Hooded Warbler *Wilsonia citrina*

Preferred breeding habitat: Mixed hardwood forests in the north, particularly moist woodlands and ravines, and cypress-gum swamps in the south. Depends critically on a well developed shrub understory, usually associated with small canopy openings, for nesting in.

Nest placement: At height of 0.3-1.4 m among shrub stems within patch of dense understory vegetation 1-2 m high.

Clutch size / Fledging brood size (±SD)**:**

- Non-parasitized nests: clutch 3.38 ± 0.72; brood 3.06 ± 0.86
- Cowbird parasitized nests: clutch 2.88 ± 0.94; brood 1.10 ± 1.16

Number of broods per season: Two

Annual adult survival rates: Males 62%, females 53%

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

- Fledge at least 2.1 young per female per season.
- In the presence of nest parasitism, nest parasitism rate < 40% and daily nest predation rate < 3-4%.
- In the absence of nest parasitism, daily nest predation rate < 5%.

Nest mortality and parasitism rates in relation to landscape context:

- Nest parasitism rate > 40% when percent forest cover within 50 km radius < 50%

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

- Nest parasitism rate decreases with increasing distance from forest edges, and increases as the degree of forest fragmentation at landscape scales increases. Nest parasitism risk within a local patch is constrained by the degree of forest fragmentation at broader landscape scales, particularly within a 50 km radius.

General conclusions:

- Nest parasitism has a severe effect on Hooded Warbler breeding productivity, reducing host fledging success by 62% among parasitized nests.
- Nest parasitism rate is most strongly determined by the degree of forest fragmentation at spatial scales of 10-50 km radii.
- There is no predictable relationship between nest predation rate and any index of forest fragmentation at any spatial scale.
- Lambda is negatively correlated with degree of forest fragmentation at local landscape scales, particularly within a 5 km radius.

Management guidelines:

- In forests with limited gap availability, habitat suitability for Hooded Warblers can be increased by using single-tree or small-group-selection logging treatments that create gaps no larger than 0.05 ha, leaving the resulting shrub layer untouched. The larger gaps created by group-selection logging (0.05-0.2 ha) are at the upper limit of those used by Hooded Warblers. Managers should retain some mature trees, leaving a residual basal area in the large tree size class (DBH > 38 cm) of at least 12 m^2/ha., as a mature forest component is important for Hooded Warblers (Crawford et al. 1981, Whittam et al. 2002). In forest blocks exceeding 100 ha, logging should not occur simultaneously across the entire forest, but be staggered over a period of several years, preferably decades, to ensure long-term habitat suitability for Hooded Warblers (Whittam et al. 2002).

- Given the severe effect of cowbird parasitism on Hooded 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.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

The Hooded Warbler is a Neotropical migrant that breeds in the eastern United States and extreme south-eastern Canada, and winters in Central America. The breeding range extends from southeastern Nebraska to the southern Great Lakes region (including southernmost Ontario), south to southeastern Texas, the Gulf Coast, and northern Florida. (Evans Ogden & Stutchbury 1994).

On their breeding range, Hooded Warblers inhabit mixed hardwood forests in the north, usually dominated by maple (*Acer*), beech (*Fagus grandifolia*), or oak (*Quercus*), and cypress-gum swamps in the south (Evans Ogden & Stutchbury 1994). A southern Ontario population occupied a deciduous forest with a mean canopy height of 28 m, mean canopy cover of 88%, and mean shrub cover of 87% (Gartshore 1988). Deciduous forests inhabited are usually mature to the point where trees are large enough to create tree-fall gaps, as they depend critically on a well developed shrub understory for nesting in. Thus, in mature forests, territories usually include small clearings, particularly those created by periodic tree death, where a shrub understory is available for nesting (Evans Ogden & Stutchbury 1994, Whittam et al. 2002). They are often associated with moist woodlands and ravines, and will commonly invade selectively logged deciduous forests 1-5 years after harvesting, remaining as long as there are sufficient understorey shrubs for nesting (Whitcomb et al. 1977, Gartshore 1988, Annand & Thompson 1997, Robinson & Robinson 1999). Local populations have declined dramatically in forests with a disappearing shrub layer (Evans Ogden & Stutchbury 1994, Whittam et al. 2002). In less mature forests, judicious selective logging that creates openings of 0.02-0.4 ha can mimic natural gaps and facilitate the maintenance of Hooded Warbler populations (Gartshore 1988, Whittam et al. 2002). In southern Illinois, Hooded Warblers colonized selectively logged deciduous forest 1-4 years after logging, then disappeared (Robinson & Robinson 1999). In southwestern Ontario, Hooded Warblers colonized an area with extensive pine plantations only after substantial group-selection and singe-tree selection logging had taken place, using gaps 1-14 years old and preferring stands with higher logging intensity (Whittam et al. 2002). Selectively logged pine plantations can maintain viable Hooded Warbler populations, and can thus provide important opportunities for their conservation, provided that a substantial deciduous shrub layer is present (Whittam et al. 2002). On the other hand, selective logging accompanied by heavy cutting of understory shrubs and saplings (to promote regeneration of desirable tree species) reduces Hooded Warbler populations (Rodewald & Smith 1998), suggesting that the dense shrub and herb layer generated by the canopy opening, rather than the opening itself is the key habitat feature to which they respond (Whittam et al. 2002). Nonetheless, a mature forest component is important for Hooded Warblers (Crawford et al. 1981, Whittam et al. 2002). A mixture of mature trees and shrubby canopy openings provide the horizontal and vertical habitat structure preferred by Hooded Warblers: a patchwork of shrubby understory for nesting in; a relatively open subcanopy used for song perches; and a relatively closed upper canopy (Whittam et al. 2002). There are no data to suggest that the habitat requirements of juveniles or post-breeding adults on the breeding range differ from those of breeding adults.

Breeding territories range from 0.5-0.75 ha in size (Evans Ogden & Stutchbury 1994). The overall density of territorial males varies greatly among geographic areas and habitats, with higher densities generally found in forests with a more extensive shrub layer and larger area of continuous forest: 0.42-0.70 males/ha in a high density population in Pennsylvania (Evans Ogden & Stutchbury 1994); 0.07-0.25 males/ha in New York (Eaton 1988); 0.25 males/ha in Maryland (MacClintock et al. 1977); and 0.12-0.25 males/ha in Ontario (Gartshore 1988).

On their breeding range, Hooded Warblers are area-sensitive forest birds, meaning that they are generally found only in larger (> 15 ha) tracts of mature forest (Robbins 1979; Evans Ogden & Stutchbury 1994).

Nest site characteristics

Hooded Warblers nest within patches of shrub within forest or along the edge of forest. They preferentially select nest sites beneath a gap in the overstory canopy, where there is a denser understory vegetation of 1-2 m high shrubs and saplings, the height range of plants generally used to support nests (Kilgo et al. 1996, Bisson & Stutchbury 2000, Whittam et al. 2002). In a South Carolina bottomland hardwood forest (70-100 years old), Hooded Warblers showed a distinct preference for nesting within 50 m of group-selection or clearcut logging edges, where dense patches of switchcane (*Arundinaria gigantea*) stems, the preferred nesting substrate, were most common. Few nests were located at distances greater than 150 m from edges (Moorman et al. 2002). Switchcane forms extensive thickets (canebreaks) in southeastern swamps, and is the preferred substrate species throughout much of the southeastern United States (Kilgo et al. 1996).

The open cup nest is often placed near the edge of a distinct patch of shrub, at a height of 0.29-1.43 m, in crotches of the main stem with primary branches as supports (Evans Ogden & Stutchbury 1994, Kilgo et al. 1996). In Pennslyvania, average (±SE) nest characteristics (n = 97) were: nest height: 53 ± 1.8 cm; nest plant height: 1.02 ± 0.03 m; and 23.7 ± 1.3 stems/m^2 within 1 m of nest (Howlett & Stutchbury 1996). In South Carolina, nest characteristics (n = 45) were: nest height: 98 ± 36 cm; nest plant height: 1.76 ± 0.10 m; potential substrate (all woody stems 1-3 m tall) density: 3.79 ± 0.6 (Kilgo et al. 1996).

Laying seasons

Earliest and latest Hooded Warbler nests in the BBIRD database were initiated on 25 April and 25 July respectively, although most laying took place during a 7-8 week period: 7 May to 1 July at latitudes 30-40°N and 14 May to 1 July at latitudes 40-45°N (Figure

1). Although egg laying peaks approximately two weeks later at latitudes of 40-45°N than at latitudes of 35-40°N, there is little difference in the length of the laying season (61 and 62 days respectively), with the average laying season estimated at 62 days.

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (Evans Ogden & Stutchbury 1994). BBIRD data indicate a mean clutch size in unparasitized nests of 3.38 (SD = 0.72; n = 330), ranging from 3.25-3.69 across sites (Table 1). It is further reported as 3.5 (SE = 0.2; n = 22) in southwestern Ontario (Bisson & Stutchbury 2000), and 3.2 (SE = 0.1; n = 86) in South Carolina (Moorman et al. 2002). The modal incubation period has been reported as 11 days (Evans Ogden & Stutchbury 1994), although a mean incubation period of 11.9 days (n = 54) has been reported in Arkansas (Li 1994). The modal nestling period is reported as 9 days in Pennsylvania (Evans Ogden & Stutchbury 1997), although a mean nestling period of 7.9 days (n = 68) has been reported in Arkansas (Li 1994). BBIRD data indicate a mean incubation period of 11.8 days (range 9-12; n = 51) and a mean nestling period of 9.2 days (range 7-11 days; n = 51). There is no published information on re-nesting intervals following nest loss, but nests take 2-6 days to build (Evans Ogden & Stutchbury 1994). In Pennsylvania, 45% of females that successfully fledge their first brood attempt a second brood, with an average re-nesting interval of 11 days (range 3-22 days; n = 15: Evans Ogden & Stutchbury 1997). To calculate breeding productivity, we used a 23-day nesting period (2-day laying, 12-day incubation, 9-day nestling), a 6-day re-nesting interval following nest loss, and an 11-day re-nesting interval following successful fledging.

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

Monthly survival among Hooded Warblers (all sexes and age classes included) wintering in a southern Belize tropical forest was estimated at 0.93, which if extrapolated over 12 months, yields an annual survival estimate of 42% (Conway et al. 1995).The return rate of banded breeding males in a Pennsylvania population was 63.6% (n = 33) in one year and 45.2% (n = 31) in the following year, yielding an average return rate of 54.7%. Similarly, males exhibited a return rate of 62% (n = 34) in southern Ontario (Evans Ogden & Stutchbury 1994). The average return rate of banded breeding females was 39% over two years in Pennsylvania (n = 71), and 42% in southern Ontario (n = 38). Although >90% of returning males occupy the same territory, 68% of returning females move to a different territory, suggesting that the lower return rates of banded females relative to males may be due to greater breeding dispersal between years (Evans Ogden & Stutchbury 1994). We assume annual adult survival rates of 62% for males and 53% for females (85% of male survival, as observed for other North American passerines), and an annual juvenile survival rate of 35%.

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

Although Hooded Warblers select nest sites non-randomly (Kilgo et al. 1996, Bisson & Stutchbury 2000), there has been little evidence that nest microhabitat influences nest predation or parasitism. Howlett & Stutchbury (1996) found that seven nest micro-habitat characteristics (nest visibility, vegetation density surrounding the nest, nest height, nest-substrate height, nest-substrate species, height of the cryptic dead-leaf base of the nest, and proximity to a microedge did not differ between successful and depredated nests. Futhermore, nests whose visibility was experimentally increased by 86% through the removal of concealing vegetation did not suffer elevated predation (Howlett & Stutchbury 1996). In a similar study, Kilgo et al. (1996) found only one significant difference between successful and failed nests: fern cover was greater around successful nests, yet there was no difference in fern cover between nest sites and random, non-use sites. Moorman et al. (2002) found that successful nests were surrounded by a greater number of switchcane stems, and were more concealed from below than unsuccessful nests.

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

The average Hooded Warbler clutch size was 15% lower among parasitized nests (Mean = 2.88; SD = 0.94; N = 252), than non-parasitized nests (Mean = 3.38; SD = 0.72; N = 330). This is almost certainly the result of the removal of one or more host eggs by the female cowbird (Evans Ogden & Stutchbury 1994). Consequently, host fledging success was 62% lower among parasitized nests (Mean = 1.10; SD = 1.16; N = 167) than non-parasitized nests (Mean = 3.06; SD = 0.86; N = 204). The mean number of Brown-headed Cowbird eggs laid per parasitized Hooded Warbler nest increased significantly ($F_4 = 15.96$; $P = 0.03$), and the mean number of host young fledged per successful nest decreased significantly ($F_7 = 31.05$; $P = 0.001$) as the site-specific parasitism rate increased (Figure 2).

Effects of landscape-level habitat variables on nest parasitism

Using data from all plots with ≥5 nests, nest parasitism was significantly related to various indices of fragmentation across all spatial scales, from the patch within which the plot was embedded, to within 1-10 km radii of plot centers (Table 2, Figure 3). There was sufficient variation in fragmentation index among plots to test for a within-site relationship between parasitism rate and fragmentation at one or more scales at only two sites, namely northern Ohio and Hoosier National Forest (Figure 4). In northern Ohio, there was a significant positive relationship between nest parasitism rate and percent grassland cover within a 1 km radius (Table 3). At Hoosier National Forest, a similar relationship existed at the 5 km radius scale (Table 3, Figure 4).

Among sites, percent forest cover was negatively related, and percent cropland cover positively related to nest parasitism rate at each of the six spatial scales (Table 4). In the multiple regression analysis, single parameter models were most parsimonious, with the single parameter model of percent core forest at the 50 km radius scale serving as the best predictor of nest parasitism rate in relation to landscape structure across sites ($F = 36.3$, $P = 0.001$, $R^2 = 0.93$: Table 2, Figure 5).

In the only other study to have examined edge-related effects on the breeding success of Hooded Warblers, Moorman et al. (2002) found that nest parasitism rate decreased with increasing distance from group-selection (0.06-0.5 ha; 2-4 years old) and clearcut (25-32 ha; 10-14 years old) logging edges. However, no parasitism was recorded at distances greater than 150 m from the nearest edge, and the overall parasitism level was low (13%). The Hooded Warbler is a preferred cowbird host, and high parasitism rates have been recorded elsewhere: 75% in Illinois; 54-62% in Pennsylvania; and 45% in southern Ontario (Evans Ogden & Stutchbury 1994).

With only two study sites outside the East region, a comparison of nest parasitism rate among regions was not possible.

Table 1. Summary of Hooded Warbler 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]	Daily predation rate (%)[3]	Nest success (%)[4]	Fledglings/ nest[5]	Annual fecundity[6]	Lambda
Hoosier Natl Forest, IN	137	3.37	57.7	3.62	35.3	2.13	2.55	0.89
Western Maryland	11	3.50	63.6	7.55	16.5	0.80	0.54	0.61
Wayne Natl Forest, OH	155	3.47	31.6	3.19	38.59	2.71	3.89	1.02
Ouachita Natl Forest, AR	9	3.43	0.0	3.49	44.2	3.33	4.56	1.19
NW Monongahela Natl Forest, WV	46	3.69	8.7	4.63	29.7	3.12	3.25	1.01
Ozark Natl Forest, AR	204	3.50	5.88	3.75	38.7	3.20	4.02	1.11
Northern Ohio	453	3.25	51.9	3.94	33.4	1.76	1.99	0.82
Nantahala Natl Forest, NC	17	3.69	0.0	7.32	17.4	3.00	2.10	0.84

[1]Number of host eggs incubated in non-parasitized nests

[2]Percentage of nests that received 1 or more cowbird eggs

[3]Percentage of nests lost to predators per day

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

[5]Number of host young fledged per successful nest

[6]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 ≥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: patch size; the distance between the plot center and nearest cowbird habitat (grassland/cropland/developed) edge; edge density; percent core forest; percent cropland; and percent grassland. In all cases, single parameter models were most parsimonius. 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 R^2	Slope	Dependent variables	Adjusted R^2	Slope
Patch	Parasitism	Edge density	0.32***	0.68	To cowbird edge	0.68**	-0.43
	Lambda	Edge density	0.22*	-0.25	To cowbird edge	0.66**	0.21
1 km	Parasitism	% core	0.28***	-0.58	% core	0.54*	-0.95
	Lambda	% core	0.09		% developed	0.52*	-0.76
5 km	Parasitism	Fractal shape	0.53***	4.50	% cropland	0.53*	4.21
	Lambda	Patch size	0.35**	0.093	Edge density	0.53*	-0.32
10 km	Parasitism	Patch size	0.45***	-0.2	% cropland	0.79**	3.33
	Lambda	% developed	0.25*	-0.42	Edge density	0.52*	-0.32
50 km	Parasitism				% core	0.83***	-1.21
	Lambda				% core	0.27	0.39
100 km	Parasitism				% core	0.82**	-1.44
	Lambda				% core	0.24	0.45

Table 3. Adjusted R^2, slope (b) and significance (P) of the relationship between nest parasitism rate or nest predation rate and fragmentation index for either plot patch area or percent forest cover at each of three different radii from plot centers at two sites.

Site		Patch [a]	1km [b]	5km	10km [b]	Patch	1km	5km	10km
		Nest parasitism				Nest predation			
Northern Ohio	R^2	0.01	0.26	0.01 [a]	0.03				
	b	0.58	0.95	0.36	-0.76				
	P	0.30	0.045*	0.32	0.27				
Hoosier NF				0.65 [b]					
				2.66					
				0.03*					

Independent variables: [a]edge density of forest; [b]percent grassland; [c] percent core forest.
*$P < 0.05$.

Table 4. 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 1-100 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		-0.72*			-0.43		0.80*
1 km	0.68	-0.74*	0.77*	-0.06	-0.32	0.07	0.75*
5 km	0.71*	-0.80*	0.90**	-0.29	-0.26	-0.09	0.72*
10 km	0.75*	-0.84**	0.91**	-0. 41	-0.22	-0.16	0.72*
50 km	0.61	-0.89**	0.76*	-0.59	0.15	-0.33	0.50
100 km	0.67	-0.89**	0.78*	-0.30	0.15	-0.21	0.48
150 km		-0.86**			0.18		0.46

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

Effects of landscape-level habitat variables on nest predation

No significant relationships between nest predation and any index of forest fragmentation at any spatial scale were found using BBIRD data. Daily predation rates on Hooded Warbler nests in a South Carolina bottomland forest were not associated with proximity to group-selection or clearcut edges, despite significant clumping of their nests near edges (Moorman et al. 2002).

In summary, the available evidence suggests there is no predictable relationship between nest predation rate and either patch-level edge effects or degree of landscape-level forest fragmentation.

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

Among all plots, lambda was most closely related to average forest patch size within a 5 km radius (Table 2, Figure 6). Similarly, variation in lambda across BBIRD sites was closely related to percent developed land within a 1 km radius, and average forest edge density at both the 5 km and 10 km radii scales (Table 2, Figure 7). Although lambda across BBIRD sites was closely related to the average distance between plot centers and the nearest cowbird habitat edge (grassland/cropland/other developed land cover type) (Table 2, Figure 7), lambda across plots was not at all related to distance from nearest cowbird edge ($F = 0.12$, $P = 0.74$, $R^2 = -0.05$), suggesting this is not a reliable predictor of parasitism risk. In summary, lambda was best predicted by the degree of forest fragmentation at the local landscape scale of the 5 km radius. Considerable residual variation in lambda among sites with similar extents of forest fragmentation can be largely explained by variation in nest predation rate, which was unrelated to any index of fragmentation.

Effects of silviculture on nest predation and nest parasitism

In southern Illinois, daily nest predation rates were twice as high in forest disturbed by group selection logging cuts (2-6 years after cutting, 0.1-0.4 ha) than they were in other kinds of interior forest-edge habitats, such as tree-fall gaps and stream beds (Suarez et al. 1997, citing unpublished data). In contrast, daily mortality rates (3.6-4.7%) on Hooded Warbler nests in a South Carolina bottomland forest were not associated with proximity to group-selection or clearcut edges, despite significant clumping of their nests near edges (Moorman et al. 2002).

Effects of burning on nest success

No data. Repeated prescribed burning of a mixed-oak forest (1-4 years of annual burning), that reduced the density of small shrubs and saplings, resulted in incremental reductions in Hooded Warbler breeding density (Artman et al. 2001).

Effects of grazing 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 broader, landscape scales, particularly within a 50 km radius of sites. The relationship between lambda and index of forest fragmentation is less clear cut than that between parasitism rate and degree of fragmentation because 1) nest predation exerts an equally important effect on lambda; and 2) nest predation is not related to any index of forest fragmentation at any scale. Nonetheless, lambda is significantly negatively related to the degree of forest fragmentation at local landscape scales, particularly the 5 km radius scale.

Mapping predicted source and sink habitat

The relationship between lambda and landscape structure is insufficiently resolved to permit accurate mapping of predicted source and sink habitat.

MANAGEMENT GUIDELINES

The Hooded Warbler is a gap-dependent species of mid-successional to mature forest. In forests with limited gap availability, habitat suitability for Hooded Warblers can be increased by using single-tree or small-group-selection logging treatments that create gaps no larger than 0.05 ha, leaving the resulting shrub layer untouched. The larger gaps created by group-selection logging (0.05-0.2 ha) are at the upper limit of those used by Hooded Warblers. Managers should retain some mature trees, leaving a residual basal area in the large tree size class (DBH > 38 cm) of at least 12 m^2/ha., as a mature forest component is important for Hooded Warblers (Crawford et al. 1981, Whittam et al. 2002). In forest blocks exceeding 100 ha, logging should not occur simultaneously across the entire forest, but be staggered over a period of several years, preferably decades, to ensure long-term habitat suitability for Hooded Warblers (Whittam et al. 2002).

Given the severe effect of cowbird parasitism on Hooded 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.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

Single-tree and group-selection logging treatments are recommended as a method for increasing habitat suitability for Hooded Warblers. However, the effect of these silvicultural practices on nest parasitism and predation rates have not been widely investigated, particularly in relation to broader landscape contexts. One study, citing unpublished data, suggests that daily nest predation rates are twice as high in forest disturbed by group selection logging cuts than in natural, interior forest-edge habitats, such as tree-fall gaps and stream beds (Suarez et al. 1997). Another study, in a location with relatively low nest predation rates, suggests that nest predation is not related to proximity to edges of group-selection and clear-cut logging cuts (Moorman et al. 2002). Further studies investigating such edge effects are needed from sites that vary in the degree of forest fragmentation at the broader landscape level (within a 5-10 km radius).

Our confidence in the modeled relationship between lambda and landscape characteristics could be improved with an increased sample of breeding success data from more sites across the range of the Hooded Warbler. 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. Hooded 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).

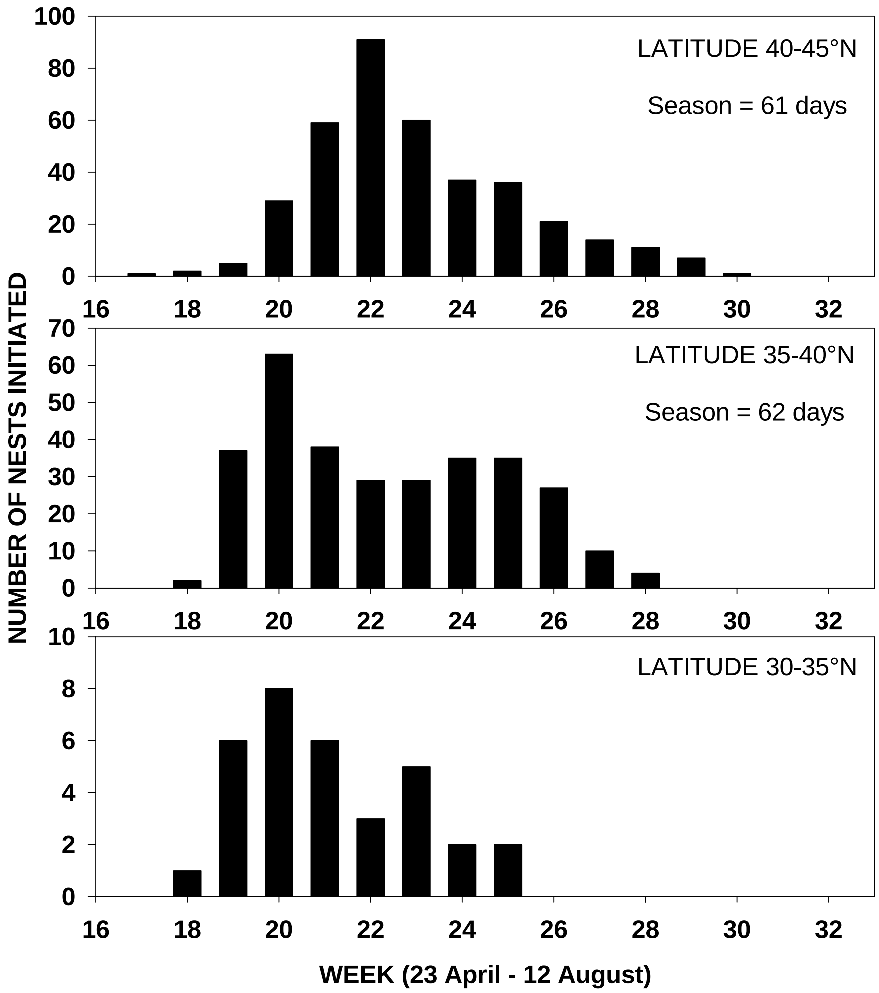

Figure 2. The mean number of Brown-headed Cowbird eggs laid per parasitized Hooded Warbler nest (top) increases significantly (F_4 = 15.96; P = 0.03), and the mean number of host young fledged per successful nest (bottom) decreases significantly (F_7 = 31.05; P = 0.001) as the site-specific parasitism rate increases.

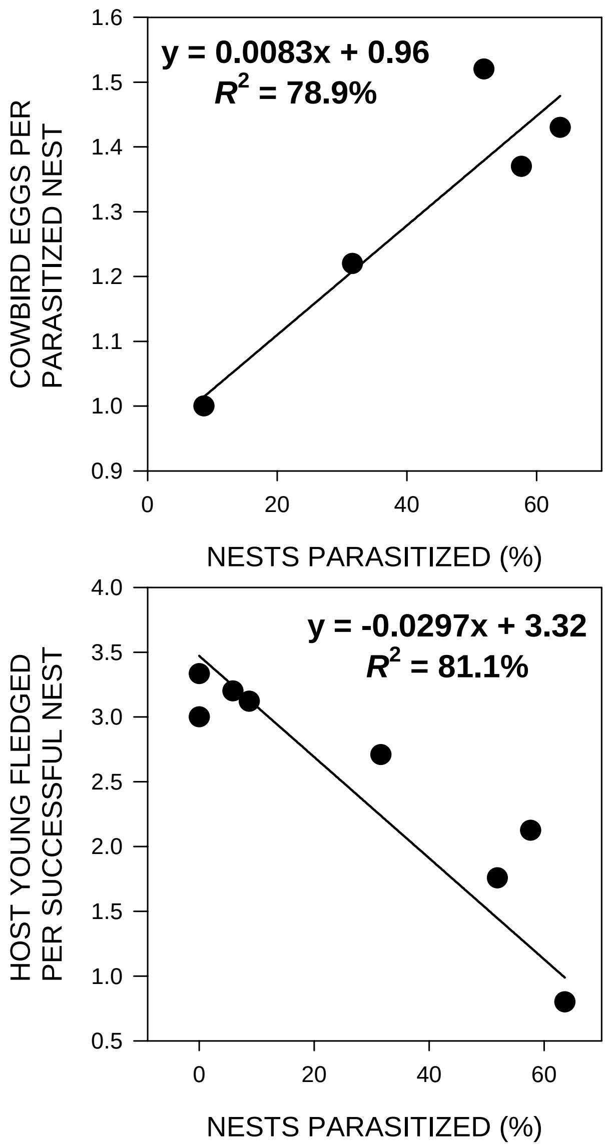

Figure 3. Relationship between nest parasitism rate (arcsine transformed) and each of: A) edge density of the forest patch (ln-transformed); B) percent core forest cover (arcsine transformed); and C-D) mean forest patch size (ln-transformed) at the spatial scales of 1-10 km radii of plot centers, for 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).

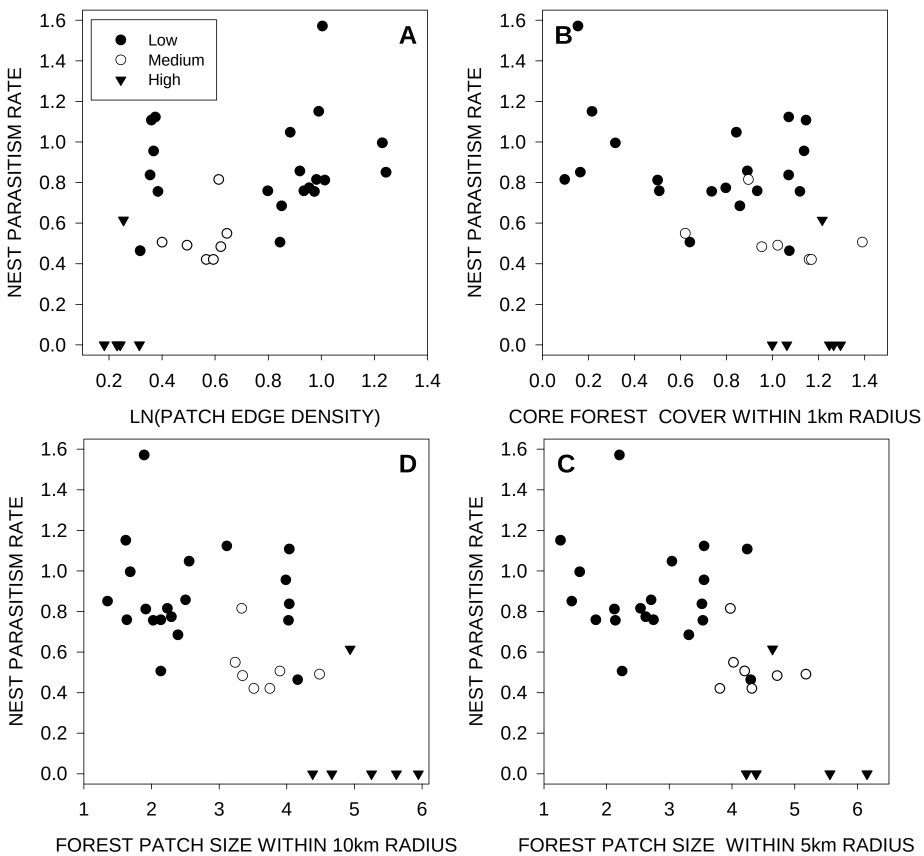

Figure 4. Relationship between nest parasitism rate (arcsine transformed) and each of edge density of the forest patch (ln-transformed), and percent grassland cover (arcsine transformed) at the spatial scales of 1-10 km radii of plot centers at Hoosier National Forest and northern Ohio.

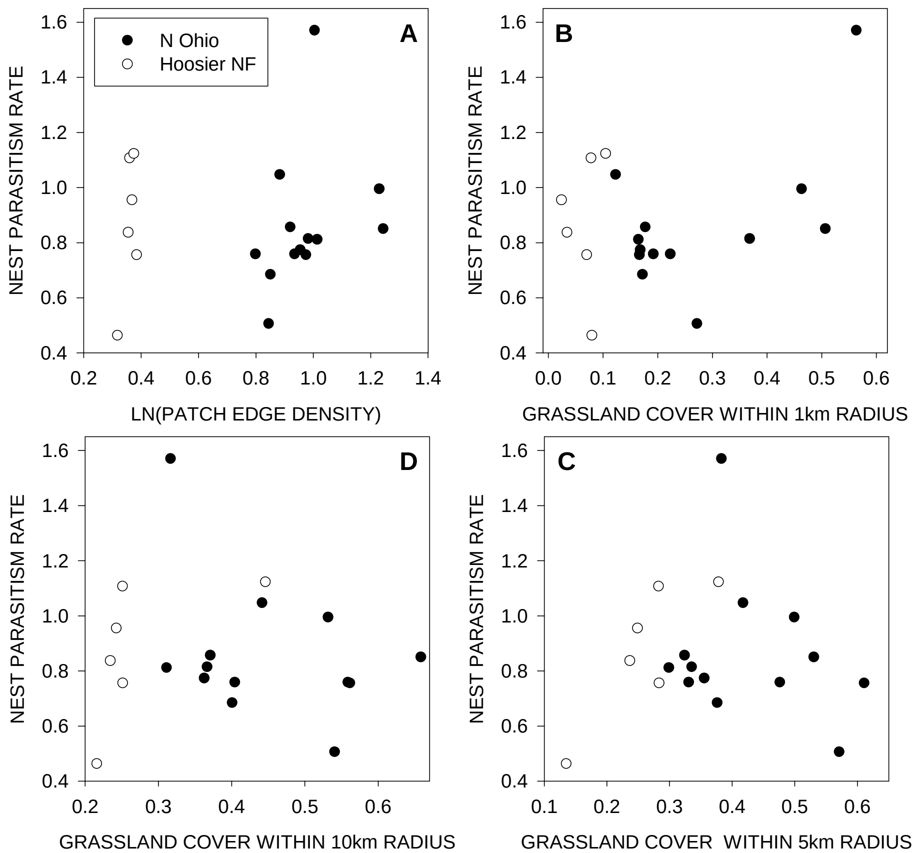

Figure 5. Relationship between nest parasitism rate (arcsine transformed) and forest fragmentation index (ln or arcsine transformed) at spatial scales of the plot patch and 1-10 km radii of plot centers (site averages), and 50-100 km radii of site centers. Relative percent forest cover at the 100 km radius scale is classified as low, medium, or high.

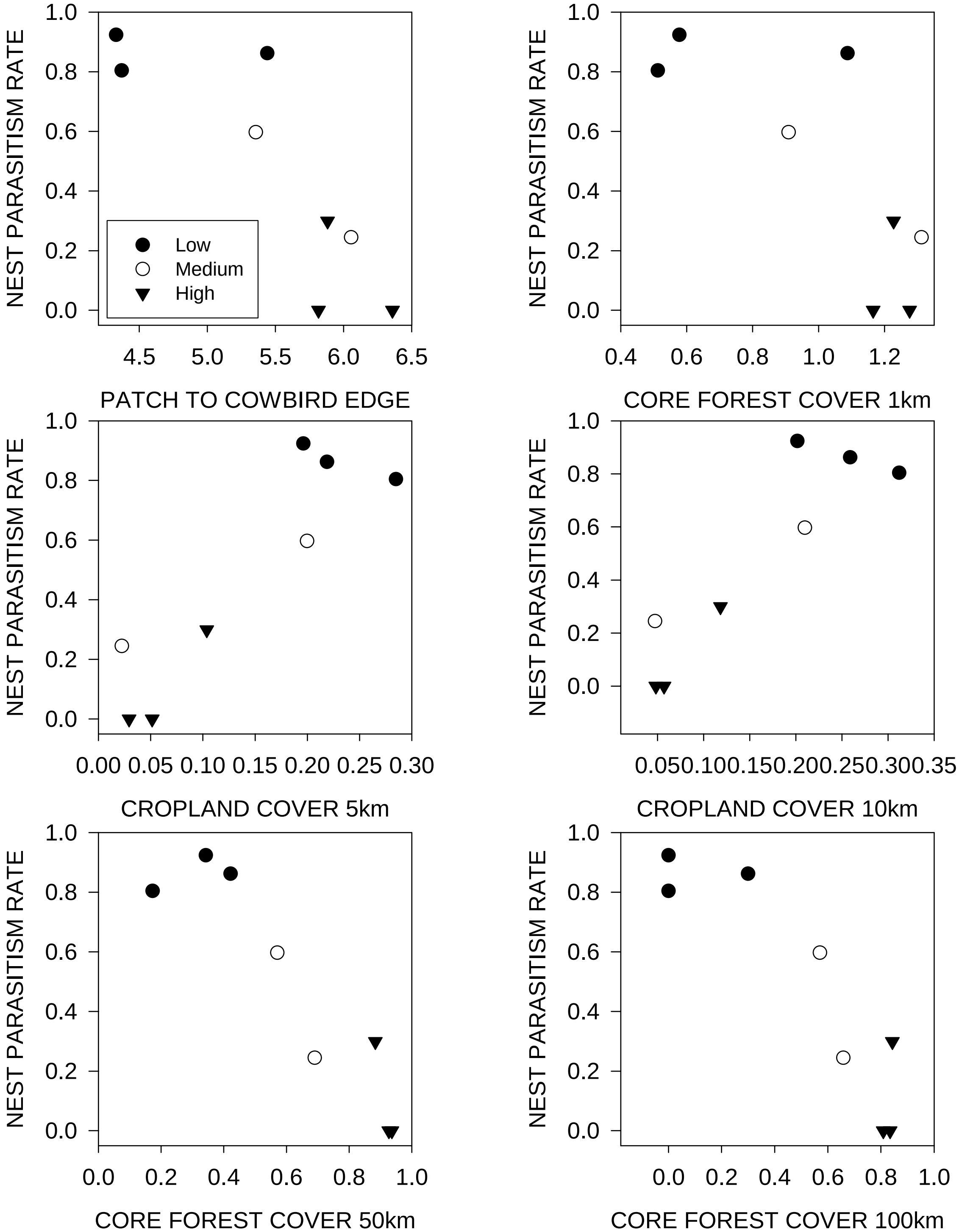

Figure 6. Relationship between lambda and average forest patch size (ln-transformed) within a 5 km radius of plot centers, for all plots with ≥5 nests surviving to fledging.

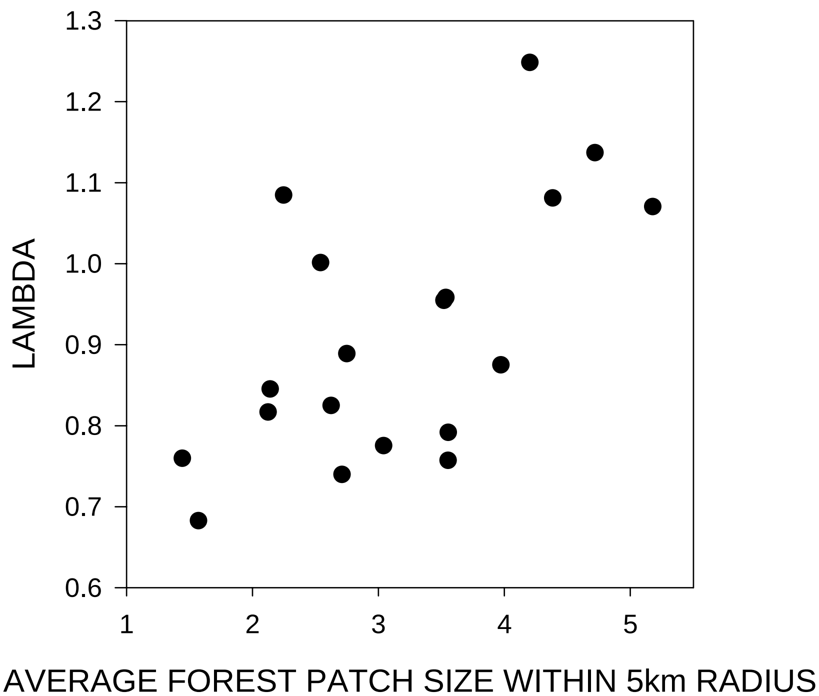

Figure 7. Relationship between lambda and each of distance from plot center to nearest cowbird (cropland/grassland/developed) edge (ln-transformed), and mean forest edge density (ln-transformed) within a 5 km radius of plot centers (site averages) for Hooded Warblers among BBIRD sites.