

Ovenbird *Seiurus aurocapillus*

Preferred breeding habitat: mature forests with large trees, high canopies (10-22 m), high percent canopy closure (60-90%), and open understories with relatively low shrub cover and 20-50% herbaceous cover

Nest placement:

- Ground, in leaf litter and low herbaceous cover
- Ca. 30 woody shrub stems (<8 cm dbh) within 5 m radius circle
- 10-30 tree stems (>8 cm dbh) within 11 m radius circle

Clutch size / Fledging brood size:

- Non-parasitized nests: 4.4 / 3.9
- Cowbird parasitized nests: 3.2 / 2.4

Number of broods per season: 1.0

Annual adult survival rates: Males 61%, females 51%

Requirements for population stability:

- Fledge at least 2.7 fledglings per year (varied from 1.7 to 3.5 across BBIRD sites, with only 5 of 14 sites meeting the minimum)
- Cowbird brood parasitism $\leq 10\%$
- Daily nest mortality $\leq 3.6\%$ (nest success $\geq 41\%$) assuming zero parasitism
- Daily nest mortality $\leq 2.6\%$ (nest success $\geq 54\%$) when $> 20\%$ parasitism
- Percent forest cover $\geq 60\%$ within 100 km radius of focal patch

Cowbird brood parasitism:

- ranged from 0% to 63% across BBIRD sites
- parasitized nests fledge fewer Ovenbird fledglings than non-parasitized nests (2.37 vs 3.91 respectively)
- parasitism effects are particularly strong because birds do not renest if they fledge young, even if only cowbird young, whereas they will renest following predation

Daily nest mortality / Cowbird parasitism rates in relation to landscape context:

- Highly sensitive: Nest predation increases with any fragmentation, but parasitism increases primarily with grass/agriculture fragmentation
- 5.4-7.8% / 16-72% within 100-200 m (predation) and up to 2 km (parasitism) of forest/agricultural edges
- 3.9-5.4% / 0-8% within 200 m of recent clear-cut edges within forests
- 1.7-2.7% / 0-4% within interior forest
- >10% within landscapes with <60% forest cover within 100 km radius

Landscape features that increase/decrease predation and parasitism at local (1-10 km) and large (50-100 km radius) scales:

- an increased proportion of forest edge as forest cover is reduced increases nest predation
- increased agriculture/human dwellings/grassland habitats increase parasitism

Further effects of habitat fragmentation:

- breeding densities rapidly decline within 100-300 m of forest edges and when forest patch size is reduced below 2,000 ha.
- pairing success of males also declines in these same forest edges and fragments, reaching as low as 25% in patches smaller than 50 ha

General conclusions:

- Forest edge habitats within 200 m of recent clear-cuts and within 200 m to 2 km of agricultural edges are population sinks for Ovenbirds
- Ovenbird populations breeding in moderately fragmented landscapes with less than 60% 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 for Ovenbirds
- Based on our assumptions, source populations ($\lambda > 1$) exist only at sites with greater than 60% forest cover in a 100 km radius scale

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

The Ovenbird is a wood-warbler that migrates between grounds in North America and wintering grounds in the southern United States and the Neotropics. Its breeding distribution is restricted to mature deciduous and mixed deciduous/coniferous forests of North America, largely in the eastern US and southeastern Canada. Ovenbirds generally nest in mesic climax forests where deciduous trees are dominant, but will breed in younger deciduous forests in ecoregions where conifers form the climax vegetation (Van Horn & Donovan 1994).

The components of vegetation structure associated with Ovenbird territory occupancy and food supply have been relatively well studied. Ovenbirds are typically associated with mature forests having large trees, high canopies (10-22 m), high percent canopy closure (60-90%), relatively low percent herbaceous cover (20-50%), low shrub density/cover, higher basal area of deciduous trees relative to conifers (overall basal area 25-30%), high percent litter cover (50-95%) and deep leaf litter (Thompson & Capen 1988; Robbins et al. 1989; Van Horn & Donovan 1994; King et al. 1996; Burke & Nol 1998; Holmes & Sherry 2001). In deciduous forests, and mixed deciduous/coniferous forest where the successional gradient is from coniferous to deciduous species, occupancy and territory quality (as determined by arthropod food availability) increase as forest structure varies from forest having a relatively open canopy and dense shrub-understory layer, to forest dominated by larger trees having a closed canopy and sparse understory (Smith & Shugart 1987). The only study finding an opposite pattern (Stenger & Falls 1959) was conducted in forest with a successional gradient from early successional deciduous species to late successional coniferous species. The difference in these patterns is thought to be due to a negative effect of conifer dominance on the microclimate and ecology of the forest floor (Smith & Shugart 1987). Arthropod food availability for Ovenbirds decreases, and territory size increases, as the relative basal area

of conifer species increases, probably because conifer litter provides a poorer carbon source for the forest-floor arthropods upon which Ovenbirds feed (Smith & Shugart 1987). Within deciduous forests, Ovenbird abundance generally increases as forests mature (Morgan & Freedman 1986; Yahner 2000; Holmes & Sherry 2001).

Because Ovenbirds both feed and nest on the ground in thick leaf litter and associated herbaceous cover, they are sensitive to the thinning and trampling of forest-floor vegetation associated with livestock grazing within forests, and generally avoid nesting in grazed areas (Hann 1937). Similarly, Ovenbird breeding abundance is substantially reduced for at least the first 1-2 years following prescribed fires that reduce understorey vegetative cover in mature oak forests (Aquilani et al. 2000; Artman et al. 2001).

Ovenbird territory densities (territories per 10 ha) in suitable habitat range from 3-11 in New Hampshire (Holmes & Sherry 2001), to 8.3 in Michigan (Hann 1937), 4.82 in Tennessee (Smith & Shugart 1987), 0.3-8.3 in southern Ontario woodlots (Burke & Nol 1998) and 0.66-2.6 in Missouri (Wenny et al. 1993; Porneluzi & Faaborg 1999). A 30-year study in a mature deciduous forest in New Hampshire found that Ovenbird breeding densities would occasionally double or halve between years (Holmes & Sherry 2001). Relatively large short-term, inter-annual fluctuations in population density of this nature are likely regulated by a strong inverse relationship between territory size and food availability (Stenger 1958; Smith & Shugart 1987; Burke & Nol 1998), and the combined effects of food availability and nest mortality on breeding success and subsequent recruitment into the breeding population the following year (Martin 1992; Sillett et al. 2000; Holmes & Sherry 2001). Inter-annual variation in food abundance for wood warblers in eastern deciduous forest has been linked to El Nino Southern Oscillation (ENSO) macro-climatic variation (Sillett et al. 2000).

Nest site characteristics

All Ovenbird nests recorded in the BBIRD database were sited on the ground (n = 959), either in the open among the leaf litter, or against or under live vegetation or plant stems

constituting the green ground cover (Table 1), in areas where green ground cover was less than 40% (Table 2). When live vegetation constituted part of the nesting substrate, this vegetation was generally less than 25 cm in height, with the nests placed either right up against/under the foliage, or against the central stem of the plant. Average counts of tree stems within an 11.3 m radius of nest sites were lower than those at nearby non-use sites (Table 3), suggesting that Ovenbirds select nest sites in areas with slightly reduced tree density. These observations are in agreement with published studies that suggest Ovenbirds prefer to nest in mature forest with a relatively open understory.

Table 1. Number of nests coded with different nest-site characteristics among study sites. See Figure 1b for site locations.

Site	Nest substrate ¹		Substrate height (cm)				
	Leaf litter	Vegetation	0	10-25	26-50	60-100	>100
Chippewa Natl Forest, MN	60	302	104	167	56	4	20
St Croix R. Valley, MN & Chequamegon Natl Forest, WI	45	0					
South-eastern Minnesota	12	0	12	0	0	0	0
Mississippi R., MN/WI	15	3	16	1	0	0	0
Central Missouri	13	1					
Ozarks, Missouri	15	47	0	1	0	7	6
Ozark Natl Forest, AR	0	27	23	10	11	0	4
Wayne Natl Forest, OH	114	155	31	48	29	13	5
Nantahala Natl Forest, NC	39	1					
Monongahela Natl Forest, WV	0	18					
Westvaco Wildlife & Ecosystem Research Forest, WV	10	0	5	0	0	0	0
Eastern West Virginia			7	0	0	0	0

¹Nest in leaf litter alone or against/under green vegetation

Table 2. Average characteristics of Ovenbird nest sites measured in 5-m radius plots centered on the nest, quantified as percent overhead cover (% of nest obscured by vegetation from 1 m above nest), average percent side cover (average of 4 measurements of side cover from 1 m to N, S, E, W of nest at ground level), leaf-litter depth, percent of ground covered by green vegetation below 50 cm in height, percent of ground covered by dead leaves, height of the average height of the top canopy within an 11.3 m radius above the nest, percent cover of high canopy (above 5 m in height), and percent total canopy cover that includes sub-canopy cover. Nest sample size in parentheses.

Site	% Overhead cover	Average % side cover	Litter depth (cm)	% Green ground cover	% Leaf ground cover	Average top canopy ht (m)	% High canopy cover (>5m)	% Total canopy cover
Chippewa Natl Forest,								
MN	38.4 (44)	49.1 (44)	3.0 (47)	27.1 (47)	96.3 (47)	20.3 (47)	93.1 (48)	93.5 (48)
Ozarks, Missouri	32.3 (13)	25.7 (13)	15.7 (15)	11.9 (13)				
Wayne Natl Forest, OH	64.4 (41)	36.2 (15)	1.7 (59)	39.1 (60)	70.6 (60)			

Table 3. Average counts of stems of different diameters within a 5-m radius (shrub stem counts) or 11.3-m radius (tree stem counts) at Ovenbird nest sites.

Site	Tree stem counts			Sample size	Shrub stem counts			Sample size
	8-23cm	23-38cm	>38cm		<2.5cm	2.5-8cm	Class 3	
Chippewa Natl Forest, MN	14.58	5.43	1.68	320				
Nantahala Natl Forest, NC	16.89	5.89	2.56	9				
Ozarks, Missouri	17.14	7	1.75	14				
Mississippi R., MN/WI	9.75	6.75	12	4				
Wayne Natl Forest, OH	6.88	3.01	1.64	136				
South-central NY	16.63	9.32	2.89	19				
Ozark Natl Forest, AR					28.14	4.92	5.38	14

BREEDING PRODUCTIVITY

Breeding seasons

Earliest and latest nests in the BBIRD database were initiated on 28 April and 21 July (excluding a nest initiated on 6 August), with most nests initiated in the period 30 April – 10 June (Figure 2). Ovenbirds breeding in northern Minnesota started laying three weeks later than those at sites in southern Indiana and Ohio, and consequently exhibited a shorter breeding season (Figure 2). The breeding season in northern Minnesota is similar to that described for southern Michigan (Hann 1937), suggesting that birds breeding at higher latitudes experience shorter breeding seasons. The overall length of the laying season of Ovenbirds was estimated at 64 days.

Assumptions in calculations of breeding productivity

We used a nesting period of 23.6 days (3.4 days laying, 12.2 days incubation (Hann 1937), and 8-day nestling period (Hann 1937)). We assumed a 64-day laying season, a 5-day delay between loss of a clutch or brood and the laying of the first egg in a replacement clutch (Hann 1937) and a 45-day delay between successful fledging and clutch initiation (to simulate the rarity of double-brooding among Ovenbirds).

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

Accurate estimates of the finite rate of population increase depend critically on accurate estimates of annual adult and juvenile survival. Adult survival estimates for Ovenbirds vary widely, even among studies using capture-recapture models that control for recapture probabilities. DeSante et al. (2001), using a mark-recapture model that ignored transient individuals in populations, estimated the average annual survival rate of adult Ovenbirds (both sexes) to be 49% in both the western (Kansas, Missouri) and eastern Midwest (Indiana, Kentucky) over a 6-year period. Porneluzi & Faaborg (1999) estimated overall annual adult survival of color-banded males at 52% from an average

return rate of 41% (n=115) in central Missouri. In that study, nearly all paired males that failed to raise young did not return the following year, suggesting that they dispersed from the study site. Because birds that permanently disperse away from a study site are assumed to have died in a capture-recapture model, this is likely to lead to bias, producing a low estimate of annual survival. When paired males that failed to raise young were removed from the analyses, the estimated annual survival rate, averaged over four years, was 61% (Porneluzi & Faaborg 1999). This latter estimate of survival matches the observed 0.61 proportion of after-second-year males in this population where second-year and after-second-year males could be distinguished. The proportion of adults within a certain age class can be a reliable alternative estimate of the mean survival rate of adults (Ricklefs 1997). However, monthly survival among Ovenbirds (all sexes and age classes included) wintering in a southern Belize tropical forest was estimated at 0.89, which if extrapolated over 12 months, yields an annual survival estimate of 25% (Conway et al. 1995). Reanalysis of a smaller, 10-year mark-resighting dataset of Hann (1948) using program MARK (Lebreton et al. 1992; White & Burnham 1999), yielded estimates of annual survival rate of 57% for males (n = 23) and 48% for females (n = 15). Adult female passerines generally have lower survival than adult males, and the 84% ratio of female-male survival from the data of Hann (1948) for Ovenbirds is similar to the 86% observed in the Black-throated Blue Warbler *Dendroica caerulescens* (Holmes & Sherry 1992). The assumption of lower survival among female Ovenbirds is also supported by the numerous observations of males failing to find mates due to a paucity of females (Gibbs & Faaborg 1990; Villard et al. 1993; Wenny et al. 1993; Van Horn et al. 1995; Burke & Nol 1998; Bayne & Hobson 2001). For the purposes of this assessment, adult male Ovenbird survival is assumed to be 61%, based on the larger, inter-annual dataset of Porneluzi & Faaborg (1999), and adult female survival is assumed to be 84% of male survival, i.e. 51%.

The survival rate of fledglings, from the time they leave the nest to independence at the age of 30-40 days, was estimated at 56% (n = 70) in one study (Hann 1937). If the survival of fledglings is assumed to be 0.56 in the first month, and the equivalent of annual adult male survival (0.61) adjusted over the remaining eleven months, then the

survival of juvenile females through their first year is estimated to be 36%. Given that the winter survival of first-year birds is commonly lower than that of older birds (e.g. Holmes et al. 1989), this estimate is likely optimistic, although it is similar to estimates of 28-35% for first-year survivorship among other small tropical migrants (Saether 1989). Under these survival-rate assumptions, the annual breeding productivity required for the maintenance of a stable Ovenbird population ($\lambda = 1$) is 2.72 fledglings per female.

Breeding productivity and Ovenbird population stability among BBIRD sites

The average Ovenbird clutch size differed between non-parasitized and parasitized nests (4.36 vs 3.17), being lower in parasitized nests probably as a result of removal of host eggs by female cowbirds when visiting the nest to lay their eggs (Hann 1937).

Consequently, brood parasitism resulted in fewer Ovenbird fledglings (2.37 vs 3.91) per successful nest. The mean number of cowbird eggs laid in parasitized nests increased as the rate of cowbird parasitism increased (Figure 3). Seasonal productivity ranged from 1.35 to 3.48 fledglings per female, with only 5 of the 14 BBIRD sites meeting the minimum of 2.7 fledglings per female required for population stability (Table 4).

Table 4. Summary of Ovenbird 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 pred rate (%) ³	Nest Succ (%) ⁴	Fledglings/ Nest ⁵	Annual Prod ⁶	λ
Central Missouri	19	3.56	63.2	3.92	21.8	2.62	1.35	0.75
Mississippi R., MN/WI	15	4.00	40.0	2.74	40.6	2.37	1.65	0.80
St Croix R. Valley, MN & Chequamegon Natl Forest, WI	27	3.48	22.2	4.64	27.1	3.31	1.89	0.85
Western Maryland	19	3.75	36.8	4.62	25.8	3.56	2.01	0.87
Wayne Natl Forest, OH	232	4.09	16.4	5.36	25.7	3.58	2.03	0.87
South-central NY	15	4.15	20.0	3.42	32.1	3.70	2.33	0.92
Chippewa Natl Forest, MN	240	4.42	2.1	4.25	33.8	3.75	2.43	0.94
Hoosier Natl Forest, IN	142	4.07	30.3	3.79	40.0	3.54	2.44	0.94
Ozarks, Missouri	72	4.34	4.2	4.37	30.7	4.18	2.60	0.97
Chequamegon Natl Forest, WI	41	4.20	4.9	2.34	46.6	4.00	2.94	1.03
Nicolet Natl Forest, WI	24	4.40	4.2	2.83	40.7	4.34	3.03	1.05
Monongahela Natl Forest, WV	18	4.50	5.6	2.14	60.2	3.83	3.09	1.06
Ozark Natl Forest, AR	55	4.80	1.8	2.26	58.3	4.10	3.34	1.10
Nantahala Natl Forest, NC	39	4.77	0.0	2.60	48.0	4.65	3.48	1.13

¹Number of Ovenbird eggs incubated

²Percentage of nests that received 1 or more cowbird eggs

³Percentage of nests lost to predators per day

⁴Percentage of nests that produced at least 1 fledgling

⁵Number of Ovenbird young fledged per successful nest

⁶Number of Ovenbird young fledged per female per year across all females

Nest parasitism rate and daily nest predation rate were not significantly correlated ($r = 0.34$, $P = 0.26$) among sites, suggesting that factors leading to greater nest parasitism rates do not also lead to greater nest predation rates at an overall site level. This broader-scale assessment should, however, not be taken as a contradiction of finer-scale studies that generally find correlated increases in both brood parasitism and nest predation within 200 m of forest edges (see below). The relative influence of brood parasitism is simply more severe at broader scales of assessment. The correlation between population growth rate (λ) and each of the two nest mortality factors was stronger for nest parasitism rate after controlling for predation rate ($r_p = -0.90$, $P < 0.001$) than for predation rate after controlling for parasitism rate ($r_p = -0.65$, $P = 0.021$; Figure 4). This suggests that Ovenbird populations are more severely affected by increases in cowbird brood parasitism than by increases in daily nest predation rates. Indeed, no population was a source ($\lambda > 1$) if cowbird parasitism exceeded 10%. Our emphasis on a relatively reduced role for nest predation in this single-brooded species is partially influenced by our assumption that females will renest repeatedly following nest loss during the length of the laying season (i.e. we set no upper limit on the number of renesting attempts). This assumption contrasts with another Ovenbird productivity model that assumed that females attempt only one renest following nest loss (Donovan et al. 1995), but is in agreement with the suggestion that females breeding at sites with high nest predation will renest persistently (Porneluzi & Faaborg 1999).

Effects of forest fragmentation on Ovenbird nesting success

Ovenbird nesting success and breeding productivity (number of fledglings produced per female per year) are sensitive to habitat edges and forest patch size, largely due to changes in the rate of brood parasitism by Brown-headed Cowbirds and the rate of nest predation within forest edges.

Cowbird parasitism: In forest fragments surrounded by agriculture in southern Ontario, the cowbird parasitism rate on Ovenbird nests was 68% within 100 m of forest fragment edges, but only 4% in forest fragment interiors greater than 100 m from agricultural

edges. As a result, cowbird parasitism averaged 29% in small woodlots (mostly less than 100 ha) and 16% in larger woodlots (mostly 100 – 2 300 ha) where local forest cover (within 10 km radius) was typically 15-40%, but was absent in the interior of contiguous forest with >80% local forest cover (Burke & Nol 2000). In the Midwest of the US, both small (mean patch size 550-670 ha) and large forest fragments (2 000 – 4 000 ha) experience severe brood parasitism (19-67% and 72% respectively), whereas parasitism rates in contiguous forests are similarly low (2-4%: Li ?; Donovan et al. 1995; Porneluzi & Faaborg 1999; Flaspohler et al. 2001). In southern Indiana, Ovenbirds at a forest-interior site (roughly 2 km from closest agricultural edge, with 87% forest cover within a 3 km radius) suffered relatively high brood parasitism (24%: Ford et al. 2001), suggesting that cowbirds can intrude several kilometers into contiguous forest to parasitise host nests. Nonetheless, there is a strong negative correlation between percent forest cover within a 10 km radius and cowbird brood parasitism on Ovenbird populations across the Midwest (Robinson et al. 1995). Other reported cowbird parasitism rates on Ovenbird nests are 52% in forest bordering pasture fields in Michigan (Hann 1937), 54% in forest bordering livestock pastures in New York (Hahn & Hatfield 2000), and 9% in fragmented forest dominated by suburban development in Maryland (Dowell et al. 2000). Rates of brood parasitism in forest edges adjoining clear-cuts embedded in contiguous forests are generally low (0-8%: King et al. 1996; Flaspohler et al. 2001; Rodewald & Yahner 2001), and little different from parasitism levels in undisturbed contiguous forest, suggesting that clear-cuts are substantially less attractive than agricultural lands as feeding habitats for cowbirds.

Nest predation: In the Midwest and Great Lakes regions of the US and Canada, and in the north-eastern US, nest predation rates on Ovenbird nests have consistently been found to be greater within 200 m of forest edges and in more fragmented habitats. In southern Ontario forests fragmented by agriculture, where edge-adapted corvids (especially Blue Jay *Cyanitta cristata*) and Raccoons *Procyon lotor* are prominent nest predators, there was a threshold in nest predation rates on Ovenbird nests at around 100 m, with higher nest predation within 100 m of forest edges (43%) than at distances greater than 100 m (24%). Furthermore, daily nest mortality (due largely to predation) declined significantly

with increasing size of forest fragments, being 7.9% in small woodlots (mostly less than 100 ha), 3.6% in large woodlots (mostly 100-2 300 ha) and 1.8% in contiguous forest (Burke & Nol 2000). In Pennsylvania, daily nest mortality was greater within forest edges (mostly 100-200 m from edge) bordering agriculture (7.8% daily mortality) than forest edges bordering clear-cuts (5.4% daily mortality). This difference is attributed largely to a greater abundance of corvids in forest bordering agriculture (Rodewald & Yahner 2001). In northern Wisconsin, the edge-mediated predation threshold adjoining recent clear-cuts extended to around 200 m, with greater Ovenbird nest predation within 200 m of forest edges (around 39% nest success) than at distances of 200-950 m (around 67% nest success: Flaspohler et al. 2001). In the north-eastern US, where squirrels and chipmunks are major nest predators, predation rates were higher within 200 m of forest clear-cut edges (39% nest success) than in forest interiors greater than 200 m from such edges (54% nest success: King et al. 1996). In the Midwest, where a general trend of increasing Ovenbird nest predation with declining forest cover (an index of fragmentation) has been found (Robinson et al. 1995), daily nest predation was higher in forest fragments (mean patch size 550-670 ha) surrounded by agriculture (4.2-4.6% daily predation) than in contiguous forest (2.2-2.7% daily predation) in one study (Donovan et al. 1995), but daily nest mortality was non-significantly lower in larger forest fragments of 2 000 – 4 000 ha (3.5% daily mortality) than in contiguous forest (5.3% daily mortality) in another study (Porneluzi & Faaborg 1999).

Landscape effects on Ovenbird breeding productivity and population viability

Ovenbirds breeding in most forest-edge habitats bordering agriculture have been found to suffer brood parasitism rates of 16-72%. BBIRD data indicate that any population that suffers a brood parasitism rate greater than 10% is not viable in the long term. This leads us to the conclusion that forest edges act as universal sinks on Ovenbird populations. This elevated, edge-mediated brood parasitism can extend up to 2 km from agricultural edges, and occur in forest fragments up to 4,000 ha in area. The ubiquity of unsustainable levels of cowbird brood parasitism on Ovenbirds breeding in forests fragmented by agriculture

and suburban developments highlights the threat that forest fragmentation poses to the viability of Ovenbird populations in many regions.

In the absence of parasitism, an average population is a sink if the daily nest mortality rate exceeds 3.6%, i.e. if nest success is lower than 41%. Most studies of Ovenbird nesting success in forest-edge habitats report daily mortality rates (mostly from predation) greater than 3.6%. These include daily mortality rates of 5.4-7.8% in forest within 100-200 m of agricultural edges, 3.9-5.4% in forest within 200 m of clear-cut edges, and 3.6-7.9% in fragmented landscapes generally. This ensures that fragmented landscapes and forest edges, particularly those bordering agriculture, function as population sinks, even if cowbird parasitism were to be absent.

The combination of unsustainably high levels of cowbird brood parasitism and nest predation in forest edges and fragmented habitats in general means that forests fragmented by, and bordering agriculture and suburban developments are strong sinks on Ovenbird populations. In contrast, low daily mortality rates (1.7-2.7%) and negligible cowbird brood parasitism (0-4%) within the interiors of contiguous forests highlight the importance of large, unfragmented forests as sources for maintaining regional Ovenbird populations. The negative effect of forest edges and fragments on population dynamics is ameliorated somewhat by the strong preference that females show for forest interior habitats when selecting breeding territories.

The pervasive association of cowbirds with fragmented habitats and their strongly negative influence on Ovenbird population viability are supported by the strong correlations between percent forest cover within a 100 km radius of study sites and each of population growth rate ($r = 0.91$, $P = 0.001$) and the rate of cowbird brood parasitism ($r = -0.89$, $P = 0.001$; Figure 5). At this broad landscape level, percent forest cover was not a good predictor of nest predation rate ($r = -0.43$, $P = 0.25$). Among BBIRD sites, no Ovenbird population was a source if percent forest cover within a 100 km radius was less than 60% (Figure 5). In a comparison of forested landscapes within the Midwest, Robinson et al. (1995) found that the rate of brood parasitism on Ovenbirds exceeded

10% and the daily rate of nest predation exceeded 3.6% in any landscape with less than 80% forest cover within a 10 km radius. In combination with our assessment of the nesting success requirements for population viability (parasitism less than 10% or daily predation less than 3.6% in the absence of parasitism), these results suggest that most Ovenbird populations breeding in moderately to highly fragmented forests, such as those of the Midwest, are not viable in the long term. These broad landscape effects on Ovenbird breeding productivity are undoubtedly the result of increased parasitism and nest predation within forest edges, given that forest fragmentation and the proportion of edge habitat increases as percent forest cover is reduced.

Further effects of forest fragmentation on Ovenbird populations

Effects on population density: As inhabitants of mature, temperate deciduous forest interiors, Ovenbirds are sensitive to forest edges (Wenny et al. 1993; Van Horn et al. 1995). The proportion of habitat occupied by breeding pairs is significantly lower within 100m of a forest edge than at distances greater than 200m from edges (Wenny et al. 1993; Porneluzi & Faaborg 1999). In an extensively forested region of Vermont, Ovenbird territory densities were 40% lower within 0-150 m of unpaved roads than within interior areas (150-300 m from roads), illustrating the extreme sensitivity of Ovenbirds to forest-edge effects (Ortega & Capen 1999). Reduced Ovenbird density at forest edges is thought to be mediated by reduced arthropod abundance in the leaf litter due to reduced humidity, increased desiccation and reduced litter depth near forest edges (Burke & Nol 1998). This may explain the failure to detect reduced Ovenbird densities at the edges of recent forest clear-cuts (King et al. 1995; Flaspohler et al. 2001), if forest-floor microenvironments equilibrate slowly to newly created edge conditions. Although Ovenbirds will occupy forest fragments as small as 10 ha, population densities increase as forest patch size increases (Wander 1985; Temple 1986; Gibbs & Faaborg 1990; Porneluzi et al. 1993; Wenny et al. 1993; Villard et al. 1993; Van Horn et al. 1995; Burke & Nol 1998; Porneluzi & Faaborg 1999), and population densities are reduced in more fragmented landscapes (Kluza et al. 2000; Mancke & Gavin 2000). This undoubtedly occurs as a consequence of edge-reduced density.

Effects on male pairing success: Several aspects of the breeding success of Ovenbirds are also sensitive to forest fragmentation. The pairing success of territorial male Ovenbirds is frequently substantially reduced in smaller forest patches (Gibbs & Faaborg 1990; Villard et al. 1993; Wenny et al. 1993; Van Horn et al. 1995; Burke & Nol 1998; Bayne & Hobson 2001) and at forest edges in comparison to forest interiors (Van Horn et al. 1995; Bayne & Hobson 2001). In Missouri, only 25% of males occupying territories in forest fragments of around 300 ha were paired, in contrast to 75% pairing success in a larger, 4 000 ha patch (Wenny et al. 1993). In Saskatchewan, Canada, the pairing success of males was similarly lower in forest fragments created by either agriculture (86% pairing success) or forestry (87% pairing success) than in contiguous forest (97% pairing success; Bayne & Hobson 2001). In southern Ontario, Canada, male pairing success decreased sharply from around 95% to below 25% as forest fragment area declined from 2 300 ha to below 50 ha (Burke & Nol 1998).

MANAGEMENT RECOMMENDATIONS

The viability of Ovenbird populations is threatened largely by Brown-headed Cowbird brood parasitism rates greater than 10%, although elevated nest predation within 200 m of forest edges is also severe enough to limit population viability in such habitats. Cowbird parasitism is directly related to the degree of forest fragmentation, particularly when the cleared forest is transformed to agricultural and suburban habitats.

Our principal management recommendation is therefore to maintain the integrity of source forest habitat by halting/minimizing the processes leading to further fragmentation of source forest patches, broadly defined as core forest greater than 2 km from agricultural edges. These processes include the clearing of forest for agriculture and housing development in particular, and, to a lesser extent, the construction of roads and utility corridors and clear-cut harvesting of timber.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

Most BBIRD sites with sufficient Ovenbird data are in either minimally fragmented (well forested) regions or highly fragmented (relatively low forest cover) regions (see Figure 5). Breeding productivity estimates from moderately fragmented sites are also needed.

A major influence on estimating annual productivity is numbers of breeding attempts per year. This is influenced by both predation and parasitism in differing ways and we have had to make certain simplifying assumptions due to the absence of real data on reneating rates. More studies of reneating rates for populations under different predation and parasitism regimes are needed.

Although based on a single study, the estimated adult male survival rate is considered to be robust. However, the ratio used to then estimate adult female survival rate is based on a relatively small sample from a single study. It would therefore be useful for bird-banding studies to directly estimate survival rates for both sexes at a variety of breeding sites with stable populations.

The estimate of the survival rate of juveniles through their first year is based on a single estimate of survival through the first month post fledging, and on guesswork thereafter. It would be useful to estimate juvenile relative to adult survival on the wintering grounds as the rate of change in the ratio of juvenile to adult birds through the winter season.

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Figure 1a. Distribution of 41 BBIRD sites across the United States.

Figure 1b. BBIRD sites with sufficient Ovenbird data relative to forest cover. 1) Chippewa Natl Forest (NF), MN; 2) Chequamegon NF, WI; 3) Nicolet NF, WI; 4) St Croix R. Valley, MN & Chequamegon NF, WI; 5) South-eastern Minnesota; 6) Mississippi R., MN/WI; 7) Central Missouri; 8) Ozarks, Missouri; 9) Ozark NF, AR; 10) Hoosier NF, IN; 11) Wayne NF, OH; 12) Nantahala NF, NC; 13) Monongahela NF, WV; 14) Westvaco Wildlife & Ecosystem Research Forest, WV; 15) Eastern West Virginia; 16) Western Maryland; 17) South-central NY

Figure 2. Ovenbird laying seasons, as number of new nests initiated each week.

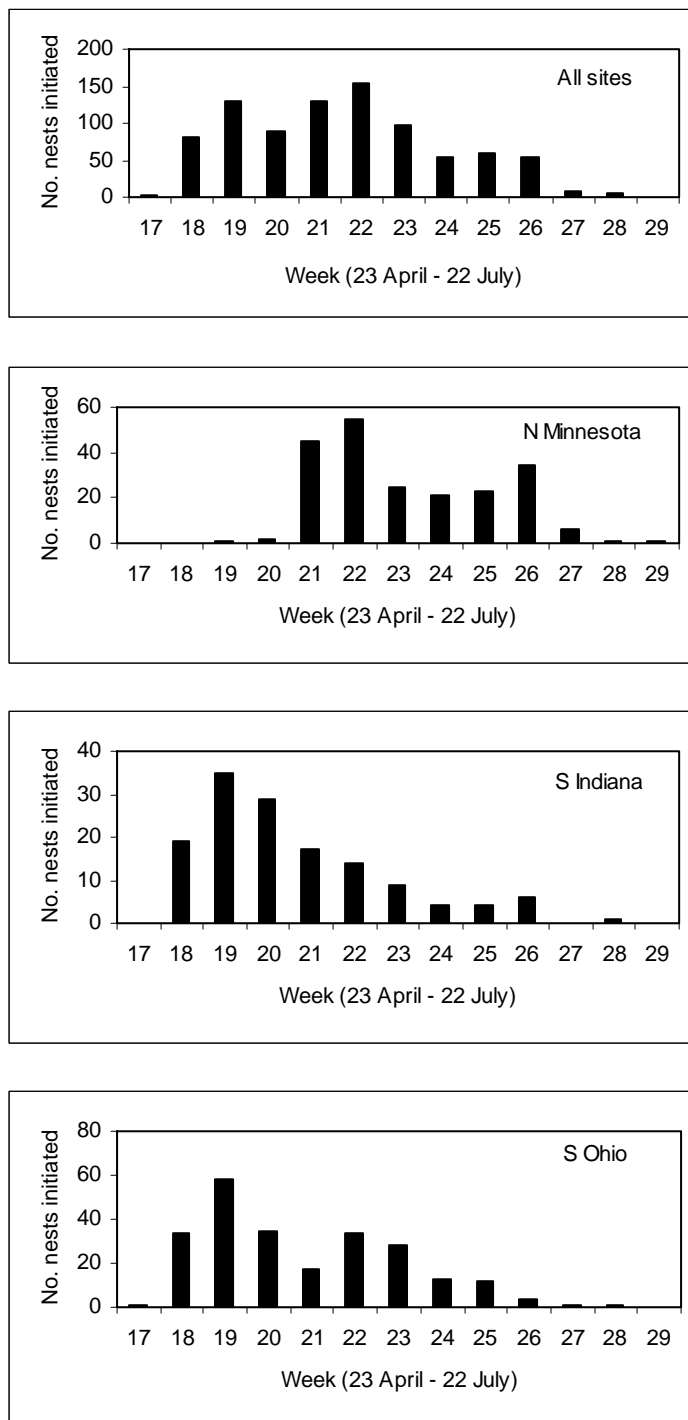


Figure 3. Relationship between the number of Cowbird eggs laid in Ovenbird nests and the site-specific cowbird parasitism rate of Ovenbird nests.

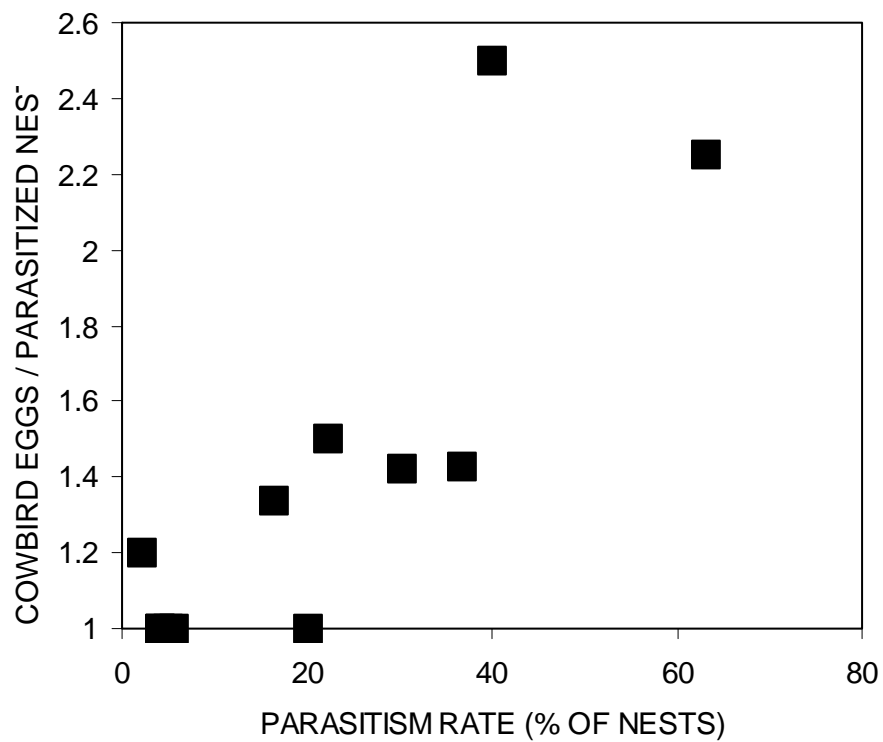


Figure 4. Partial regression plots of finite rate of Ovenbird population increase (lambda) relative to brood parasitism rate and daily predation rate among BBIRD sites. Lambda is more strongly influenced by brood parasitism ($r_p = -0.90$, $P < 0.001$) than nest predation ($r_p = -0.65$, $P = 0.021$).

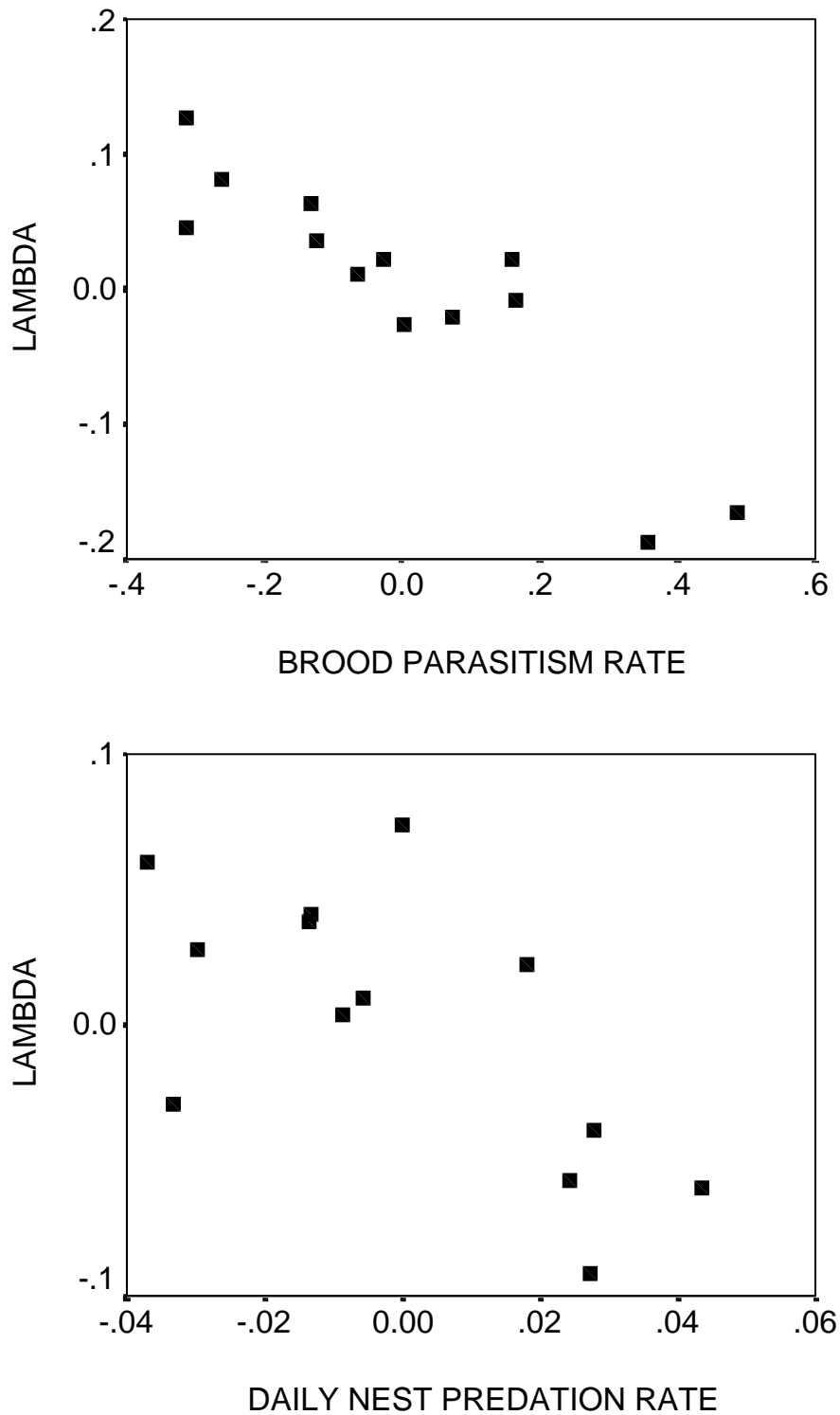


Figure 5. Finite Ovenbird population growth rate (λ) and parasitism rate relative to percent forest cover (forest of any age class) within a 100 km radius of BBIRD sites.

