Kentucky Warbler *Oporornis formosus*

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EXECUTIVE SUMMARY

Preferred breeding habitat: Mature bottomland hardwood forests and mature deciduous-forested stream valleys with a dense understory and well-developed ground cover.

Nest placement: On the ground in low and dense understory vegetation, or 2-3 cm off the ground if wedged in dead twigs near the ground.

Mean clutch size and fledging brood size (±SD**):**

- Non-parasitized nests: clutch 4.32 ± 0.90; brood 4.01 ± 0.93
- Cowbird parasitized nests: clutch 3.33 ± 1.18; brood 1.63 ± 1.60.

Number of broods per season: One to two.

Annual adult survival rates: Males and females 62%.

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

- Fledge at least 2.2-2.5 own young per female per year
- Daily nest mortality ≤5.5-6.2% (≥22-26% nest success) assuming zero parasitism
- Percent forest cover approximately ≥60% within a 10 km radius

Nest mortality and parasitism rates in relation to landscape context:

- Daily nest predation rate 1.6-4.2% in forest interior, particularly in landscapes with >60% forest cover within a 10 km radius.
- Daily nest predation up to 7-16% in regenerating clearcuts and other relatively large internal forest openings
- Nest parasitism rate up to 60% within 300 m of developed edges, but <5% at distances greater than 1.5 km of developed edges in a fragmented landscape

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

- Nest predation rate may not be particularly influenced by edge effects, but increases with increasing degree of forest fragmentation at landscape scales, suggesting that fragmentation effects at landscape scales may constrain the extent of local edge effects.
- Nest parasitism rate increases with reduced distance to the developed land cover edges, but the severity of local edge effects appear to be constrained by the degree of forest fragmentation at landscape scales.

General conclusions:

- Nest parasitism has a severe effect on breeding productivity, reducing host fledging success by an average of 59% among parasitized nests.
- Nest parasitism rate is strongly influenced by distance to cowbird feeding habitats, and the degree of forest fragmentation at landscape scales.
- Nest predation rate is strongly influenced by the degree of forest fragmentation at landscape scales.
- Lambda is negatively correlated with degree of forest fragmentation across multiple spatial scales, particularly landscape scales.

Management guidelines:

- Although it is primarily an inhabitant of the interiors of mature forests, the Kentucky Warbler's critical requirement for a dense understory for nesting in means that breeding densities are generally enhanced by the presence of a mosaic of relatively small internal openings in the canopy. It will thus tolerate, and even flourish in response to, a fairly broad range of silvicultural practices, ranging from group selection, small or narrow clearcuts, thinning to remove overmature trees, or single tree selection. However, the creation of openings greater than at least 1 ha in forests within heavily fragmented landscapes should be avoided, since such internal openings can facilitate the penetration of cowbirds into the forest interior and elevate nest parasitism rates. Furthermore, given the evidence suggesting that nest predation rates are elevated within small clear-cuts, but not within forest subjected to group- and single-tree selection logging, the latter methods of harvesting should be preferred.
- Given the severe effect of cowbird parasitism on Kentucky 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 thrush populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of breeding habitat by minimizing (1) the extent of agriculture and development (particularly human dwellings) within or adjoining forests (not always feasible); (2) the extent of short grass openings, such as along road verges, utility corridors and around human dwellings; and (3) the presence of livestock within or adjoining forests. Where possible, logging roads should be narrow enough that they do not break the canopy, or closed and re-vegetated as soon as possible. Campgrounds should be managed to minimize extensive areas of grass, and garbage should be removed quickly to avoid attracting and subsidizing potential nest predators such as raccoons, opossums and corvids (Robinson & Wilcove 1994).
- Given the evidence of strong edge effects on nest parasitism, even in highly fragmented landscapes, a general management strategy that leaves large "core" areas of mature forest far (>1 km) from potential cowbird foraging sites, will help to increase nest success. In regions where the Kentucky Warbler 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 and other cowbird food sources, within forested areas) of the larger forest tracts within the region to ensure that percent forest cover within a 10 km radius of focal forest tracts is maintained above approximately 60%.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

A Neotropical migrant, the Kentucky Warbler occupies a breeding range through much of the eastern United States, and winters from Mexico south through Central America to the northern portions of Columbia and Venezuela. The northern limits to the breeding range extends from north-central New Jersey, central Pennsylvania, northern Ohio, central Indiana, north-central Illinois, southeastern Iowa, and north-central Missouri. It also breeds from extreme northern Illinois to extreme north-eastern Iowa and southwestern Wisconsin, and in extreme southeastern New York. The breeding range extends south along the Atlantic coast to southern South Carolina and southern Georgia (except southeastern coastal plain), the panhandle of Florida, west to eastern Texas (but absent from coast). The western limits of the breeding range extend (particularly along wooded river valleys) from the eastern quarter of Texas to eastern Oklahoma, eastern Kansas, extreme southeastern Nebraska and extreme south southwestern Iowa (McDonald 1998).

On the breeding range, it occupies mature bottomland hardwood forests and mature deciduous-forested stream valleys, often at low elevations (McDonald 1998). A dense understory and well-developed ground cover for nesting are essential (Wenny et al. 1993, McDonald 1998). Average percent ground cover was 46%, average ground cover height 16 cm, and percent canopy cover 97% at nest sites in Missouri (Wenny et al. 1993). Although generally considered a forest-interior songbird, it will nest in a variety of disturbed habitats, due to the enhanced growth of a dense understory that such disturbances stimulate. Breeding densities are typically positively affected by a variety of silvicultural practices (Annand & Thompson 1997, Robinson & Robinson 1999). Breeding densities were significantly greater in a >800 ha forest patch than in two 300 ha forest patches in Missouri (Wenny et al. 1993), but both density and male pairing success did not differ between small (<140 ha), isolated forest fragments and larger (>500 ha) contiguous forest in Missouri (Gibbs & Faaborg 1990). Kentucky Warbler densities were not sensitive to forest edge in Missouri (Wenny et al. 1993).

Average territory size is 2.21 ha (range 1.21-3.75, n = 493) in Virginia (McDonald 1998). Breeding densities are variously reported as 0.91-1.82 males/10 ha in Missouri (Wenny et al. 1993), 1.9-2.1 males/10 ha in Missouri (Gibbs & Faaborg 1990), 5.4 territories/40 ha in Mississippi mature bottomland hardwoods (Twedt et al. 1999), and 0.4 pairs/40 ha in Ohio mixed-oak forest (Artman et al. 2001).

Nest site characteristics

The well concealed, open-cup nest is usually sited on the ground in low and dense understory vegetation, or 2-3 cm off the ground if wedged in dead twigs near the ground (McDonald 1998).

BREEDING PRODUCTIVITY

Laying seasons

Earliest and latest nests in the BBIRD database were initiated on 1 May and 27 June respectively, with a single, exceptional nest initiated on 13 July. Most laying occurs within a 6-week period 7 May to 17 June, with a peak in the week of 14-20 May (Figure 1). The overall length of the laying season across latitudes 30-40°N was estimated as 45 days. This season is somewhat different from that described for a population in northern Virginia, where first eggs are laid 16 May to 1 July, females may re-nest through mid-July, and peak hatching occurs mid- to late June (McDonald 1998), 2-3 weeks later than the late May to mid-June peak in hatching expected from BBIRD nest initiation data.

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (McDonald 1998). The mean clutch size of unparasitized nests is 4.32 (SD = 0.90). The mean incubation period has been reported as 11-13 days in Virginia (McDonald 1998), with a mean of 12.0 days (SD = 0, n = 4) in Arkansas (Li 1994), and the nestling period as 8-9 days in Virginia (McDonald 1998), with a mean of 9.2 days (SD = 0.69, n = 6) in Arkansas (Li 1994). The re-nesting interval following nest loss has not been reported on, but nests are usually built in a single day, occasionally 2 days, and the first egg is usually laid 1 day after nest completion, so we assume an interval of 5 days (as for the Ovenbird). The Kentucky Warbler is reported to only occasionally be double-brooded (1-2 out of 40 pairs/year) if the first brood fledges before about 15 June in Virginia (McDonald 1998), and raises 1-2 broods in Maryland (Whitcomb et al. 1981). The re-nesting interval after successful fledging is about 10 days (McDonald 1998). To calculate annual breeding productivity, we used a 45-day laying season, 24-day nesting period (3-day laying, 12-day incubation, 9-day nestling), and re-nesting intervals of 5 days after nest loss, and 10 days after successful fledging. We calculated annual breeding productivity using two different models, one assuming single-brooding, and the other assuming double-brooding.

Our annual breeding productivity estimates at 3 sites with 0-13% nest parasitism and 1.6-4.1% nest mortality ranged 2.9-3.8 fledglings/female if double-brooded, 2.2-3.0 if single-brooded, but 2.1 and 1.8 fledglings/female respectively at a site with 46% parasitism and 4.6% daily mortality (Table 1). Annual productivity at sites in southern Illinois range from 1.24 fledglings/female at a site with >30% parasitism and >6% daily nest predation, to 2.95 fledglings/female at a site with <20% parasitism and 4.2% daily predation (Morse & Robinson 1998). These field estimates are roughly equivalent to our model estimates that assume double-brooding, suggesting the assumption of double-brooding is necessary for adequate model performance.

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

The annual adult survival rate of color-banded birds (males and females combined) is reported as 62% (n = 6 years), which is thought to be a conservative estimate given that breeding dispersal of up to 1 km has been observed (McDonald 1998, citing unpublished data). Conway et al. (1995) estimated monthly survival of Wood Thrushes on the wintering grounds as 0.89 (SE = 0.025), which extrapolates to annual survival of 25%, but this estimate is likely heavily biased low by the problem of accounting for dispersal in a mark-recapture study. We therefore assume an annual adult female survival rate of 62%. We further assume a juvenile survival rate estimate of 31% (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 (3.33, SD = 1.18, n = 15) was 23% lower than that of non-parasitized nests (4.32, SD = 0.90, n = 85). Mean fledging success was 59% lower from successful parasitized nests (1.63, SD = 1.60, n = 5) than from non-parasitized nests (4.01, SD = 0.93, n = 87).

Table 1. Summary of Kentucky Warbler breeding productivity and estimated finite rate of population increase (λ) across BBIRD sites, under assumptions of both single-brooding and double-brooding.

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
Central Missouri	13	4.71	46.15	3.92	32.50	3.00	1.79	2.05	0.90	0.94
Hoosier Natl Forest, IN	79	4.45	12.66	4.13	36.32	3.89	2.23	2.86	0.97	1.06
Ozark Natl Forest, AR	27	4.30	7.41	2.99	48.24	3.50	2.43	3.07	1.00	1.10
Wayne Natl Forest, OH	27	4.30	7.41	4.05	37.07	4.32	2.52	3.22	1.01	1.12
Ouachita Natl Forest, AR	24	4.00	0	1.55	68.73	3.52	2.99	3.81	1.08	1.21

[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, daily nest predation rate, and lambda (assuming double-brooded) among BBIRD sites (plot averages for scales of patch and 1-10 km radii) using multiple regression analysis. Spatial scales included: the patch of forest within which the study plot was embedded; 1-10 km radii of study plot centers; and 50-100 km radii of study site centers. Non-significant results included for comparison across scales. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Scale	Dependent variables	Independent variables	Adj. R2	Slope
Patch	Parasitism	Core forest area	0.72*	-0.23
	Predation	To nearest developed edge	0.9**	-0.023
	Lambda	Forest patch size	0.64	
1 km	Parasitism	% cropland	0.53	
	Predation	% cropland	0.49	
	Lambda	% cropland	0.43	
5 km	Parasitism	Avg forest patch size >10 ha	0.78*	-0.24
	Predation	Fractal dimension	0.5	
	Lambda	Avg forest patch size >10 ha	0.7*	0.084
10 km	Parasitism	% cropland	0.71*	1.62
	Predation	Fractal dimension	0.76*	0.2
	Lambda	% cropland	0.65	
50 km	Parasitism	Avg forest patch size	0.94**	-0.31
	Predation	Fractal dimension	0.87*	0.48
	Lambda	Avg forest patch size	0.97**	0.11
100 km	Parasitism	Avg forest patch size	0.77*	-0.36
	Predation	Fractal dimension	0.83*	0.68
	Lambda	Avg forest patch size	0.83*	0.13

Effects of landscape-level habitat variables on nest parasitism

Among sites, nest parasitism is strongly positively correlated with the degree of forest fragmentation across all spatial scales, but particularly at the broad landscape scales of within a 50km radius (Table 2, Figure 4). Robinson et al. (1995) found a non-significant negative correlation between nest parasitism rate and percent forest cover within a 10 km radius of nine sites across the Midwestern United States, with parasitism rates in the order of 20-50%. Morse & Robinson (1999) found the extent of nest parasitism to be strongly negatively related to the distance from the nearest agricultural edge at a site in southern Illinois with a high degree of forest fragmentation at the broad landscape scale – nest parasitism decreased steadily across 300-m-width intervals, from 60% parasitism within 300 m of the nearest agricultural edge, to 44%, 35%, 27% and 16% parasitism at successively deeper 300-m intervals, and finally <5% parasitism at distances greater than 1.5 km from the nearest agricultural edge. Winslow et al. (2000) similarly found higher nest parasitism in forest near exterior, agricultural edges (25.0%, n = 4), than in interior forest (11.1%, n = 9) in southern Indiana.

Effects of landscape-level habitat variables on nest predation rate

Among sites, daily nest predation rate is particularly negatively correlated with average distance from the nearest developed land cover edge, and positively correlated with the degree of forest fragmentation at the broad landscape scales of within a 50-100 km radius. Given the strong positive correlations between these indices of fragmentation, it is not possible to distinguish which spatial scale is primarily responsible for this influence. Robinson et al. (1995) found a non-significant negative correlation between daily nest mortality rate and percent forest cover within a 10 km radius of nine sites across the Midwestern United States, with daily mortality rates in the order of 4-6%. On the other hand, at a site embedded in a fragmented landscape in southern Illinois, neither distance to the nearest major agricultural edge, nor distance from internal edges associated with regenerating clear-cut openings and residential clearing, had any significant effect on daily nest predation rate (Morse & Robinson 1999). In this latter study, predation rates varied strongly with forest type, however (see under effects of silviculture).

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

Among sites, lambda is negatively correlated with the degree of forest fragmentation across all spatial scales, but particularly at the broad landscape scales of within a 50-100 km radius (Table 2, Figure 4).

Effects of silviculture on nest predation and nest parasitism

At a site embedded in a fragmented landscape in southern Illinois, daily nest predation rates varied significantly with forest type. Kentucky Warblers nesting in young, even-aged forest in recent (8 years) and older (20 years) clearcuts (3.6-14.6 ha), a sweetgum plantation, and other early-successional vegetation, experienced significantly higher daily nest predation rates (average 8.2% daily predation) than did warblers nesting in mature forest adjoining these openings (average 4.2% daily predation: Morse & Robinson 1999). However, at another southern Illinois site (Robinson & Robinson 2001), daily nest predation rates were not markedly or consistently different between forest compartments subjected to recent (1-5 years) and older (10-15 years) group (0.02-0.4 ha) and single-tree selection logging (3.46% and 1.50% daily nest mortality respectively), and uncut, mature forest (2.60-4.14% daily mortality).

At a large forest embedded in a relatively highly fragmented landscape, internal edges created by clear-cut logging, residential clearing, and a sweetgum plantation had no effect on cowbird parasitism, which was instead strongly positively correlated with distance from the nearest agricultural edge (Morse & Robinson 1999). However, at another southern Illinois site (Robinson & Robinson 2001), nest parasitism was greater in selectively logged forest (45-64% parasitism) than adjoining uncut forest (25% parasitism), but not significantly greater than at another two, more distant, uncut reference sites (40-50% parasitism). Similarly, Winslow et al. (2000) found higher nest parasitism in forest near large clear-cuts (28.6%, n = 14), and exterior, agricultural edges (25.0%, n = 4), than in interior forest (11.1%, n = 9) in southern Indiana, although sample sizes were small.

Breeding densities were significantly positively affected by group (0.02-0.4 ha) and single-tree selective logging of a mature oak-hickory forest in southern Illinois, reaching peak densities 2-4 years after cutting (Robinson & Robinson 1999). Densities (individuals/10 50-m-radius point counts) in ravines and on ridges were significantly higher in recently (1-5 years: 8.67-9.17 and 5.08-6.33 individuals in ravines and on ridges respectively) and less recently cut (10-15 years: 5.00-6.52 and 1.84-2.76 individuals) forest compartments than in mature forest (3.52-3.81 and 0.86-1.04 individuals). Similarly, breeding densities (mean detections/10-min point count) were greater in mixed-oak forest subjected to clearcut (0.15), shelterwood (0.19), group selection (0.18), single-tree selection (0.16) logging, than in mature, uncut forest (0.07) in southeastern Missouri (Annand & Thompson 1997). On the other hand, breeding densities were greater in uncut, mature bottomland hardwood forest (5.4 territories/40 ha), than in selectively harvested stands (2.4 territories/40 ha) and cottonwood plantations (0.3-1.1 territories/40 ha) in the Mississippi Alluvial Valley (Twedt et al. 1999).

Effects of burning on nest success

No data on effects 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 Kentucky Warbler breeding densities (Artman et al. 2001). Similarly, breeding densities were not significantly affected by winter prescribed burning in Georgia (White et al. 1999).

Effects of grazing/browzing on nest success

No data.

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

At the local patch scale, several studies suggest that nest parasitism rate is strongly related to the distance to the nearest developed land cover edge providing cowbird foraging habitat, even in relatively highly fragmented landscapes. In turn, BBIRD data suggest that nest parasitism is most strongly correlated with the degree of fragmentation at landscape scales, particularly the broad landscape scale of within a 50-100 km radius. This suggests that the parasitism rate at the local patch scale may be constrained by the effects of fragmentation at landscape scales.

The extent to which nest predation rates are related to distance from forest edges remains uncertain. One study (Morse & Robinson 1999) found no effect of edge, but BBIRD data suggest a strong relationship between nest predation and either distance to nearest developed edge, or degree of landscape-level forest fragmentation.

Due to the severe effects of both parasitism and predation on Kentucky Warbler breeding productivity, lambda is strongly negatively related to the degree of forest fragmentation across all spatial scales examined, particularly the broad landscape scale of within a 50-100 km radius. The four BBIRD sites at which Kentucky Warbler lambda is estimated to be ≥ 1 are all well forested at the local landscape scale (75-95% forest cover within a 10 km radius), whereas the single site evaluated as a sink has just 43% forest cover within a 10 km radius. It would be useful to obtain breeding productivity data from several more fragmented sites, to get a better measure of productivity responses to a broader range of landscape-level fragmentation.

Mapping predicted source and sink habitat

Mapping predicted source and sink habitat is problematic due to insufficient confidence (due to small sample size) in the relationship between lambda and landscape metrics of forest fragmentation across BBIRD sites.

MANAGEMENT GUIDELINES

Although it is primarily an inhabitant of the interiors of mature forests, the Kentucky Warbler's critical requirement for a dense understory for nesting in means that breeding densities are generally enhanced by the presence of a mosaic of relatively small internal openings in the canopy. It will thus tolerate, and even flourish in response to, a fairly broad range of silvicultural practices, ranging from group selection, small or narrow clearcuts, thinning to remove overmature trees, or single tree selection. However, the creation of openings greater than at least 1 ha in forests within heavily fragmented landscapes should be avoided, since such internal openings can facilitate the penetration of cowbirds into the forest interior and elevate nest parasitism rates. Furthermore, given the evidence suggesting that nest predation rates are elevated within small clear-cuts, but not within forest subjected to group- and single-tree selection logging, the latter methods of harvesting should be preferred.

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

Given the evidence of strong edge effects on nest parasitism, even in highly fragmented landscapes, a general management strategy that leaves large "core" areas of mature forest far (>1 km) from potential cowbird foraging sites, will help to increase nest success. In regions where the Kentucky Warbler 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 and other cowbird food sources, within forested areas) of the larger forest tracts within the region to ensure that percent forest cover within a 10 km radius of focal forest tracts is maintained above approximately 60%.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

Most BBIRD data are derived from sites that are relatively well forested at both local and broad landscape spatial scales. 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.

BBIRD data relating to the timing and extent of the laying season (most from southern Indiana and Ohio) differ quite substantially from that observed at a site in northern Virginia (McDonald 1998). Intensive monitoring of nest initiation dates throughout a breeding season (at least 100 nests) from other sites would therefore be useful to obtain greater clarity on this important parameter for any breeding productivity model.

The extent of double-brooding has been studied in detail at only one site, where it was found to be minimal. Our breeding productivity model suggests that if this species is largely single-brooded, only populations breeding within very extensively forested landscapes will be productive enough to act as sources. Given the importance of this parameter to productivity estimates, greater clarity on the degree of double-brooding in both the north, south and western extents of the breeding range is needed. This requires the intensive monitoring of color-banded females throughout a breeding season.

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

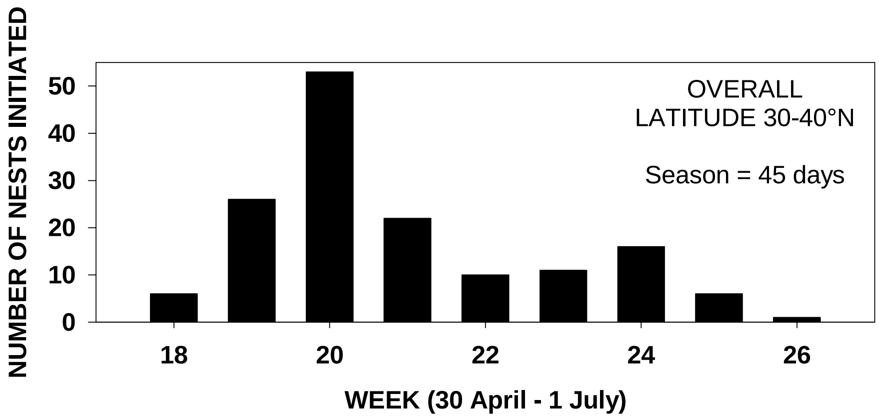

Figure 2. Relationship between nest parasitism rate (arcsine transformed) and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers.

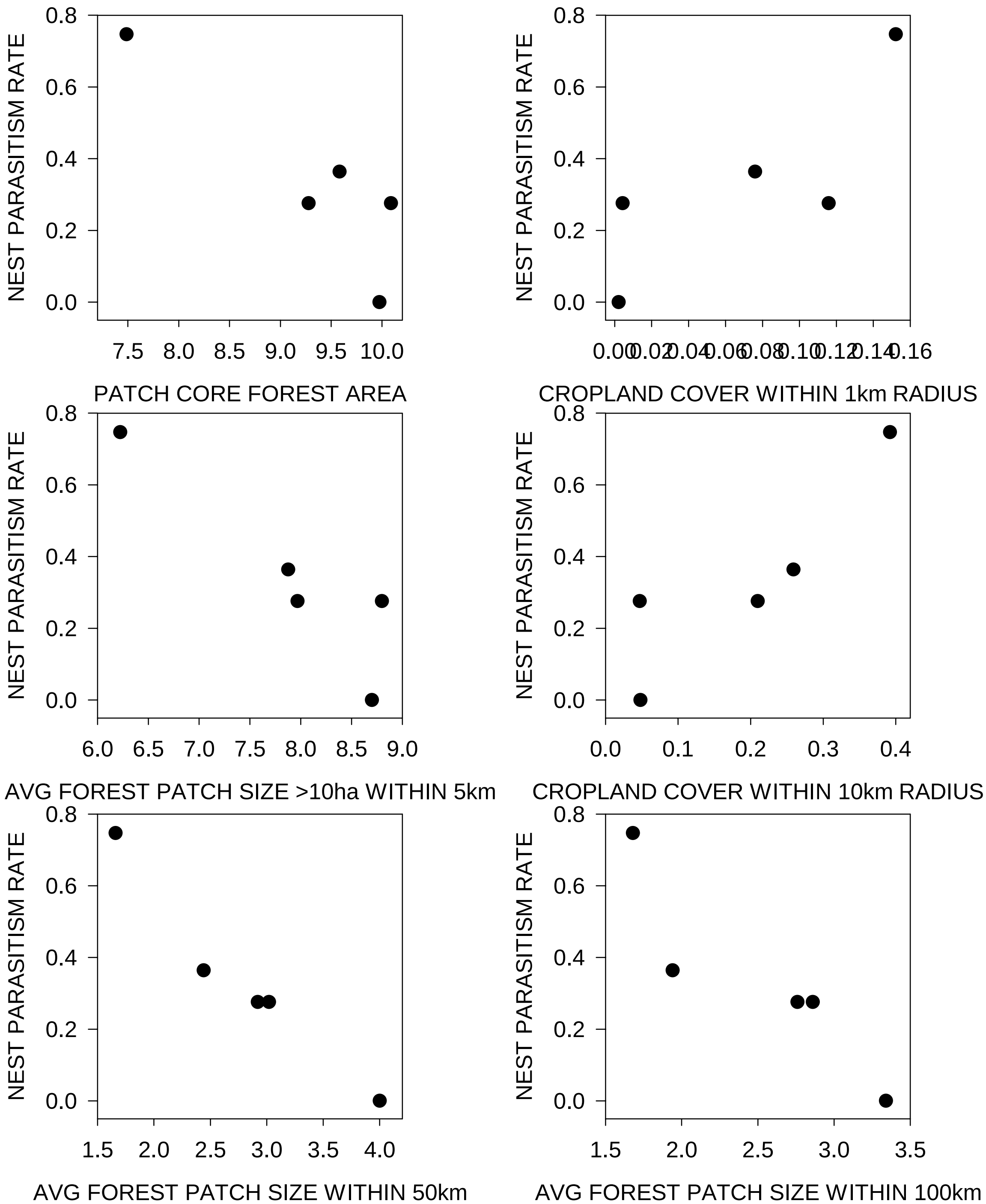

Figure 3. Relationship between daily nest predation rate and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers.

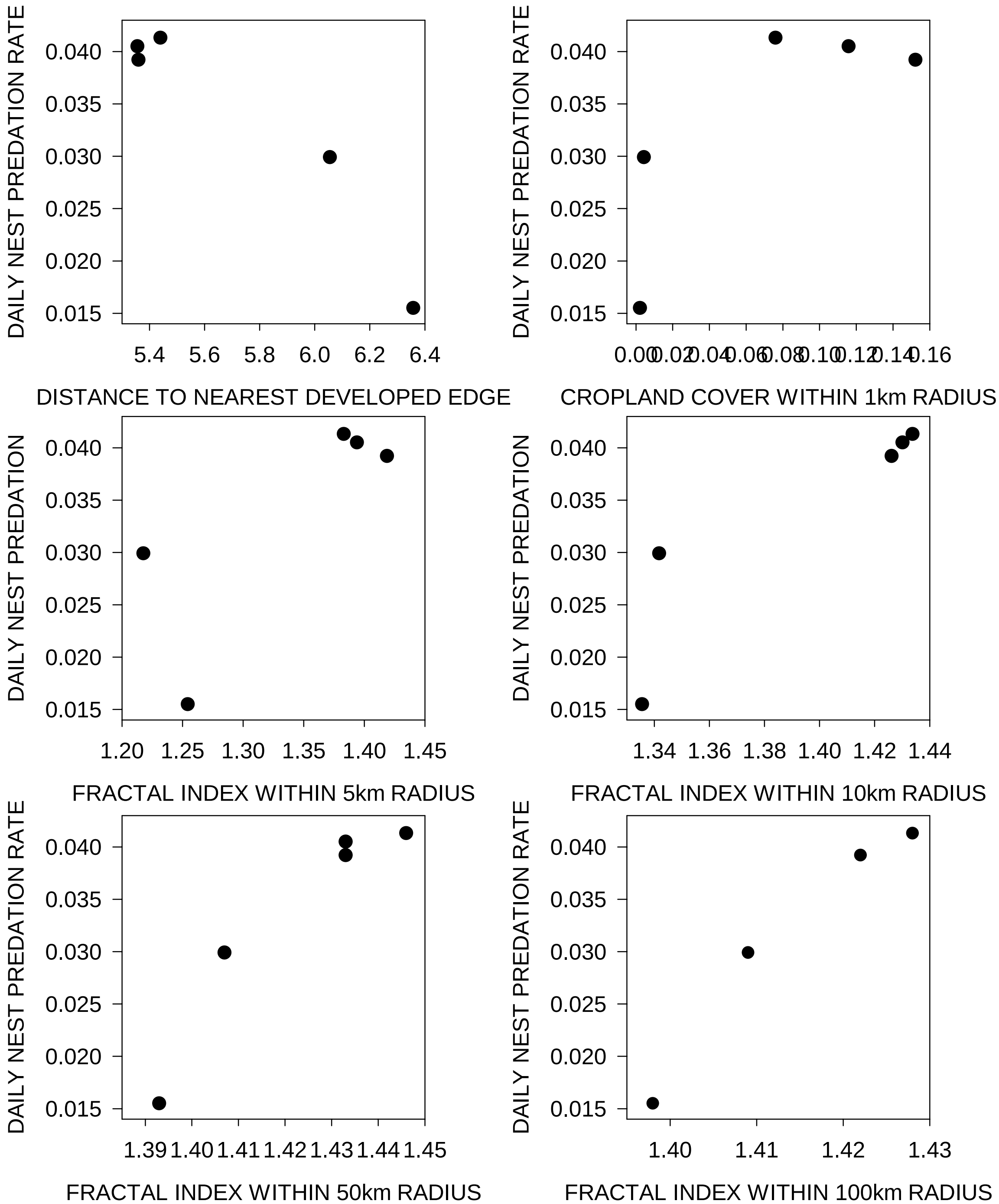

Figure 4. Relationship between lambda and various indices of forest fragmentation at spatial scales of the forest patch, within 1-10 km radii of plot centers (site averages), and within 50-100 km radii of site centers.