American Redstart *Setophaga ruticilla*

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EXECUTIVE SUMMARY

Preferred breeding habitat: Moist, deciduous, second-growth woodlands with abundant shrubs, often near water (bottomland hardwoods and swamps), and in thickets under tree-fall gaps in old-growth forest.

Nest placement: Surrounded by foliage and supported by at least three vertical stems against the main trunk of a leafy tree or shrub, usually at a height of 1-4 m, less often up to 15 m.

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

- Non-parasitized nests: clutch 3.60 ± 0.83; brood 2.84 ± 1.12
- Cowbird parasitized nests: clutch 3.05 ± 0.98; brood 0. 74 ± 1.03

Number of broods per season: One

Annual adult survival rates: Male and female 67%.

Requirements for population stability ($\lambda \geq 1$)**:** Uncertain, but possibly required to fledge at least 2.0 own young per female per year

Nest mortality and parasitism rates in relation to landscape context:

- Nest parasitism increases significantly with the degree of forest fragmentation at patch and local landscape scales (within radii of 1-10 km)
- Daily nest predation rate increases significantly as the degree of forest fragmentation across multiple spatial scales increases

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

- Daily nest predation rate appears to be strongly related to local landscape effects of forest fragmentation within the local forest patch or within a 1 km radius, but whether it may be constrained to some extent by the degree of forest fragmentation at broader local landscape scales (within a 5-10 km radius) is uncertain.
- Nest parasitism rate is most strongly related to the degree of forest fragmentation within the local landscape (within a radius of 1-10 km).

General conclusions:

- Nest parasitism has a severe effect on breeding productivity, reducing host fledging success by 74% among parasitized nests.
- Nest parasitism rate is most strongly positively correlated with the degree of forest fragmentation at spatial scales of 1-10 km radii.
- Nest predation rate is strongly positively correlated with forest fragmentation across multiple scales, particularly within a 1 km radius.
- Lambda is strongly negatively correlated with the degree of forest fragmentation at multiple spatial scales, particularly within a 1 km radius.

Management guidelines:

- In most areas, particularly northern hardwood forests, where the American Redstart is associated primarily with early-successional habitats (Hunt 1996), breeding densities can be increased using a variety of silvicultural practices, including various degrees of thinning and small patch cuts (Webb et al. 1977, Welsh & Healy 1993). However, in some areas, such as central Appalachian hardwood forests, where the American Redstart is associated primarily with closed-canopy forest, it will tolerate uneven-age management of forest stands, such as single-tree selection and thinning understory trees that compete for root space, but any intermediate or harvest cutting that opens the canopy will probably decrease populations (Crawford et al. 1981).

- Given this species' area sensitivity, and the strong effect of forest fragmentation at landscape scales on population lambda, a primary regional management focus should be to maintain a representative network of large, unfragmented forests to serve as source populations across the breeding range of the American Redstart. These forests should ideally be greater than 10,000 ha in area, and incorporate the moist, deciduous forest habitats preferred by this species. Silvicultural practices that produce a patchwork of early-successional habitat preferred by the American Redstart may enhance habitat quality within mature forests, without compromising nesting success through the negative effects of fragmentation on breeding productivity, if logging is restricted to the interiors of large forest tracts, to reduce the potential risk of cowbird parasitism.
- Given the severe effect of cowbird parasitism on American Redstart 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 American Redstart populations. A primary objective, therefore, is to minimize the availability of cowbird feeding habitat within at least a 10 km radius of American Redstart 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.
- Given that nest predation rates may be elevated close to forest edges, particularly adjoining grassland, agricultural lands and other human-developed land cover, the extent of forest/developed edges within preferred American Redstart breeding habitat should be minimized where possible.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

A Neotropical migrant, the American Redstart occupies a broad breeding range across much of the eastern and northern United States, and southern Canada, from extreme southwestern Yukon in the east, to Newfoundland in the west. It overwinters from the western coast of northern Baja and from throughout southern Baja California, the Atlantic slope of mainland Mexico, the southern tip of Florida, the Central Americas, the Caribbean, and northern South America (Sherry & Holmes 1997).

On the breeding range, it generally prefers moist, deciduous, second-growth woodlands with abundant shrubs, often near water (bottomland hardwoods and swamps) in the southern and western parts of its range (Sherry & Holmes 1997). It becomes less common as the abundance of conifers in mixed forests increases (Martin 1960, Sabo 1980, DeGraaf & Chadwick 1987, Hunt 1996). American Redstarts generally reach maximum breeding densities in early successional to mid-successional forests (Bond 1957, Webb et al. 1977, DeGraaf 1991, Westworth & Telfer 1993, Hunt 1996, Holmes & Sherry 2001). American Redstart abundance in a large, undisturbed New Hampshire forest declined significantly by an average of 4.85% over the period 1969-1998, mirroring an average decline of 3.10% among state-wide Breeding Bird Survey routes for New Hampshire over the same period (Holmes & Sherry 2001). These changes have been linked to declines in habitat availability, with the New Hampshire forest maturing from a mature second growth state at the start of the study (Holmes & Sherry 2001), coincident with similar forest maturation over much of the northeastern United States (Hunt 1998). However, a minority of studies have found maximum redstart densities in more mature forests (Ficken & Ficken 1967, Crawford et al. 1981, Morgan & Freedman 1986, Thompson & Capen 1988). In central Appalachian hardwood forests, the American Redstart is restricted to mature stands with a closed overstory canopy and dense midstory and understory (Crawford et al. 1981). Furthermore, when a combination of Dutch elm disease, drought and windstorms changed a mature, closed-canopy forest in northern Minnesota to a more open habitat with a dense undergrowth, breeding densities were reduced by an average of 27%, from 1.4-4.8 territories/10 ha to 0-4.8 territories/10 ha (Canterbury & Blockstein 1997). In old-growth forest, if frequents thickets in tree-fall gaps (Sherry & Holmes 1997).

The American Redstart appears to be area sensitive in parts of eastern North America, preferring interior woodland over edges, and large (>4,000 ha), intact tracts of habitat (Robbins 1979, Ambuel & Temple 1983, Robbins et al. 1989).

Nest site characteristics

The open-cup nest is generally surrounded by foliage and supported by at least three vertical stems against the main trunk of a leafy tree or shrub. Nest height averaged 8.2 m (SD = 6.43), with a strong mode at 1.5-3 m and a second shallow mode from 10-20 m in New Hampshire (Sherry & Holmes 1997), but 3.4 m (SD = 1.68, range 0.6-12 m) in Alberta (M.-A. Villard & S. Hannon cited in Sherry & Holmes (1997)). Most other reported nest heights are in the range 1-4 m, with some nests up to 15 m high (reviewed in Sherry & Holmes 1997).

BREEDING PRODUCTIVITY

Laying seasons

Earliest and latest nests in the BBIRD database were initiated on 7 May and 15 July respectively. Published earliest and latest "egg dates" are 12 May and 27 July (reviewed in Sherry & Holmes (1997)). Most laying takes place during a 6-week period, with the peak of laying occurring two weeks later at latitudes 45-50°N (11-17 June) than at latitudes 40-45°N (28 May – 3 June: Figure 1). This is similar to reported data showing a mid-May start to nesting in the southern part of the range, and a late-May start in the north, with most egg laying occurring during the month of June (Sherry & Holmes 1997). The length of the laying season was 37 days at latitudes 45-50°N and 51 days at latitudes 40-45°N, yielding an average laying season length of 44 days.

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (Sherry & Holmes 1997). BBIRD data indicate that the mean clutch size of unparasitised nests is 3.60. The modal incubation and nestling periods are 11 days and 9 days respectively (Sherry & Holmes 1997). The American Redstart is single-brooded, at least in the northern regions of its range where its breeding biology has been sufficiently well studied (Sherry & Holmes 1997). There are no published data on the length of the re-nesting interval after nest failure, but females may make up to four attempts in a season (Sherry & Holmes 1997). We assume a 5-day re-nesting interval, as described for the Ovenbird. To calculate breeding productivity, we used a 44-day laying season, 23-day nesting period (3-day laying, 11-day incubation, 9-day nestling), and 5-day re-nesting interval after nest failure.

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

Jolly-Seber estimate of annual survival based on banding returns (n = 232 birds of both sexes) in a large, undisturbed forest in New Hampshire was 67% (Nichols et al. 1981). However, Sherry & Holmes (1997) suggest that annual survival appears to lie in the range 50-60% for birds that have reached sexual maturity, and females may survive at a lower rate than males. These estimates may be variously confounded (biased low) by relatively low breeding-site fidelity and evidence of breeding dispersal between years (Holmes & Sherry 1992). We assume an annual survival rate for adult females of 67%, despite evidence that females appear to survive at a lower rate than males (Sherry & Holmes 1997). We further assume a juvenile survival rate estimate of 33.5% (50% of the adult survival rate estimate, following the hypothesis of Greenberg (1980) and Temple & Cary (1988) that juvenile survival is approximately 50% of adult survival among small, north-temperate passerines).

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

No data.

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

BBIRD data indicate that the mean clutch size in parasitized nests (3.05, SD = 0.98, n = 38) was 15% lower than that of non-parasitized nests (3.60, SD = 0.83, n = 150). Mean fledging success was 74% lower from successful parasitized nests (0.74, SD = 1.03, n = 43) than from non-parasitized nests (2.84, SD = 1.12, n = 140).

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

Site	No. of nests	Clutch size[1]	Parasitism rate (%)[2]	DPR (%)[3]	Nest success (%)[4]	Fledglings/ nest[5]	Annual fecundity[6]	Lambda
Chippewa Natl Forest, MN	6		0					
NE Monongahela Natl Forest, WV	21		0	0.95	80.33	2.71	2.5	1.09
Northern Ohio	76	3.46	25	4.44	32.74	2.5	1.36	0.9
Bitterroot, MT	137	3.85	34.31	3.39	29.01	2.42	1.2	0.87
Upper Mississippi, MN, WI, IL	274	3.28	17.15	4.04	29.39	2.13	1.07	0.85

[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 (assuming double-brooded) across plots (all plots with ≥5 nests) and sites (plot averages for scales of patch and 1-10 km radii) using multiple regression analysis. Spatial scales included: the patch of forest within which the study plot was embedded; 1-10 km radii of study plot centers; and 50-100 km radii of study site centers. Non-significant results included for comparison across scales. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Scale	Plots				Sites		
	Dependent variables	Independent variables	Adj. R^2	Slope	Independent variables	Adj. R^2	Slope
Patch	Parasitism	To nearest edge	0.1		Patch edge density	0.90**	0.67
	Predation	To nearest edge	0.06		Patch edge density	0.55	
	Lambda	Core forest area	0.57**	0.017	Patch edge density	0.8	
1 km	Parasitism	Forest edge density	0.06		% developed	0.97**	1.18
	Predation	Avg forest patch size >10ha	0.14*	-0.007	% cropland	0.71	
	Lambda	Avg forest patch size >10ha	0.66**	0.072	Angular second moment	0.81	
5 km	Parasitism	Total edge density	0.36**	5.22	Total edge density	0.95**	4.77
	Predation	% forest cover	0.08		% developed	0.90*	0.063
	Lambda	Avg forest patch size >10ha	-0.01		Contagion	0.98**	0.47
10 km	Parasitism	Total edge density	0.35**	5.95	Aggregation index	0.97**	-3.36
	Predation	% forest cover	0.13		% core forest	0.92*	-0.042
	Lambda	Contagion	0.54**	-1.22	% forest	0.96*	0.41
50 km	Parasitism				Total edge density	0.45	
	Predation				Shannon-Weaver diversity	0.96*	0.04
	Lambda				Angular second moment	0.66	
100 km	Parasitism				Fractal dimension	0.53	
	Predation				Aggregation index	0.58	
	Lambda				Total edge density	0.73	

Effects of landscape-level habitat variables on nest parasitism

Among all plots, nest parasitism rate increased significantly with the degree of forest fragmentation at local landscape scales (within a radius of 5-10 km: Table 2, Figure 2). Among sites, nest parasitism rate was significantly related to the degree of forest fragmentation at the patch and local-landscape scales (1-10 km radius), but not the broad-landscape scales (50-100 km radius: Table 2, Figure 3). No other published data on the relationship between nest parasitism and habitat variables are available.

Effects of landscape-level habitat variables on nest predation rate

Among all plots, daily nest predation rate was significantly related to the degree of forest fragmentation at the local-landscape scale of within a 1 km radius, increasing as the average size of forest patches >10 ha within a 1 km radius decreased i.e. predation rate increased as the degree of forest fragmentation increased (Table 2, Figure 4). This trend was apparent for plots within both the Upper Mississippi River and Bitterroot Valley study sites (Figure 4). Among sites, nest predation rate similarly increased as the degree of forest fragmentation increased across all spatial scales, but it was not possible to determine the relative influence of different spatial scales (Table 2, Figure 5). No published data on the relationship between daily nest predation rate and habitat variables are available.

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

On the basis of the most optimistic published estimates of annual adult female and juvenile survival, American Redstarts are required to fledge at least 2.0 fledglings/female/year for lambda to exceed unity. Although annual breeding productivity was estimated at 2.5 fledglings/female at one BBIRD site, productivity estimates ranged from 1.1-1.4 fledglings/female at three other sites (Table 1), and 0.4-1.8 among the 11 plots with sufficient data (Figure 6). As the great majority of the BBIRD lambda estimates are substantially below unity, we may have underestimated seasonal productivity and/or adult survival. However, annual breeding productivity in a large New Hampshire forest averaged 1.8 fledglings/territorial yearling male (n = 17) and 2.4 fledglings/territorial after-second-year male (n = 7: Procter-Gray & Holmes 1981), within the range reported among BBIRD sites.

Among all plots, lambda is particularly negatively related to the degree of forest fragmentation at the patch scale and within a 1 km and 10 km radius of plot centers (Table 2, Figure 6). Among sites, lambda is similarly negatively related to the degree of forest fragmentation across all spatial scales (Table 2, Figure 7).

Effects of silviculture on nest predation and nest parasitism

No data on effects on nest success. The American Redstart was largely absent from regenerating clear-cut areas in Nova Scotia for the first six years post harvest, but occurred in plots of age 8-74 years (Morgan & Freedman 1986). In northern hardwood forests, breeding densities increase significantly in response to a variety of silvicultural practices, including various degrees of thinning and small patch cuts (Webb et al. 1977, Welsh & Healy 1993, Lent & Capen 1995).

Effects of burning on nest success

No data on nest success. 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 breeding densities (Artman et al. 2001).

Effects of grazing/browzing on nest success

No data.

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

Both nest parasitism rate and daily nest predation rate increased as the degree of forest fragmentation at local landscape scales increased. Given that both these factors have a strong negative effect on breeding productivity, it is no surprise then that the BBIRD evidence suggests that lambda decreases strongly as the degree of forest fragmentation at these scales increases. On the basis of published nesting success estimates that averaged 50% in mature forest, and greater breeding densities in early-successional habitats than mature forest, Hunt (1998) suggested that mature forest functions as a sink on American Redstart populations, and that early-successional and edge habitats may represent important source habitat for populations, despite the lack of data on nesting success in such habitats. Our results suggest that such conclusions may be misleading, particularly if early-successional habitats occur more frequently in association with agricultural lands, and should not be taken at face value until the relative nesting success in early-successional versus mature forest has been properly quantified in relation to broader landscape context.

Mapping predicted source and sink habitat

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

MANAGEMENT GUIDELINES

In most areas, particularly northern hardwood forests, where the American Redstart is associated primarily with early-successional habitats (Hunt 1996), breeding densities can be increased using a variety of silvicultural practices, including various degrees of thinning and small patch cuts (Webb et al. 1977, Welsh & Healy 1993). However, in some areas, such as central Appalachian hardwood forests, where the American Redstart is associated primarily with closed-canopy forest, it will tolerate uneven-age management of forest stands, such as single-tree selection and thinning understory trees that compete for root space, but any intermediate or harvest cutting that opens the canopy will probably decrease populations (Crawford et al. 1981).

Given this species' area sensitivity, and the strong effect of forest fragmentation at landscape scales on population lambda, a primary regional management focus should be to maintain a representative network of large, unfragmented forests to serve as source populations across the breeding range of the American Redstart. These forests should ideally be greater than 10,000 ha in area, and incorporate the moist, deciduous forest habitats preferred by this species. Silvicultural practices that produce a patchwork of early-successional habitat preferred by the American Redstart may enhance habitat quality within mature forests, without compromising nesting success through the negative effects of fragmentation on breeding productivity, if logging is restricted to the interiors of large forest tracts, to reduce the potential risk of cowbird parasitism.

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

Given that nest predation rates may be elevated close to forest edges, particularly adjoining grassland, agricultural lands and other human-developed land cover, the extent of forest/developed edges within preferred American Redstart breeding habitat should be minimized where possible.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

Nearly all of the BBIRD lambda estimates were substantially below unity, suggesting that our modeling approach may be underestimating lambda. This is most likely due to either 1) an underestimate of the average laying season length, which, in turn, results in an underestimate of annual breeding productivity; and/or 2) an underestimate of annual adult female survival. We consider it unlikely that we have underestimated laying season length, and thus breeding productivity, as BBIRD data closely approximate other published information (see under "Laying seasons"). The most likely underestimate is that of the annual adult female survival rate, despite our use of the most optimistic published estimate. Thus, annual adult female survival rate should be determined with intensive monitoring, over a period of at least five years, of a color-banded population occupying the interior of a large forest tract where reproductive success is high, given that poor reproductive success may result in higher levels of breeding dispersal (e.g. Porneluzi & Faaborg 1999, Bayne & Hobson 2002).

Despite a lack of nesting success data from early-successional habitats, Hunt (1998) suggested that these habitats must function as important source areas, and mature forests as sinks. Given the negative relationship between lambda and the degree of forest fragmentation at local landscape scales observed among BBIRD sites, the hypothesis of Hunt (1998) requires proper validation.

BBIRD data suggest that nest predation rates are elevated close to forest edges. However, we are unable to distinguish between internal forest edges associated with silviculture, and external, hard edges associated with agriculture etc. The effects of these two edge types on nest predation rates are known to vary. Given that selective or clear-cut logging of small patches may be prescribed for increasing breeding densitites, the extent to which edge effects on nest predation might vary between internal edges created by silviculture and external, predominantly agricultural edges, needs to be determined.

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

A good estimate of the re-nesting interval following nest failure is important for any model estimating seasonal productivity. Our estimate is based on that of another paruline warbler. It would therefore be useful to gather additional data by monitoring color-banded individuals throughout a breeding season.

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

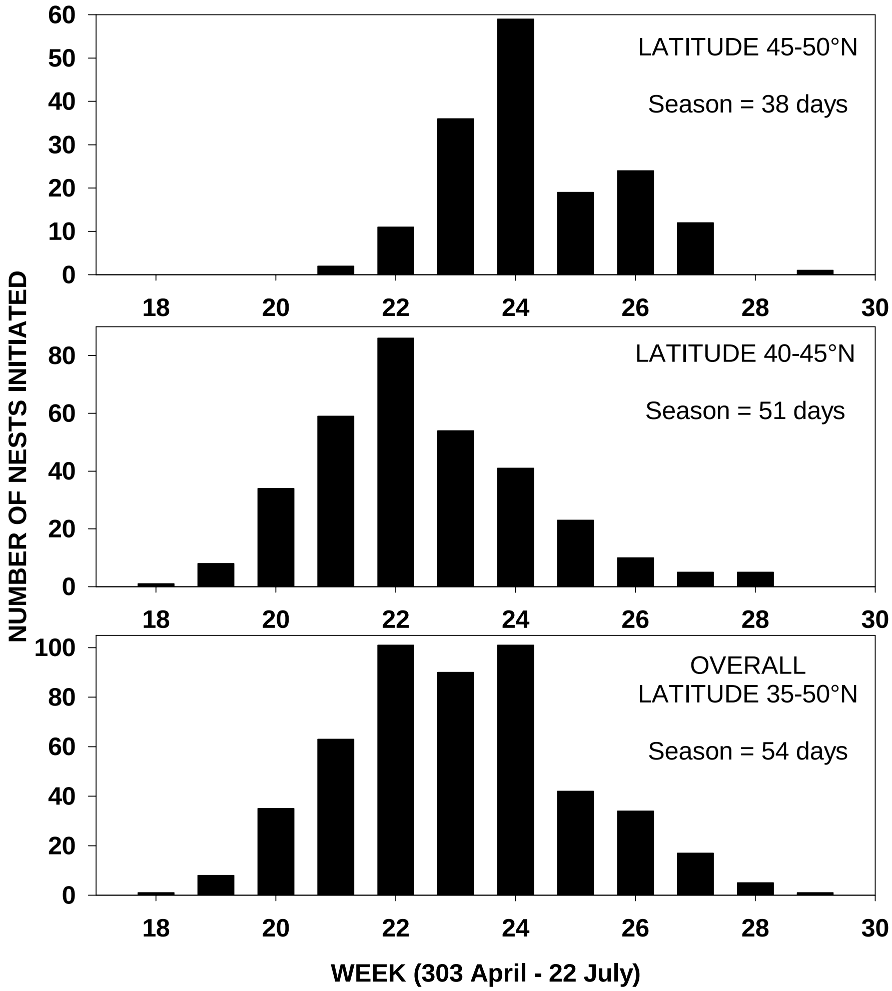

Figure 2. Relationship between nest parasitism rate (arcsine transformed) and indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km radii of plot centers, for all plots with ≥5 nests, at three different sites.

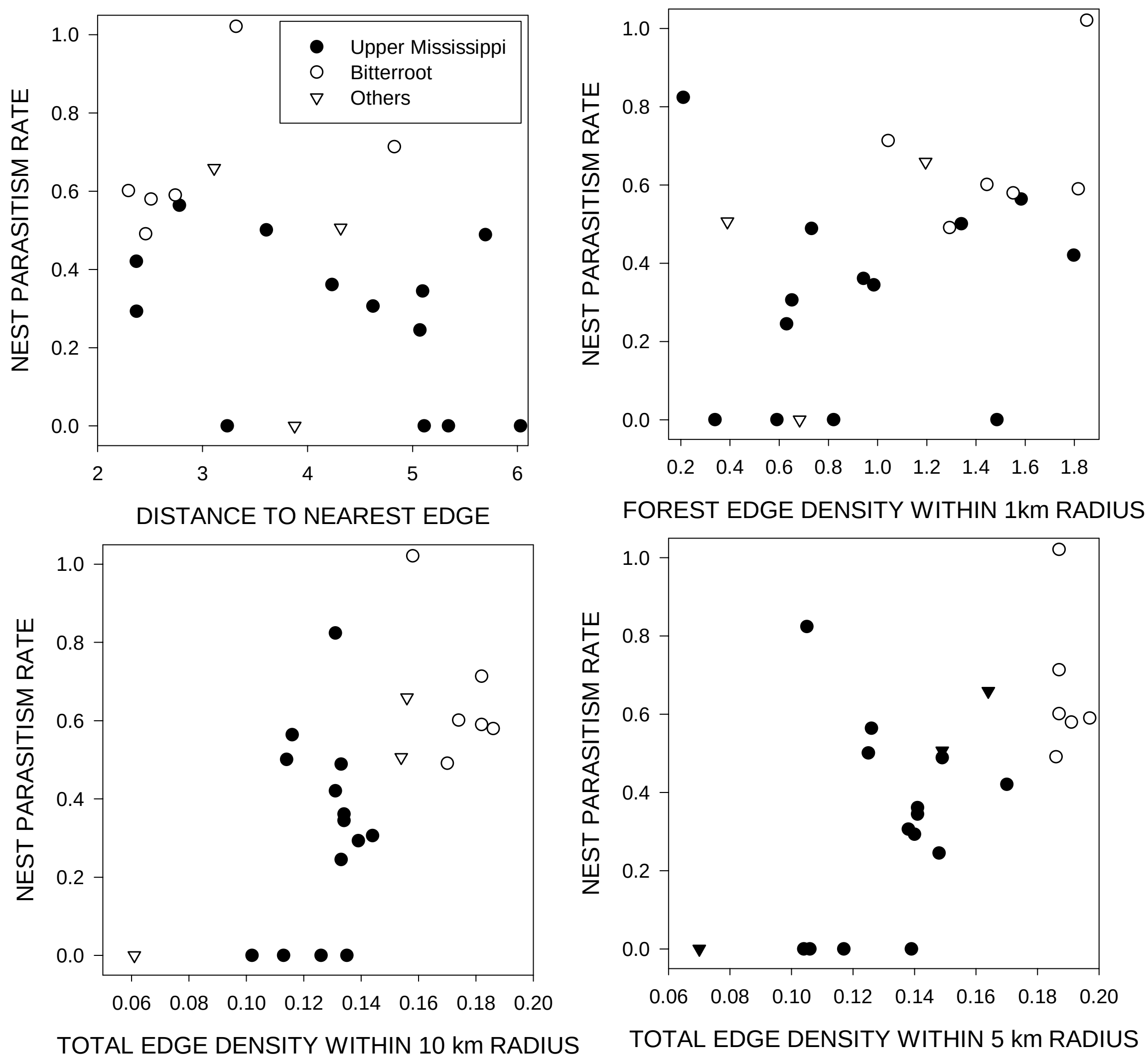

Figure 3. Relationship between nest parasitism rate (arcsine transformed) and various indices of forest fragmentation at spatial scales of the forest patch, within radii of 1-10 km of plot centers (site averages), and within radii of 50-100 km of site centers.

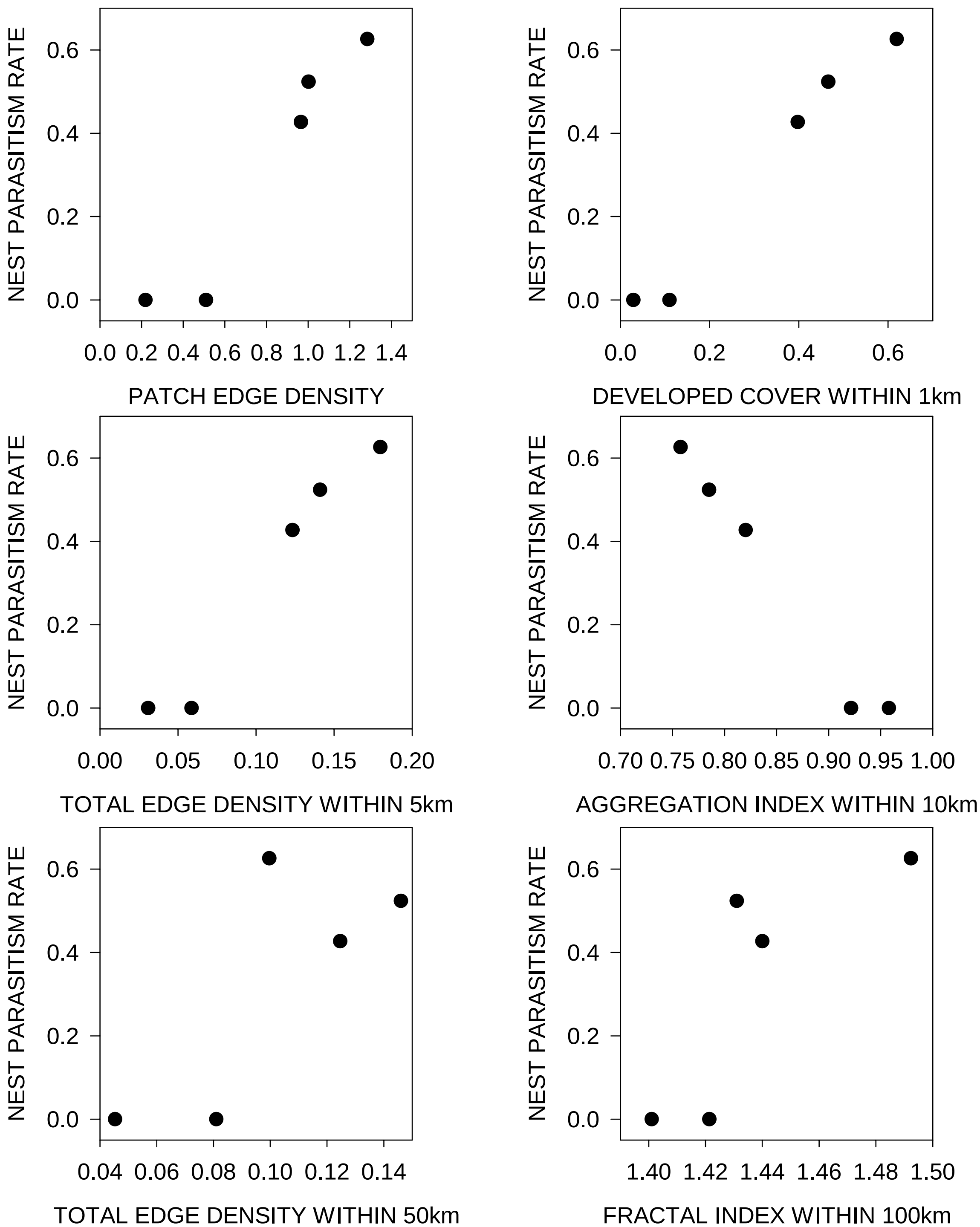

Figure 4. Relationship between daily nest predation rate and indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km of plot centers, for all plots with ≥5 nests within three sites.

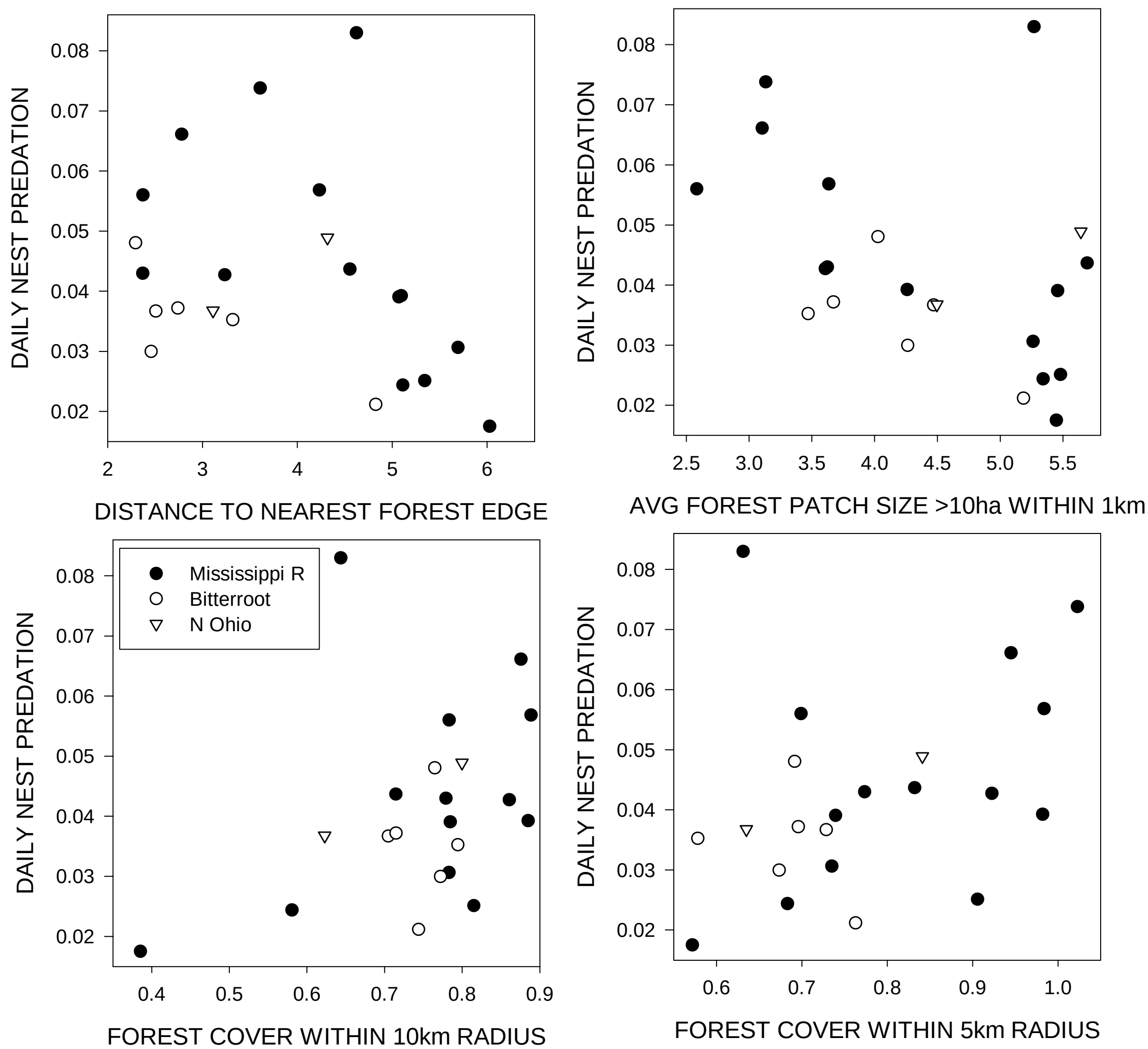

Figure 5. Relationship between daily nest predation rate and various indices of forest fragmentation at spatial scales of the forest patch, within radii of 1-10 km of plot centers (site averages), and within radii of 50-100 km of site centers.

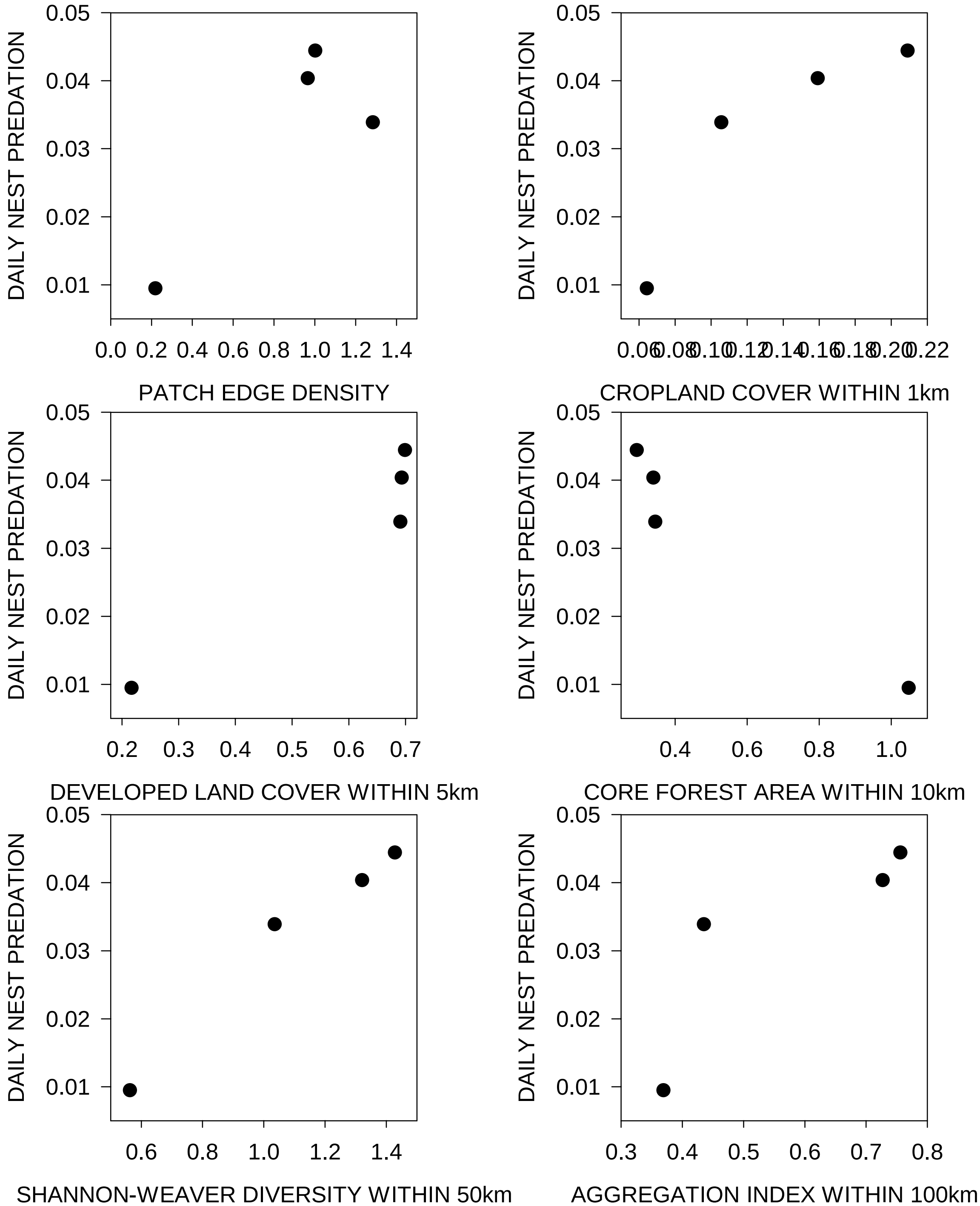

Figure 6. Relationship between lambda and indices of forest fragmentation at spatial scales of the forest patch and within 1-10 km of plot centers within three sites.

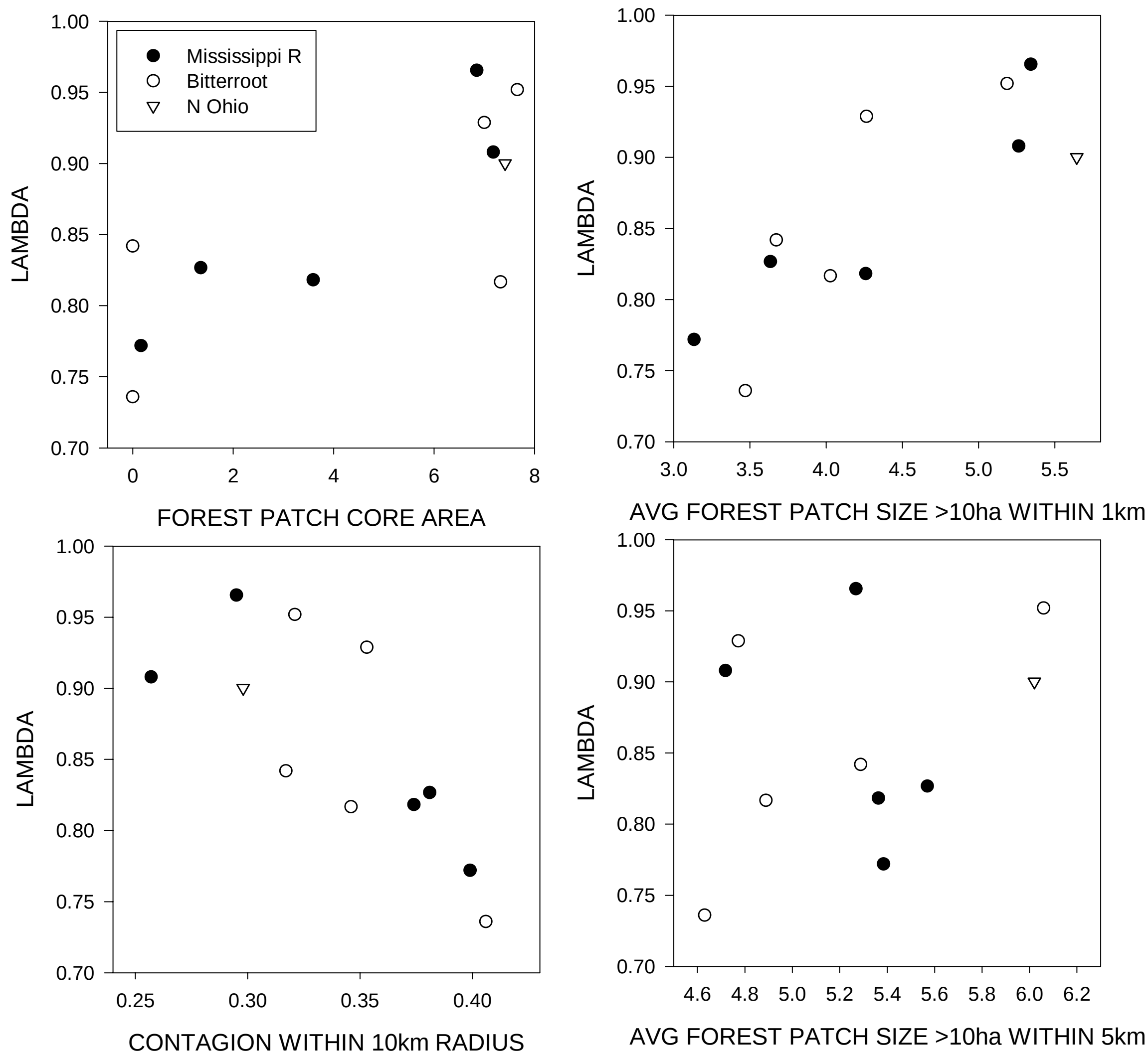

Figure 7. Relationship between lambda and various indices of forest fragmentation at spatial scales of the forest patch, within radii of 1-10 km of plot centers (site averages), and within radii of 50-100 km of site centers.