Based on our assumptions, source populations ( $\lambda > 1$ ) exist only at sites with greater than 50% forest cover within a 100 km radius.
- Populations breeding in moderately to severely fragmented landscapes with less than 50% forest cover within a 100 km radius are generally not viable in the long term.
- The interiors of large, unfragmented forests are important source habitats.

**Management guidelines:**

- Given this species' area sensitivity, and the strong effect of forest fragmentation at a broad scale on population lambda, a primary regional management focus should be to maintain a representative network of large, mature, relatively undisturbed and unfragmented forests to serve as source populations across the breeding range of the Worm-eating Warbler (Robinson et al. 1995). These forests should ideally be greater than 10,000 ha in area, and incorporate the hilly topography preferred by this species.
- Given the severe effect of cowbird parasitism on Worm-eating Warbler 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 warbler populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Worm-eating Warbler 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 forests managed for silviculture, group and single-tree selective logging should be preferred over clear-cut logging. Selective logging has little impact on breeding densities, but may increase parasitism rates in some landscapes, whereas clear-cut logging reduces breeding densities substantially.

**DETAILED and BACKGROUND INFORMATION*****Distribution and habitat preference***

A Neotropical migrant, the Worm-eating Warbler breeds in the eastern United States, and overwinters in Central America and the Caribbean. At a broad scale, it breeds throughout most of the Appalachian region, as far north as southern Massachusetts, is absent from the Mississippi River valley, but occurs again west of the Mississippi in extensively forested regions of northern Louisiana, Arkansas, and south and central Missouri. It breeds locally over a more extensive range from southeastern Texas to southwestern Wisconsin (Hanners & Patton 1998).

The Worm-eating Warbler occurs most abundantly on moderate to steep hillside slopes of large tracts of mature, closed canopy deciduous or mixed deciduous-coniferous forest with patches of dense shrub cover. Plant composition appears less important than forest age and size, presence of hillsides, and occurrence of dense patches of shrub cover (Hanners & Patton 1998). It is an area-sensitive species, reaching highest breeding densities in forests of at least several hundred hectares, with suggested minimum area requirements ranging from 21 ha to greater than 340 ha (Hayden et al. 1985, Askins et al. 1987, Robbins et al. 1989, Wenny et al. 1993, Gale et al. 1997). For example, breeding densities were significantly higher in a large forest tract (4.45 males/10 ha) than in structurally similar 21-56 ha forest fragments (0.63 males/10 ha) in Connecticut (Gale et al. 1997).

Mean territory size 1.72 ha (SD = 0.78, range = 0.60-4.95, n = 94) in Connecticut (Hanners & Patton 1998). Density of 10-15 pairs/10 ha in Maryland (Greenberg 1987), up to 7.4-9.9 males/10 ha in mature northern hardwoods of West Virginia (Hall 1983), 4.46 males/10 ha in mixed oak forest in Connecticut (Gale et al. 1997), 2.13 males/10 ha in mature secondary oak-hickory forest in central Missouri (Wenny et al. 1993), 2.0 pairs/10 ha in mixed oak forest in southern Ohio (Artman et al. 2001).

### ***Nest site characteristics***

Nests on the ground, usually on any available slope, such as hillside, ravine or riparian bank. The nest is well hidden under a drift of dead leaves at the base of a sapling, against roots of shrubs and trees, beside a rock ledge or outcrop, or in dense low shrubs such as Huckleberry (*Gaylussacia baccata*) or Blueberry (*Vaccinium vacillans*). The slope at nests is significantly greater than the slope of random points, suggesting that topography rather than vegetation is of primary importance in nest-site selection (Hanners & Patton 1998).

### ***Laying seasons***

Earliest and latest Worm-eating Warbler nests in the BBIRD database were initiated on 21 April and 15 July, respectively, although nearly all laying takes place during a 6-week period 30 April to 10 June, with a peak in the week 7-13 May (Figure 1). This is similar to the laying peak in the first two weeks of May reported for Illinois, but is somewhat earlier than the season reported for Connecticut, where most first clutches are initiated in the last two weeks of May (earliest laying dates over 4 years 13-22 May), with a peak in the last week of May; second clutches are initiated 23 May – 15 June; and third clutches initiated 23 May – 15 June (Hanners & Patton 1998). The overall length of the laying season was estimated at 43 days.

### ***Assumptions in calculations of breeding productivity***

Eggs are laid at daily intervals (Hanners & Patton 1998). The mean clutch size of unparasitised nests is 4.9 (n = 59) in Connecticut (Hanners & Patton 1998) and 4.5 (SD = 0.9) in Virginia (Dececco et al. 2000). BBIRD data indicate a mean clutch size in unparasitised nests of 4.64 (SD = 0.93, n = 333). First clutches are larger (mean 5.4; n = 30) than second and third clutches (mean 4.5; n = 29; Hanners & Patton 1998). The mean incubation period has been reported as 12.0 days (SD = 2.6) in Virginia (Dececco et al. 2000), 12.4 days (n = 28; range 11-17) in Connecticut (Hanners & Patton 1998) and 12.5 days (n = 26) in Arkansas (Li 1994), and the mean nestling period as 8.5 days (n = 40) in Connecticut (Hanners & Patton 1998), 8.6 days (SD = 1.9) in Virginia (Dececco et al. 2000), and 9.6 days (n = 32) in Arkansas (Li 1994). BBIRD data indicate a mean incubation period of 12.7 days (range 10.5-14.5 days; n = 37) and a mean nestling period of 9.2 days (range 7-12 days; n = 57). There is no published information on re-nesting intervals following clutch loss, but females re-nest rapidly, sometimes laying the first egg in the replacement clutch before the nest (which takes 4-5 days to build) is fully lined (Hanners & Patton 1998). It is reportedly a single-brooded species as far south as

Virginia (Hanners & Patton 1998; Dececco et al. 2000). To calculate breeding productivity, we used a 43-day laying season, a 26-day nesting period (4-day laying, 13-day incubation, 9-day nestling), and a re-nesting interval of 5 days following nest failure.

To corroborate the results of the productivity model, we compared model-estimated seasonal fecundity with field measurements of annual fecundity from a well-studied Connecticut population (Gale et al. 1997, Hanners & Patton 1998). Assuming a daily mortality rate of 0.025 (mean of 2 years: Gale et al. 1997) and 3.48 host young fledged per successful nest (mean of 4 years: Hanners & Patton 1998), the model estimated seasonal fecundity at 2.3 fledged young per female (66% of females successful at fledging young), which compares very favorably with the average of 2.2 young/year, and 61% of females fledging young (mean of 4 years), determined from field studies (Hanners & Patton 1998).

### ***Assumptions in calculations of finite rate of population increase ( $\lambda$ )***

Return rates of males to a 56-ha study area in southwestern Connecticut ranged from 46.9-92.8% (mean 72.6% over 4 years), whereas return rates for females ranged from 27.3-52.2% (mean 46.8% over 3 years). Female survival was thought to be biased low due to greater breeding dispersal by females, which can move  $\geq 500$  m between years (Hanners & Patton 1998). We assumed a male survival rate of 72.6%, a female survival rate of 61.7% (85% of male survival, as observed for other North American passerines, e.g. Hann (1948) and Holmes & Sherry (1992)), and a juvenile female survival rate of 36.3% (50% of the adult male 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 (3.55, SD = 1.23, n = 64) was 23% lower than that of non-parasitized nests (4.64, SD = 0.93, n = 333). Mean fledging success was 50% lower from successful parasitized nests (2.14, SD = 1.51, n = 72) than from non-parasitized nests (4.31, SD = 1.06, n = 317). Similarly, nests parasitized with one and two cowbird eggs fledged 50% and 85% fewer host young respectively than non-parasitized nests in West Virginia (Dececco et al. 2000). The mean number of Brown-headed Cowbird eggs laid per parasitized Worm-eating Warbler nest increased non-significantly ( $F = 10.10$ ;  $P = 0.086$ ), and the mean number of host young fledged per successful nest decreased non-significantly ( $F = 6.47$ ;  $P = 0.052$ ) as the site-specific parasitism rate increased (Figure 2). These trends were marginally non-significant due to small sample size and low statistical power. The relationship between the mean number of host young fledged per successful nest ( $f$ ) and nest parasitism rate ( $p$ ) is described by  $f = -1.520p + 4.074$  among sites, and  $f = -2.007p + 4.266$  among plots. At

parasitism rates of 20% and 40%, the mean number of host young fledged per successful nest is approximately 3.8 and 3.46 respectively.

### ***Effects of landscape-level habitat variables on nest parasitism***

Among all plots, nest parasitism rate was strongly positively correlated with the degree of forest fragmentation across all spatial scales, particularly at the patch scale and within 5-10 km radii of plot centers (Table 2, Figure 3). Similarly, nest parasitism rate was strongly positively correlated with the degree of forest fragmentation among sites, particularly at the 5-10 km radius scale (Table 2, Figure 4). There was no indication that nest parasitism rates differed, independently of the degree of forest fragmentation, between the East and Southern Midwest regions (Figure 4).

Percent forest cover was strongly correlated with other indices of fragmentation, leading to strong negative correlations between forest cover and parasitism rate across all spatial scales (Table 3). Robinson et al. (1995) similarly found a significant negative correlation between Worm-eating Warbler nest parasitism rate and percent forest cover within a 10 km radius of sites across the Midwest. At an extensively forested site in southern Indiana, nest parasitism was significantly greater within forest adjoining an agricultural corridor (39%), than within interior forest at least 2 km from the nearest agricultural edge (15%; Ford et al. 2001).

**Table 1.** Summary of Worm-eating Warbler breeding productivity and estimated finite rate of population increase ( $\lambda$ ) across BBIRD sites.

Site	No. of nests	Clutch size <sup>1</sup>	Parasitism rate (%) <sup>2</sup>	DPR (%) <sup>3</sup>	Nest success (%) <sup>4</sup>	Fledglings/nest <sup>5</sup>	Annual fecundity	Lambda
NW Monongahela Natl Forest, WV	5		0	10.53	5.55			
Nantahala National Forest, NC	5	5.20	0	2.56	50.90			
Columbia, MO	18	4.83	66.67	3.15	43.51	2.93	1.72	0.93
Hoosier Natl Forest, IN	266	4.70	25.19	4.20	31.14	3.78	1.74	0.93
Ouachita Natl Forest, AR	20	3.91	0	2.95	45.93	3.42	2.09	1.00
Wayne Natl Forest, OH	106	4.78	19.81	2.88	39.53	4.05	2.22	1.02
Ozarks, MO	51	4.41	3.92	3.01	42.03	4.13	2.37	1.05
SE Monongahela Natl Forest, WV	131	4.65	6.87	2.08	54.62	4.04	2.79	1.12
Ozark Natl Forest, AR	65	4.70	0	1.75	58.21	4.3	3.09	1.18

<sup>1</sup>Number of host eggs incubated in non-parasitized nests

<sup>2</sup>Percentage of nests that received 1 or more cowbird eggs

<sup>3</sup>Percentage of nests lost to predators per day

<sup>4</sup>Percentage of nests that produced at least 1 host fledgling or cowbird

<sup>5</sup>Number of host young fledged per successful nest

<sup>6</sup>Average 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  $\geq 5$  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 edge density; percent core forest; percent cropland; Fractal dimension; Contagion; Aggregation index; total edge density of all land cover types in the landscape; and average patch size of forest patches  $>10$  ha. 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		
	Dependent variables	Independent Variables	Adj. R2	Slope	Dependent variables	Adj. R2	Slope
Patch	Parasitism	Edge density	0.49***	1.28	Edge density	0.80***	1.46
	Predation	Forest patch area	0.13*	-0.026	To nearest edge	0.16	
	Lambda	Forest patch area	0.1		Edge density	0.32	
1 km	Parasitism	% core forest	0.11*	-0.46	Aggregation index	0.70**	-11.91
	Predation	% core forest	0.01		Fractal dimension	-0.01	
	Lambda	Contagion	0		Fractal dimension	0.32	
5 km	Parasitism	Total edge density	0.45***	7.2	% cropland	0.89***	2.74
	Predation	Avg patch $>10$ ha	0.17**	-0.0097	Fractal dimension	0.19	
	Lambda	Avg patch $>10$ ha	0.12*	0.083	Contagion	0.46	
10 km	Parasitism	Fractal dimension	0.48***	5.02	% cropland	0.88***	2.58
	Predation	Fractal dimension	0.12*	0.15	Fractal dimension	0.26	
	Lambda	% cropland	0.16*	-0.64	Contagion	0.42	
50 km	Parasitism				% core forest	0.67**	-1.05
	Predation				% cropland	0.39	
	Lambda				% cropland	0.43	
100 km	Parasitism				Total edge density	0.74**	9.1
	Predation				% cropland	0.75**	0.035

Lambda

% cropland

0.61\*

-0.39



**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		-0.88**			-0.28		0.58
1 km	0.83**	-0.79*	0.84**	-0.04	-0.29	0.14	0.57
5 km	0.91***	-0.92***	0.95***	-0.09	-0.36	0.06	0.65
10 km	0.91***	-0.93***	0.95***	-0.12	-0.32	0.06	0.59
50 km	0.74*	-0.83**	0.81**	-0.25	-0.43	-0.01	0.53
100 km	0.70*	-0.80**	0.77*	-0.26	-0.65	-0.08	0.66
150 km		-0.77*			-0.75*		0.71

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

#### ***Effects of landscape-level habitat variables on nest predation rate***

Among all plots, daily nest predation rate was significantly positively correlated with the degree of forest fragmentation at the spatial scale of the patch and within 5-10 km radii of plot centers, particularly within a 5 km radius (Table 2, Figure 5). These data also suggest that plot-specific nest predation is constrained by the degree of forest fragmentation at broader spatial scales, such as within a 100 km radius of sites (compare nest predation at plots from sites with low forest cover within a 100 km radius, versus those from sites with medium-high forest cover in Figure 5). Indeed, among sites, nest predation rate was significantly correlated with the degree of forest fragmentation at only the broadest spatial scale, within a 100 km radius (Table 2).

Robinson et al. (1995) found a significant negative correlation between nest predation rate and percent forest cover within a 10 km radius across sites in the Midwest, suggesting a strong effect of forest fragmentation on nest predation rate, with greater nest predation in more fragmented landscapes. No study has rigorously examined forest edge effects on Worm-eating Warbler nest predation. The daily nest mortality rate was non-significantly lower within interior forest (3.0%) than within forest adjoining an agricultural corridor (3.7%) in southern Indiana (Ford et al. 2001).

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

Among all plots,  $\lambda$  was significantly negatively correlated with the degree of forest fragmentation within 5-10 km radii of plot centers, but not at smaller spatial scales (Table 2, Figure 7). Plot-specific  $\lambda$  appears strongly constrained by the relative degree of forest cover (an index of fragmentation) at broader spatial scales, such as within a 100 km

radius (compare lambda values of plots from sites with low forest cover within a 100 km radius, versus those from sites with medium-high forest cover in Figure 7). Indeed, among sites, lambda decreased with increasing degree of forest fragmentation across all spatial scales (Figure 8), but this relationship was significant only at the broadest spatial scale, within a 100 km radius (Table 2), due to low statistical power.

### ***Effects of silviculture on nest predation and nest parasitism***

In an extensively forested region of southern Indiana, nest parasitism rates in forest adjoining large clearcuts and small (<1 ha), managed wildlife openings (25% and 33% parasitism respectively) were higher than the parasitism rate in interior forest (12%), but lower than in forest adjoining an agricultural corridor (43% parasitism: Winslow et al. 2000). No data on the effects of silviculture on nest predation.

Worm-eating Warblers were less abundant in mixed-oak and aspen forest plots with 50-75% of their area constituting regenerating (2-10 years old) clear-cuts (0.0 individuals/10 ha) than uncut forest (1.2 individuals /10 ha) in Pennsylvania (Yahner 1993). Densities were similarly reduced in clearcut and shelterwood treatments in the Missouri Ozarks (Annand & Thompson 1997). Breeding densities were significantly reduced in plots experiencing either a heavy cutting of understory vegetation or a combination of both understory cutting and selective cutting of the overstory, in comparison with densities in mature oak-hickory forest (Rodewald & Smith 1998).

However, breeding densities were not affected by recent (1-5 years previously) or older (10-15 years earlier) group-selection or single-tree selection logging that created openings of 0.02-0.4 ha in southern Illinois (Robinson & Robinson 1999). Densities were similarly unaffected by group selection (2-5 openings, 0.2-0.4 ha, every 8 ha) and single-tree selection logging in the Missouri Ozarks (Annand & Thompson 1997).

### ***Effects of burning on nest success***

No data on effects on nest success. However, breeding densities declined incrementally in response to annual (1-4 years) prescribed burns, and did not recover within 1 year of burning in a southern Ohio mixed-oak forest (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 is strongly positively correlated with the degree of forest fragmentation across all spatial scales, but especially at the local landscape scale of within a 5-10 km radius. Similarly, nest predation rate is positively correlated with the degree of forest fragmentation across multiple spatial scales, including the patch scale and local landscape scale of within a 5-10 km radius. However, there is evidence to suggest that the relative effect of fragmentation at the local landscape on nest predation

rate is constrained by the degree of fragmentation at the broader landscape scale, such as within a 100 km radius.

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. The local cowbird abundance therefore 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). Similar 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).

As lambda is more strongly determined by nest predation rate than nest parasitism rate ( $r_p = -0.86$  and  $-0.35$  respectively), lambda is more strongly correlated with the degree of forest fragmentation at broader spatial scales, especially within a 100 km radius.

### ***Mapping predicted source and sink habitat***

Mapping predicted source and sink habitat is problematic due to insufficient resolution in the relationship between lambda and landscape metrics of forest fragmentation across BBIRD sites.

## **MANAGEMENT GUIDELINES**

Given this species' area sensitivity, and the strong effect of forest fragmentation at a broad scale on population lambda, a primary regional management focus should be to maintain a representative network of large, mature, relatively undisturbed and unfragmented forests to serve as source populations across the breeding range of the Worm-eating Warbler (Robinson et al. 1995). These forests should ideally be greater than 10,000 ha in area, and incorporate the hilly topography preferred by this species.

Given the severe effect of cowbird parasitism on Worm-eating Warbler 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 warbler populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of Worm-eating Warbler 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 forests managed for silviculture, group and single-tree selective logging should be preferred over clear-cut logging. Selective logging has little impact on breeding densities, but may increase parasitism rates in some landscapes, whereas clear-cut logging reduces breeding densities substantially.

## **FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS**

The Worm-eating Warbler appears to be a strongly area-sensitive species, but more research is needed to accurately determine the relationship between breeding density and each of 1) distance to forest edge, and 2) patch area of forest fragments, within suitable habitat. Area sensitivity can counteract the negative effects of forest fragmentation on reproductive success (Donovan & Lamberson 2001), so a good understanding of such edge/area sensitivity will be important for any comprehensive modeling of source-sink dynamics in this species.

The effect of habitat edge on nest predation and parasitism rates has not been thoroughly investigated. Given the strong effect of nest predation on breeding productivity, and thus  $\lambda$ , it would be especially useful to know how nest predation risk is influenced by distance to habitat edge.

Most BBIRD data are derived from sites that are relatively well forested at both local and broad landscape spatial scales, with two sites in extensively fragmented landscapes. More data from sites with high and intermediate levels of forest fragmentation would improve resolution in our understanding of the relationship between nesting success and  $\lambda$ , and the degree of forest fragmentation across multiple spatial scales. These data are not difficult to collect – see Martin and Guepel (1993), and the BBIRD website: . A sample of ideally at least 25 nests is required, to give a sample of at least 10 successful nests for a reliable estimate of mean number of host young fledged per successful nest. These nests must be 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.

Worm-eating Warbler breeding habitat requirements have been described for the wooded hillsides typical of much of its breeding range, but not for the southern coastal plain, where it breeds in high densities on apparently flat ground (Hanners & Patton 1998).

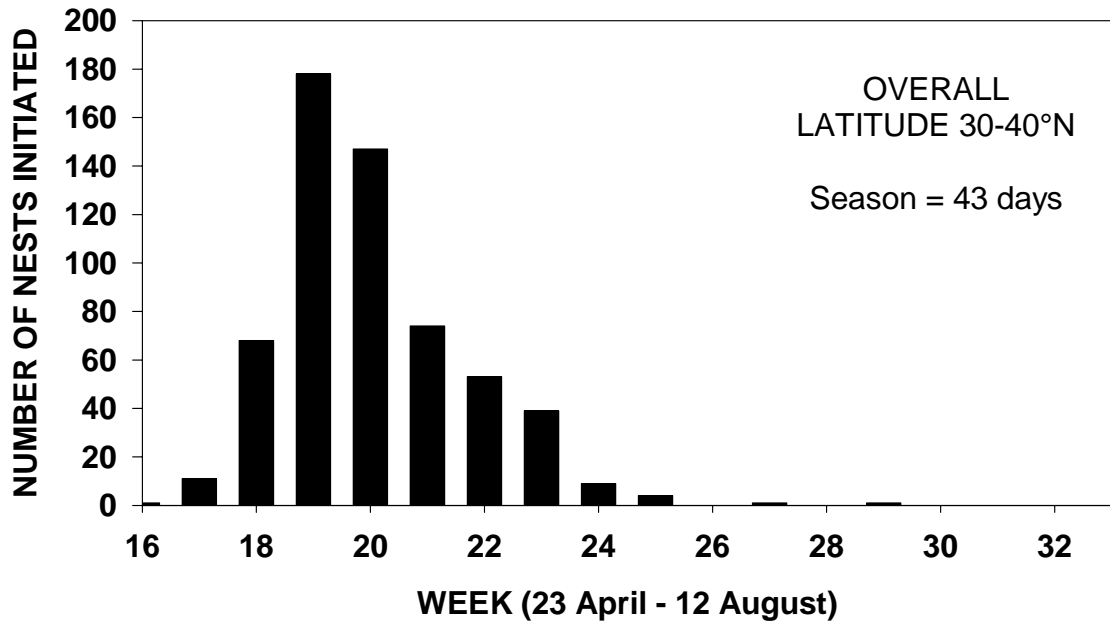
## **REFERENCES**

- 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.
- Askins, R.A., Philbrick, M.J. & Sugeno, D.S. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39: 129-152.
- 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.

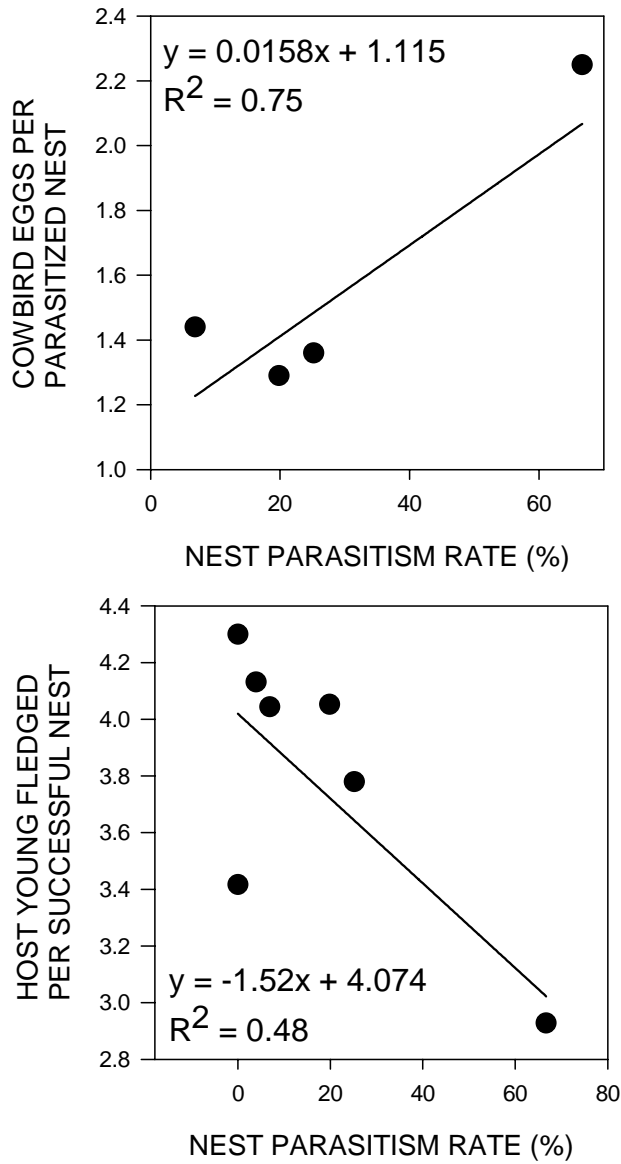
- Donovan, T.M., Jones, P.W., Annand, E.M. & Thompson, F.R. III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064-2075.
- Donovan, T.M. & Lamberson, R.H. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. *Ecology* 82: 1170-1179.
- Ford, T.B., Winslow, D.E., Whitehead, D.R. & Koukol, M.A. 2001. Reproductive success of forest-dependent songbirds near an agricultural corridor in south-central Indiana. *Auk* 118: 864-873.
- Gale, G.A., Hanners, L.A. & Patton, S.R. 1997. Reproductive success of Worm-eating Warblers in a forested landscape. *Conservation Biology* 11: 246-250.
- Greenberg, R. 1987. Seasonal foraging specialization in the Worm-eating Warbler. *Condor* 89: 158-168.
- 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.
- Hall, G.A. 1983. West Virginia birds: distribution and ecology. Carnegie Museum of Natural History Special Publication No. 7.
- Hann, H.W. 1948. Longevity of the Ovenbird. *Bird Banding* 19: 5-12.
- Hanners, L.A. & Patton, S.R. 1998. Worm-eating Warbler *Helmitheros vermivorus*. The Birds of North America, No. 367 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia.
- Hayden, T.J., Faaborg, J. & Clawson, R.L. 1985. Estimates of minimum area requirements for Missouri forest birds. *Transactions Missouri Academy of Science* 19: 11-22.
- Holmes, R.T. & Sherry, T.S. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. *In Ecology and Conservation of Neotropical Migrant Landbirds* (J.M. Hagan III & D.W. Johnson, Eds) pp. 563-575. Smithsonian Press, Washington D.C.
- 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.
- Martin, T.E. & Guepel, G.E. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64: 507-519.
- Robbins, C.S., Dawson, D.K. & Dowell, B.A. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. *Wildlife Monographs* 103: 1-34.
- 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., 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.
- 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.

- 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.
- Wenny, D.G., Clawson, R.L., Faaborg, J. & Sheriff, S.L. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. *Condor* 95: 968-979.
- 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.
- Yahner, R.H. 1993. Effects of long-term forest clear-cutting on wintering and breeding birds. *Wilson Bulletin* 105: 239-255.

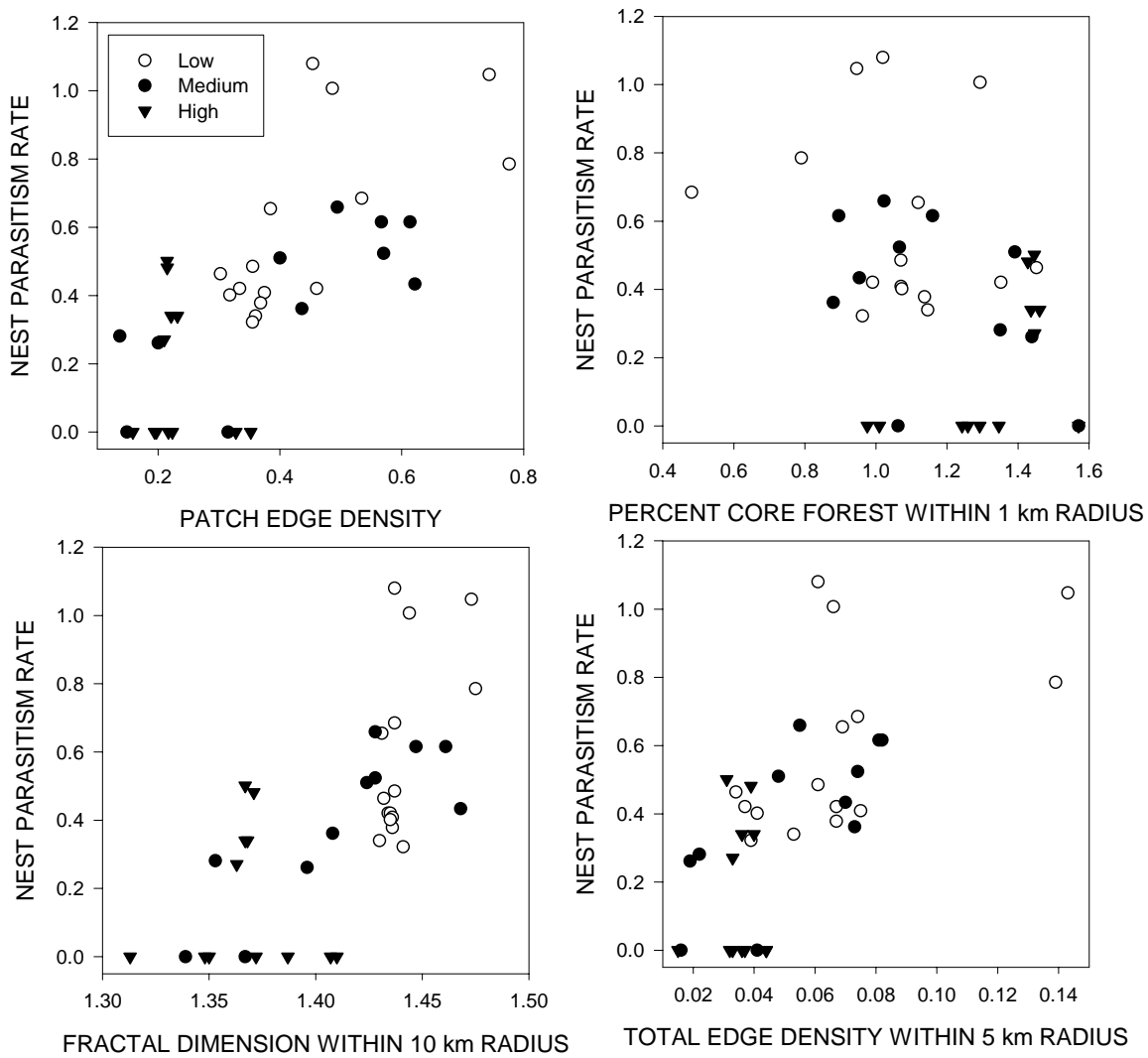
**Figure 1.** Worm-eating Warbler laying season (number of new nests initiated each week) in relation to latitude. Laying season length estimated using the MacArthur index (see text for details).



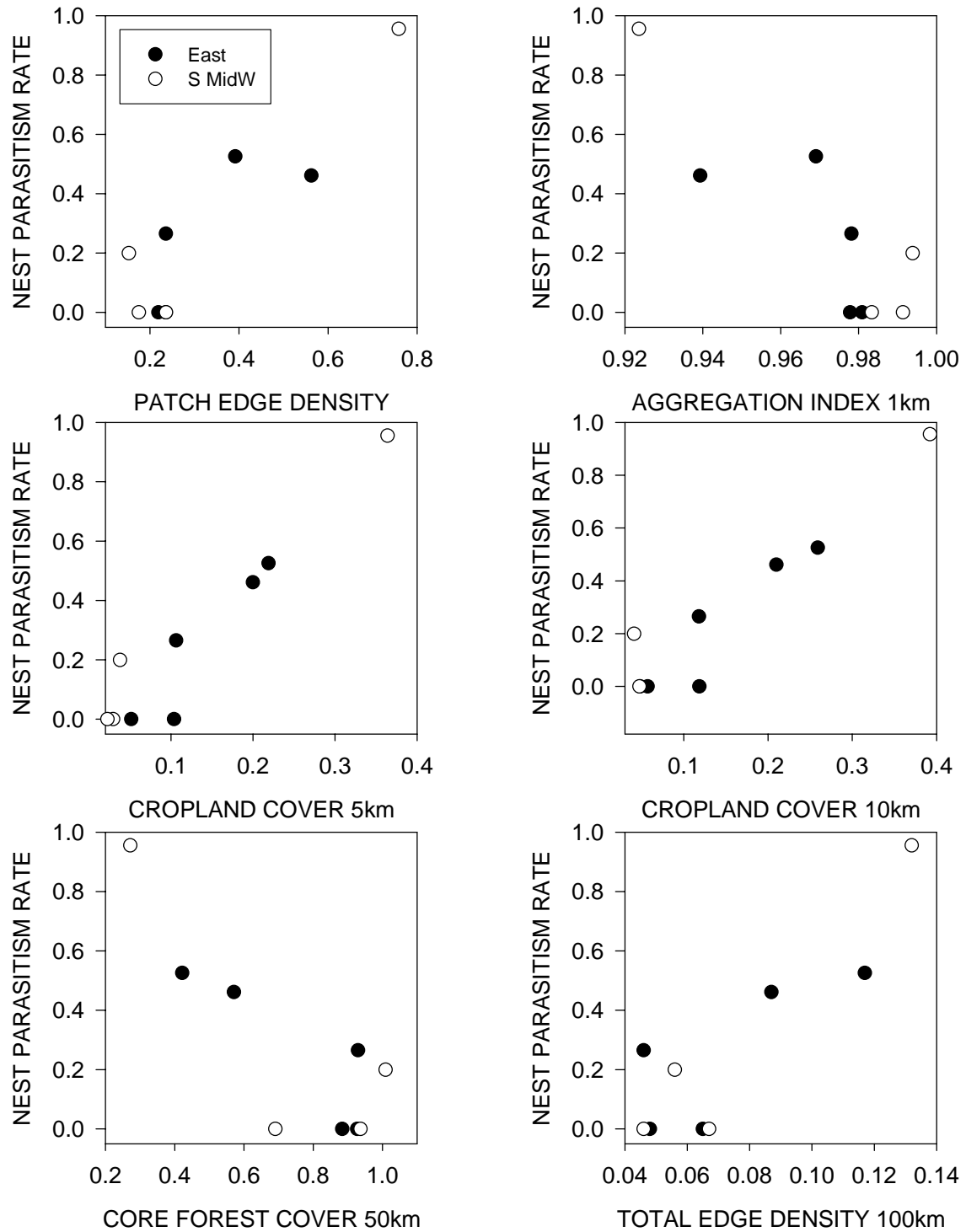
**Figure 2.** The mean number of Brown-headed Cowbird eggs laid per parasitized Worm-eating Warbler nest (top) increases non-significantly ( $F = 10.10$ ;  $P = 0.086$ ), and the mean number of host young fledged per successful nest (bottom) decreases non-significantly ( $F = 6.47$ ;  $P = 0.052$ ) as the site-specific parasitism rate increases.



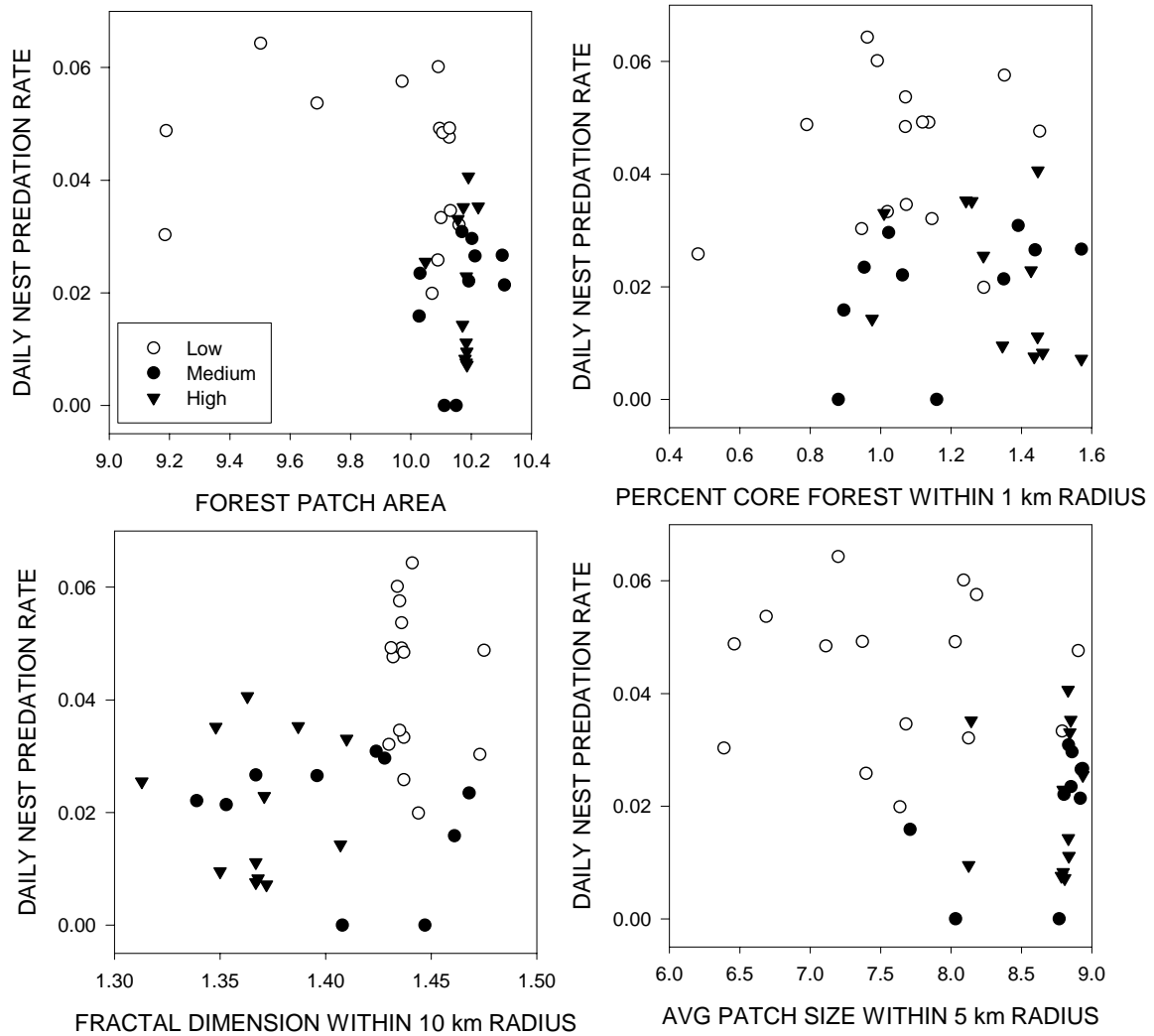
**Figure 3.** Relationship between Worm-eating Warbler nest parasitism rate (arcsine transformed) and transformed indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km radii of plot centers for all plots with  $\geq 5$  nests. Plots are grouped into three classes on 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 plot 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, and Southern Midwest.

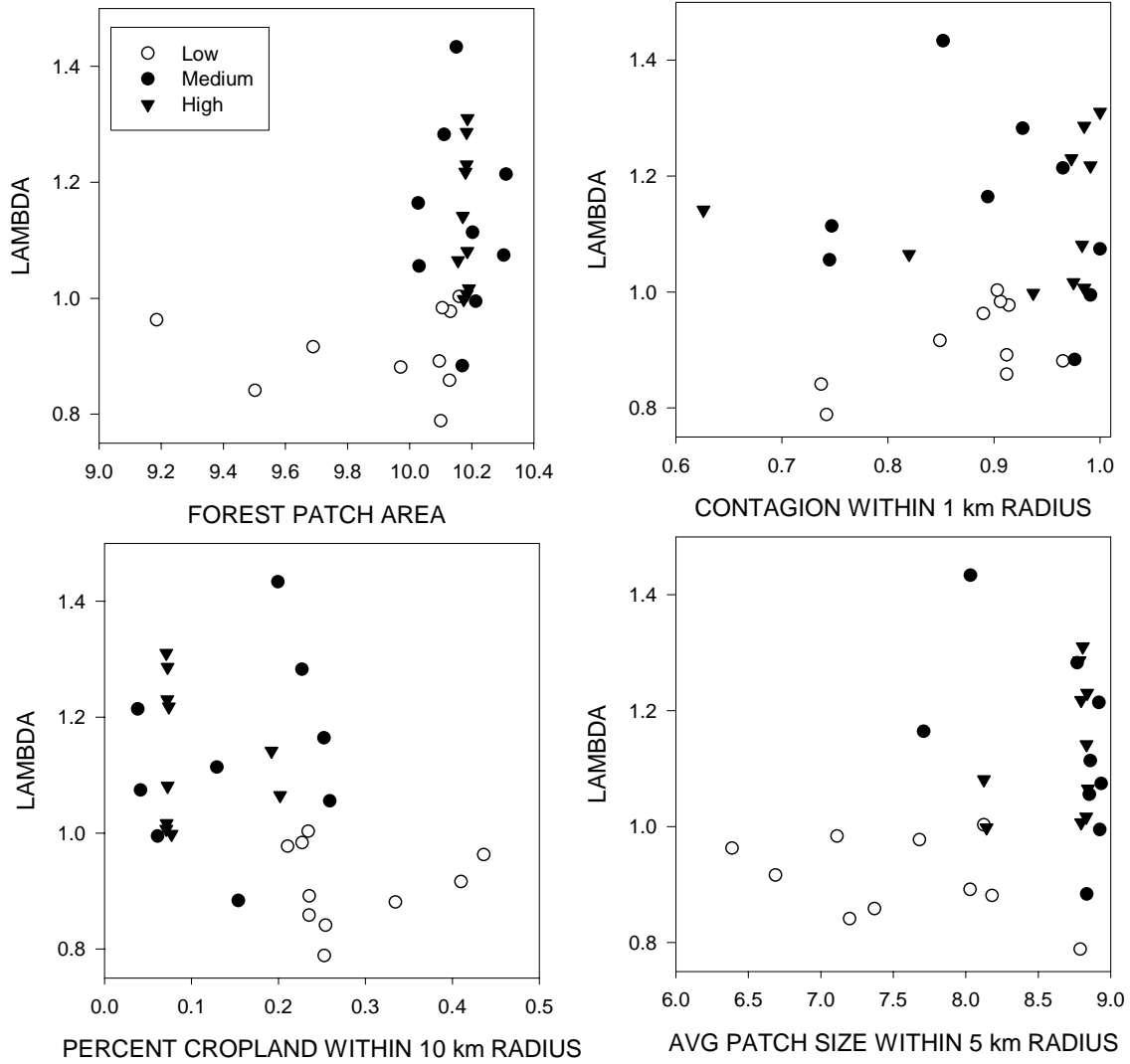


**Figure 5.** Relationship between Worm-eating Warbler daily nest predation rate and indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km radii of plot centers for all plots with  $\geq 5$  nests. Plots are grouped into three classes on the basis of relative percent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





**Figure 7.** Relationship between Worm-eating Warbler lambda and indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km radii of plot centers for all plots with  $\geq 5$  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 8.** Relationship between lambda and indices of forest fragmentation at spatial scales of the plot forest patch, within 1-10 km radii of plot centers (site averages), and 50-100 km radii of site centers.

