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COMPARATIVE SEASONAL FECUNDITY OF FOUR NEOTROPICAL MIGRANTS IN MIDDLE APPALACHIA[1]

JENNIFER A. DECECCO, MATTHEW R. MARSHALL AND ALAN B. WILLIAMS
Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, e-mail: jad3792@owl.forestry.uga.edu

GEORGE A. GALE
King Mongkut's School of Technology at Thonburi, School of Bioresources and Technology, Division of Natural Resources Management, Bangkok, Thailand 10140

ROBERT J. COOPER
Warnell School of Forest Resources, University of Georgia, Athens, GA 30602

Abstract. We estimated daily rates of nest predation and Brown-headed Cowbird (*Molothrus ater*) parasitism as well as nesting success for the Red-eyed Vireo (*Vireo olivaceus*), Blue-headed Vireo (*V. solitarius alticola*), Wood Thrush (*Hylocichla mustelina*), and Worm-eating Warbler (*Helmitheros vermivorus*) at two study sites in the middle Appalachian mountains from 1995–1998. These daily rates were then used in combination with species-specific life history parameters to estimate seasonal fecundity. Although daily predation rates were similar across species and sites, parasitism rates and nesting success differed within species between sites and among species within a site. The vireos generally experienced the highest rates of parasitism and subsequently the lowest estimates of seasonal fecundity. However, differences in parasitism and nesting success were not always an accurate predictor of seasonal fecundity. Despite significantly different estimates of nesting success, the Red-eyed Vireo and Blue-headed Vireo had similar estimates of seasonal fecundity. In contrast, estimates of nesting success for the Worm-eating Warbler and Wood Thrush were similar yet there were differences in seasonal fecundity. Life history attributes such as season length, ability to produce additional broods, and ability to raise a host young with a cowbird young were important in determining seasonal fecundity among species. We show the importance of including multiple species within a study framework and illustrate how predation and parasitism differentially affect these species with respect to seasonal fecundity.

Key words: Blue-headed Vireo, Brown-headed Cowbird, parasitism, Red-eyed Vireo, seasonal fecundity, Wood Thrush, Worm-eating Warbler.

INTRODUCTION

The ability to estimate seasonal fecundity for passerine birds is an important component of many areas of avian conservation. Questions involving life history theory, such as the cost of reproduction or source/sink dynamics, require an estimate of season-long productivity. However, the effort involved in collecting the data necessary to enumerate seasonal fecundity for one or many species can be beyond the scope of many research projects. This difficulty in directly measuring seasonal fecundity has generally resulted in inferences that are limited to nest success, the probability that an individual nesting attempt produces at least one host young.

Primary among the processes that influence seasonal fecundity of North American passerines are nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). There are numerous studies documenting the potentially devastating effects of cowbird parasitism on both endangered and non-endangered species (e.g., Mayfield 1977, Sedgwick and Knopf 1988). When parasitized, many species will experience reductions in clutch size and decreased numbers of host fledglings (Robinson et al. 1995a) while still having invested an entire nesting cycle. Those species that either experience a short breeding season, are single-brooded, or are unable to raise any of their own young along with a cowbird are most likely to be negatively affected by cowbird parasitism (Nolan 1978, May and Robinson 1985, Trine 1998). Although nest predation is often considered the leading cause of nest failure among passerine birds (Ricklefs 1969, Martin 1992), predation events usually result in the loss of the entire clutch and will therefore often cause a female to renest immediately (Pease and Grzybowski

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1995). How a particular species' seasonal fecundity is ultimately affected by nest predation or cowbird parasitism can depend on a variety of life history attributes such as the ability to produce an additional brood or the length of the breeding season (Pease and Grzybowski 1995). However, the influences of life history characteristics in combination with the effects of parasitism and nest predation are difficult to separate, and their ultimate influences on seasonal fecundity hard to predict (Woodworth 1999, Grzybowski and Pease 2000).

Many large-scale studies would benefit from the ability to examine both seasonal fecundity as well as the relative effects of predation and parasitism on more than one species within their treatment or study area. Because species can differ in their susceptibility to predation and parasitism within a community (Nolan 1963, Brittingham and Temple 1983, Donovan et al. 1995), it is important to determine whether and how individual species are able to reproductively compensate for these losses over the course of the breeding season. Research that focuses on a single species cannot investigate this variability, and conservation decisions based on such research may not be appropriate for other species that respond to parasitism and predation in dissimilar ways.

We studied the relative effects of nest predation and cowbird parasitism on seasonal fecundity of several species within two study areas. We also assessed how life history traits affect a species' ability to compensate for losses from predation and parasitism and ultimately what influences they may have on seasonal fecundity. We utilized a model developed by Pease and Grzybowski (1995) that allowed us to use our existing nesting data to examine variations in parasitism and nest predation as well as estimate seasonal fecundity without requiring a marked population. We then discuss the potentially misleading inferences that could be drawn from using a generally accepted method of estimating nesting success. Finally, we look at some of the benefits and conservation implications that result from incorporating multiple species into a study design.

METHODS

STUDY SPECIES

We examined four species of three different genera to represent much of the diversity of life history traits that occurred in our study areas within the Appalachian Mountains of West Virginia and Virginia. All four species have been reported as cowbird hosts, and the genus *Vireo* in particular appears very susceptible to parasitism (Franzreb 1989, Marvil and Cruz 1989, Barber and Martin 1997). The Red-eyed Vireo (*Vireo olivaceus*) is a single-brooded species and populations in the Midwest can experience high rates of nest failure due to cowbird parasitism and nest predation (Southern 1958, Robinson et al. 1995b). There is little information regarding the particular subspecies of Blue-headed Vireo (*V. solitarius alticola*) that occurs on our study sites; their range is primarily limited to the Appalachian Mountains where they historically have had little exposure to cowbirds. The Wood Thrush (*Hylocichla mustelina*) is a shrub-nesting species that typically is capable of producing two broods within the middle portions of their range (Roth 1996). As with the Red-eyed Vireo, midwestern populations of the Wood Thrush suffer high levels of parasitism in fragmented forests (Donovan et al. 1995, Trine 1998), although populations in the East generally have experienced lower rates (Hoover and Brittingham 1993, Roth and Johnson 1993). The Worm-eating Warbler (*Helmitheros vermivorus*) is a single-brooded, ground-nesting species that occurs primarily in the eastern portion of the United States. Their susceptibility to parasitism varies widely within their range; information regarding nest success and seasonal fecundity primarily is limited to sites in Connecticut, near the northern extent of their range (Gale et al. 1997, Hanners and Patton 1998).

STUDY AREA

Study sites were located within the Monongahela National Forest (MNF) in southeastern West Virginia and the George Washington National Forest (GWNF) in southwestern Virginia. Eighteen 30-ha study plots were established within the national forests (nine plots within each forest). The MNF sites range from approximately 800 to 1,300 m in elevation and are dominated by chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), sugar maple (*Acer saccharum*), and red maple (*A. rubrum*). The GWNF sites range from approximately 400 to 900 m in elevation and also are dominated by chestnut oak, red oak, and red maple but consist of a greater proportion of pines (*Pinus* spp.) than the

MNF. The MNF sites are generally more mesic and contain more variability in vegetation than the GWNF sites. Although both of these sites are located within large areas of contiguous forest, the larger landscape surrounding the GWNF sites contains a greater percentage of agriculture (T. Keyes, unpubl. data).

Six of the 18 study plots were sprayed with *Bacillus thuringiensis* var. *kurstaki* (*B. t.*), a larval lepidopteran-specific insecticide, in May of 1997 and 1998 to control gypsy moth (*Lymantria dispar*) populations as part of a larger study. Our analyses have found no effects of *B. t.* application on reproductive success, nest visitation rates, or survivorship in either year and therefore we have included nests from those plots in all of our analyses. In a similar study, Nagy and Smith (1997) found only minimal effects of *B. t.* application on reproductive parameters of Hooded Warblers (*Wilsonia citrina*) within study sites in Arkansas. Although Rodenhouse and Holmes (1992) did find a treatment effect with respect to the frequency of additional broods by Black-throated Blue Warblers (*Dendroica caerulescens*), their study design called for the suppression of prey throughout the summer and *B. t.* was subsequently applied several times throughout the breeding season. We recognize that there may be influences on factors other than those listed, and we are currently analyzing these data. However, for the purposes of this paper, we believe that it was appropriate to combine data from treated and untreated plots.

DEMOGRAPHY

Nest searching was conducted on the 18 study plots from 25 April to 1 August of 1995–1998, although the most intensive searching was done in May and June. Nests were found at all stages of the nesting cycle and were checked every three days until they either failed or fledged young according to BBIRD (Breeding Bird Inventory and Research Database) protocols (Martin et al. 1997).

The Pease and Grzybowski (1995) model uses nests monitored throughout the breeding season in conjunction with the timing of events in the breeding cycle to estimate daily rates of predation and parasitism and a predicted seasonal fecundity. The model separates the relative effects of depredation versus that of parasitism; thus, unlike the Mayfield (1975) method, these factors are not necessarily incorporated into a single failure rate. Because nests also can be abandoned in response to a parasitism event, the model also estimates the likelihood that a parasitized nest will be abandoned by the host.

The simple-case model (using the D-D option, Pease and Grzybowski 1995), which does not account for variations in predation or parasitism rates over the course of the nesting season, was used in all analyses. This model assumes that both predation and parasitism events occur only during certain time periods within the nesting cycle, or within a "window of susceptibility" that will vary depending on the length of the egg-laying, incubation, and nestling stage of the host (see below). For the initial stage of the model, the variables t_e, t_i, and t_f describe points in the nesting cycle at which the window of susceptibility to parasitism begins (t_e), and ends (t_i), and the point at which susceptibility to predation ends (t_f). Each of these values was determined from our own nesting data for each species (Tables 1 and 2).

The parasitism and predation rates represent the daily rate by which nests are either parasitized or depredated within the susceptible period. Any event that causes a female to renest (including weather or predation events, as well as abandonment not caused by cowbirds) is used to determine the daily predation rate, and any further reference to this rate will include these typically non-traditional "predation" events. In estimating the probability of abandonment, only those nests that are abandoned by the host immediately following a parasitism event are included. Statistical comparisons of daily rates and seasonal fecundity among species were made by comparing 95% confidence intervals. Rates for which confidence intervals did not overlap were considered significantly different.

Only those nests in which the contents were able to be seen directly were used in the analysis because the model requires the ability to assess exact nest contents on each visit to the nest. Therefore, high nests (usually > 8 m) were not used because it was too difficult to see any of the eggs or young (whether cowbird or host) and our sample was therefore biased towards lower nests and potentially different parasitism/predation levels. Nest heights were greatest for the Red-eyed Vireo ($\bar{x} \pm$ SD $= 7.0 \pm 5.7$ m) and therefore many nests (56 of 182 monitored nests) were not used in determining daily rates (and hence seasonal fecundity). Because there

TABLE 1. Estimates used in the model to determine seasonal fecundity (Pease and Grzybowski 1995) for the Red-eyed Vireo, Blue-headed Vireo, Wood Thrush, and Worm-eating Warbler using nesting data from 1995–1998. See Pease and Grzybowski (1995) for a more complete explanation of variables.

Variable	Definition	Species-specific values			
		Red-eyed Vireo	Blue-headed Vireo	Wood Thrush	Worm-eating Warbler
t_e	Day nest first becomes susceptible to parasitism	5	6	5	6
t_i	Day window of susceptibility to parasitism ends	10	13	10	11.5
t_f	Day window of susceptibility to predation ends	35.5	36.5	34	32
t_r	Day of nesting cycle that a female will initiate a nesting attempt following a successful brood	39[a]	41	40	48[a]
s_s	Length of breeding season	38	73	60	47
f_u	Mean number host young fledged from a successful unparasitized nest	2.5	2.9	2.8	4.0
f_p	Mean number host young fledged from a successful parasitized nest	1.6	0.03	2.5	1.4

[a] Because both the Red-eyed Vireo and Worm-eating Warbler are single-brooded species, the value of t_r has been set to one day greater than the value of s_s.

were no differences in either daily predation or parasitism rates between years (all 95% confidence intervals generated by the model overlapped), all nests from the four-year period for each species within each site were combined for all analyses.

Seasonal fecundity (defined as the number of young fledged per female per season) was estimated by incorporating the daily rates of predation, parasitism, and probability of abandonment with additional life history parameters (Table 1). These life history parameters were species- and site-specific and were summarized from the nesting data from our study sites. Our data for determining the species-specific values of t_r, the length of time before a female begins to renest after raising a successful brood, were limited to a single observation for the double-brooded Wood Thrush and Blue-headed Vireo. We also had difficulty in estimating species-specific season length (s_s), due to variation in weather and timing of leaf-out in early spring, which altered the first egg date for each species in a given year. Therefore, we determined the date that an egg from the first initiated nest of the year was laid as well as the date from the first egg of the last initiated nest of each season, and used the median value of this time interval over the 4-year period for each species. Although we may have overestimated the length of the breeding season using this method, it also is likely that we did not always find both the first

TABLE 2. Selected life history characteristics for the Red-eyed Vireo, Blue-headed Vireo, Wood Thrush, and Worm-eating Warbler from the Monongahela National Forest in West Virginia and the George Washington National Forest in Virginia during 1995–1998. Parameters (except breeding season length) are expressed as $\bar{x} \pm$ SD.

Parameter	Red-eyed Vireo	Blue-headed Vireo	Wood Thrush	Worm-eating Warbler
Incubation stage length (days)	14.0 ± 0.9	14.5 ± 1.0	13.0 ± 1.4	12.0 ± 2.6
Nestling stage length (days)	11.5 ± 1.4	11.9 ± 1.0	12.0 ± 1.6	8.6 ± 1.9
Breeding season length: median days (range)	38 (28–43)	73 (48–92)	60 (47–66)	47 (35–54)
Clutch size: 0 cowbird eggs	3.2 ± 0.6	3.8 ± 0.4	3.6 ± 0.6	4.5 ± 0.9
Clutch size: ≥ 1 cowbird eggs	2.2 ± 1.1	2.8 ± 1.8	3.1 ± 0.8	3.8 ± 0.9

and last female's nest during the breeding season.

MAYFIELD METHOD

The traditional Mayfield (1975) method of estimating reproductive success was used for comparative purposes. We considered a nest as failed at the time of host failure, even if the cowbird young survived in the nest until fledging. In contrast, the Pease and Grzybowski (1995) model considers a nest active as long as at least one young (either cowbird or host) is alive in the nest. The probability of overall nest success was calculated for each species on each site combining years. Survival probabilities at each stage of the nesting cycle (egg-laying, incubation, and nestling) were calculated separately and weighted by the number of days in the respective stage for each species. These separate probabilities were then multiplied together for an overall probability of nest success, and standard errors were calculated following Hensler (1985). All nests in which an outcome could be reliably assessed were used in the analysis and differences were tested using the program CONTRAST (Hines and Sauer 1989). We compared the Mayfield estimates to the seasonal fecundity estimates using Spearman rank order correlations (Dowdy and Wearden 1991).

RESULTS

A total of 927 nests of all four species was found within both sites over the 4-year period. Red-eyed Vireos were not very abundant on the GWNF and not enough nests were found on that site to be used for any estimates of daily parasitism, predation, or fecundity, although we were able to estimate Mayfield nest success. Approximately twice as many Blue-headed Vireo and Wood Thrush nests were located on the MNF compared with the GWNF, but approximately three times as many nests of the Worm-eating Warbler were found on the GWNF compared with the MNF. Nest-searching effort was similar in each forest, and both point count and plot-mapping data reflected the same trends in abundance as did the total number of nests found for each species on both plots and sites (R. Cooper, unpubl. data).

LIFE HISTORY CHARACTERISTICS

Brood status. Approximately 200 Red-eyed Vireos were banded on our study sites during the 4-year period, and there was never an observed instance of a second brood attempt in any year. Similarly, our observations of the approximately 200 Worm-eating Warblers that were banded on both sites also confirmed their status as a single-brooded species within our study area. Although no Blue-headed Vireo females were banded during the study period, one banded female successfully fledged a second brood in 1999. In addition, although there were no banded Wood Thrushes during the study period, one female was observed building a new nest while the male was observed feeding young nearby, supporting the assumption that they are double-brooded as well.

Length of season. The breeding season of the Red-eyed Vireo was the shortest of all four species (Table 2). Initial nesting attempts appeared to correlate with the timing of full leaf-out, which can occur from mid-May to as late as early June on some plots. Both the Wood Thrush and Worm-eating Warbler began breeding within the middle of May, with the Wood Thrush attempting additional nests until mid-July. The Blue-headed Vireo had the longest and most variable breeding season, typically beginning in late April and extending into August for a few individuals.

Parasitism and fledging success. Red-eyed Vireo and Wood Thrush nests were typically only singly parasitized (91% and 100% of all parasitized nests, respectively). Both the Blue-headed Vireo and Worm-eating Warbler were commonly multiply parasitized, although the frequency of multiple parasitism events varied between sites. Of all observed Blue-headed Vireo nests on both sites, 39 nests contained one cowbird egg, 18 nests contained two cowbird eggs, 3 nests contained three cowbird eggs, and 1 nest contained four eggs. Although 13% of parasitized Blue-headed Vireo nests on the MNF contained multiple cowbird eggs, nearly 45% of those on the GWNF were multiply parasitized. Of the parasitized Worm-eating Warbler nests on the GWNF, nearly 40% contained two cowbird eggs, although no nest contained more than two eggs.

For a successful singly parasitized nest of the Red-eyed Vireo (a nest that fledged at least one host or cowbird young), < 2.0 host young also fledged from the nest (Table 3). However, in two of these nests in which host young were fledged, the cowbird egg was believed to either have

TABLE 3. Number of host young fledged ($\bar{x} \pm SD$) from a successful nest (fledged ≥ 1 Brown-headed Cowbird or host young) with either 0 or ≥ 1 cowbird eggs. Nests that were either singly or multiply parasitized but unsuccessful were not used.

Species	Cowbird eggs	Number of nests	Host fledged/ successful nest
Red-eyed Vireo	0	70	2.53 ± 0.94
	1	7	1.85 ± 1.57
	3	1	0
Blue-headed Vireo	0	37	2.92 ± 0.95
	1	20	0.05 ± 0.22
	2	6	0
	3	2	0
Wood Thrush	0	79	2.85 ± 1.04
	1	2	2.50 ± 0.70
Worm-eating Warbler	0	124	4.04 ± 1.16
	1	6	2.00 ± 1.09
	2	5	0.60 ± 0.55

been ejected by the vireo, removed by a cowbird, or removed by a predator between nest checks (therefore, there were no cowbird eggs in the nest once the host young had hatched). For the Blue-headed Vireo, we only made one observation of a host young that fledged from a nest that also contained a cowbird young. The majority of the few Wood Thrush nests with cowbird eggs (a total of 11 nests on both sites in 4 years) were depredated during incubation. The two parasitized nests that were successful fledged on average 2.5 Wood Thrush young. Of six singly parasitized nests of the Worm-eating Warbler on the GWNF that eventually fledged a cowbird, five also fledged at least one host young. However, of the five successful nests that contained two cowbird eggs, only two also fledged a host young.

Probability of abandonment. The probability of an individual female abandoning a parasitized nest was < 0.15 for all species. Of the 18 parasitized nests of the Red-eyed Vireo, only 2 were considered abandoned after the cowbird egg was laid. For the Blue-headed Vireo, although we attributed six nest abandonments to cowbirds, in each of these cases abandonment came only after > 1 cowbird egg was laid in the nest. Ultimately, 30% of those nests that contained > 1 cowbird egg were eventually abandoned by the female. For the Wood Thrush, only one nest that was parasitized after the first host egg was laid was ultimately abandoned. However, because the Wood Thrush did not abandon immediately following the parasitism event, the cause of failure was not attributed to cowbirds. We did not observe a Worm-eating Warbler abandon a nest immediately following the parasitism event in a nest that was either singly or multiply parasitized.

DAILY PARASITISM AND PREDATION RATES

Daily parasitism rates for the Blue-headed Vireo, Wood Thrush, and Worm-eating Warbler were higher on the GWNF than on the MNF (Table 4). Within each site, the Blue-headed Vireo had the highest parasitism rate among species, and the Blue-headed Vireo on the GWNF had a significantly higher daily parasitism rate than any species on either site. Daily parasitism rates for the Worm-eating Warbler were significantly higher on the GWNF than on the MNF, where only two nests were found with cowbird eggs in 4 years (Table 4).

Only two failed nests of the Red-eyed Vireo on the MNF were attributed to cowbird parasitism in the 4-year period, and occurred when the Red-eyed Vireo young disappeared from the nest between checks and were assumed to have either starved or been ejected by the cowbird young. The higher parasitism rates for the Blue-headed Vireo also were accompanied by higher nest failures; 9 failures on the MNF and 19 on the GWNF were attributed to cowbird parasitism. In those parasitized nests where a host young did hatch, it was generally after the cowbird young had hatched and it usually did not survive with the larger cowbird.

Although both daily and seasonal predation rates included failures due to abandonment, weather, and unknown causes, $> 80\%$ of all

TABLE 4. Daily parasitism rates, predicted seasonal fecundity (both with 95% confidence intervals), and Mayfield estimates (± SE) of nesting success for the Red-eyed Vireo, Blue-headed Vireo, Wood Thrush, and Worm-eating Warbler on the Monongahela National Forest (MNF) in West Virginia and the George Washington National Forest (GWNF) in Virginia for the years 1995–1998 combined. For Mayfield estimates, different letters are considered different at $P < 0.05$.

Species	Site	n[a]	Daily parasitism rate	Seasonal fecundity	Nesting success
Red-eyed Vireo	GWNF	0/23	–	–	0.099 ± 0.08A
	MNF	126/182	0.047 (0.023–0.076)	2.13 (1.84–2.35)	0.430 ± 0.04B
Blue-headed Vireo	GWNF	57/85	0.160 (0.100–0.240)	1.35 (0.74–2.16)	0.114 ± 0.04A
	MNF	92/139	0.055 (0.031–0.093)	2.08 (1.44–2.80)	0.226 ± 0.04A
Wood Thrush	GWNF	51/73	0.016 (0.00[b]–0.070)	3.45 (2.43–4.37)	0.377 ± 0.06B
	MNF	110/160	0.007 (0.00[b]–0.021)	3.53 (2.93–4.11)	0.378 ± 0.04B
Worm-eating Warbler	GWNF	193/201	0.055 (0.019–0.110)	2.65 (2.20–3.10)	0.369 ± 0.04B
	MNF	58/64	0.00[b] (0.00–0.00)[b]	3.58 (3.08–3.86)	0.495 ± 0.09B

[a] Number of nests used: daily parasitism and seasonal fecundity estimates/Mayfield estimates.
[b] Estimate was < 0.001 and has been expressed as 0.00.

known failures of the Red-eyed Vireo, Wood Thrush, and Worm-eating Warbler were due to predation events. There were no significant differences in daily predation rates either between sites or among species. Predation rates were highest for the Blue-headed Vireo on the MNF (daily rate = 0.044, 95% CI = 0.032–0.056, n = 92) and lowest for the Red-eyed Vireo on the MNF (daily rate = 0.025, 95% CI = 0.019–0.033, n = 126).

SEASONAL FECUNDITY AND MAYFIELD ESTIMATES

Seasonal fecundity estimates were higher for the Blue-headed Vireo, Wood Thrush, and Worm-eating Warbler on the MNF as compared to the GWNF (Table 4). The Blue-headed Vireo on the GWNF recorded the lowest seasonal fecundity, with estimates significantly lower than the Wood Thrush and Worm-eating Warbler on either site. The Worm-eating Warbler on the MNF recorded the highest seasonal fecundity, and was significantly greater than the Blue-headed Vireo on the MNF and GWNF and the Red-eyed Vireo on the MNF.

Mayfield estimates of nest success for the Red-eyed Vireo on the MNF were significantly higher than the Red-eyed Vireo on the GWNF ($P < 0.05$) and the Blue-headed Vireo on the MNF ($P = 0.001$) and the GWNF ($P < 0.001$) (Table 4). Nest success rates for the Blue-headed Vireo on the GWNF were significantly lower ($P < 0.05$) when compared to all other species within either site with the exception of the Red-eyed Vireo on the GWNF and the Blue-headed Vireo on the MNF. The Blue-headed Vireo on the MNF also had a lower probability of nest success ($P < 0.06$) than all other species within that site. There were no differences in Mayfield estimates for either the Wood Thrush or the Worm-eating Warbler when comparing between the MNF and the GWNF. Mayfield estimates of nest success showed a moderately strong correlation with the seasonal fecundity estimates ($r_s = 0.75$, $P < 0.06$).

DISCUSSION

Although daily predation rates were similar for all of our study species both within a site as well as between sites, parasitism rates varied significantly. Both the Blue-headed Vireo and the Worm-eating Warbler had significantly higher rates of parasitism on the GWNF as compared to the MNF. Within a site, the vireos experienced significantly higher rates of parasitism as compared to the other species. Our low parasitism levels for the Wood Thrush on both sites were consistent with other findings in the East (Hoover and Brittingham 1993). Seasonal fecundity estimates were consistently higher on the MNF as compared to the GWNF for the three species for which it was estimated. The Blue-headed Vireo on the GWNF recorded the lowest seasonal fecundity and the Worm-eating Warbler on the MNF recorded the highest seasonal fecundity, producing an estimated 3.8 young per season. Mayfield estimates also varied significantly both between and within a site and were not always a good predictor of seasonal fecundity.

Many studies have documented high parasitism levels for the genus *Vireo* (Grzybowski et

al. 1986, Franzreb 1989, Woodworth 1997), and this was evident in our findings as well. The reasons that they are heavily parasitized are largely speculative, but may include behavioral differences or nest-site preferences (Marvil and Cruz 1989, Barber and Martin 1997). However, there are large differences in life history traits between the Red-eyed and Blue-headed Vireos that may either moderate or exacerbate the effects of parasitism. The longer incubation interval of both vireos as compared to other genera can place them, in part, at a higher risk of brood reduction due to parasitism (Robinson et al. 1995a). In particular, the 14.5-day incubation period of the Blue-headed Vireo in combination with their larger clutch size resulted in the largest window of susceptibility to parasitism of all species. Their long incubation period also allowed a cowbird to hatch much earlier than the host young and therefore almost always caused a nesting failure for the host. Although the Red-eyed Vireo appeared to be able to raise more young with a cowbird, this estimate was influenced by the two nests in which cowbird eggs disappeared, thereby eliminating the opportunity for a cowbird to hatch.

Despite many disadvantages, the Blue-headed Vireo still has more opportunities than the Red-eyed Vireo to produce a brood of entirely their own young due to their longer breeding season and ability to produce ≥ 2 broods. The Red-eyed Vireo's short breeding season only allows a limited time frame to successfully raise a single brood. Therefore, attempting to raise a cowbird young, despite their ability to produce nearly two of their own young in those nests, will almost always result in a reduced seasonal fecundity. As a result, the Blue-headed Vireo on the MNF, despite higher parasitism and predation rates, may produce about the same number of young over the course of the season as the Red-eyed Vireo on the MNF. For the Blue-headed Vireo on the GWNF, however, significantly higher rates of parasitism, despite lower predation rates than either the Red-eyed Vireo or Blue-headed Vireo on the MNF, resulted in a seasonal productivity of < 1.5 young/season. Although we were not able to calculate a daily parasitism rate for the Red-eyed Vireo on the GWNF, it is likely that their parasitism rates also are higher on the GWNF. For a single-brooded species with a very short season and small clutch size, even slight increases in parasitism would likely have a pronounced effect on seasonal fecundity.

A long breeding season and the ability to double-brood were clearly important for the Blue-headed Vireo to produce any young on the GWNF. Holmes et al. (1992) concluded that multiple brooding by the Black-throated Blue Warbler (*Dendroica caerulescens*) was a significant factor in their ability to achieve a high seasonal fecundity. Of the two factors they cited (time and food) that may limit the frequency of multiple broods, they attributed time constraints as potentially of greater importance in areas with high parasitism and predation levels. Higher parasitism levels require a bird to invest more time in a likely unsuccessful nesting attempt and thereby decrease the amount of time available to produce an additional brood. Events such as extreme weather in the spring may further reduce the available time for an individual Blue-headed Vireo to be able to produce a second (or possibly third) brood in a given year. We are unsure as to the frequency with which individual Blue-headed Vireos attempt an additional brood (the model we used incorporates this individual variability in the parameter s_s; as probabilities of re-nesting or double-brooding decrease, so will the empirical estimate of s_s). However, because any parasitized nest of the Blue-headed Vireo will likely be a host failure, a long season is very important for the Blue-headed Vireos on the GWNF.

For the Wood Thrush on our sites, predation levels will likely be more influential than parasitism rates on seasonal fecundity. The ability of the Wood Thrush to successfully raise nearly all of their own young in a parasitized nest, as well as their ability to produce ≥ 1 brood, gives them the greatest advantage in overcoming the effects of parasitism among our study species. Similarly, Trine (1998) concluded that it would require high levels of multiple parasitism and nest predation to depress populations below the source/sink threshold within their heavily parasitized study areas of the Midwest. In Delaware, Roth et al. (1996) report that despite a wide range of parasitism levels, the effect on Wood Thrush productivity was minimal and that ultimately parasitized and unparasitized females fledged the same number of young per season. Therefore, even higher rates of parasitism on our study area would likely have little effect on the

productivity of the Wood Thrush, given their current predation levels.

Due to their single-brooded status, higher parasitism rates for the Worm-eating Warbler would likely result in the same detrimental effects on seasonal fecundity as it did for the Red-eyed Vireo. Although the longer egg-laying interval of the Worm-eating Warbler may have resulted in a longer window of susceptibility to parasitism, their relatively short incubation and nestling intervals correlated more closely with that of the cowbird young (11 and 9 days, respectively), thereby decreasing the advantage for the cowbird young. The Worm-eating Warbler also has a longer breeding season than the Red-eyed Vireo (and therefore the potential for more nesting attempts), is able to produce more young per successful brood, and therefore was able to produce more young per season than the Red-eyed Vireo on both sites. However, we believe that an increase in the frequency of the already high proportion of multiple parasitism events on the GWNF may eliminate their advantage due to their inability to produce even one young in nests with ≥ 1 cowbird eggs. Lower parasitism and predation rates on the MNF versus the GWNF resulted in a Worm-eating Warbler on the MNF having the ability to produce almost one additional young per season. Information regarding their seasonal fecundity on other sites is limited to Connecticut, where Hanners and Patton (1998) reported an annual fecundity of 2.2 young (range of 1.1–3.0) where parasitism rates were similar to our study. Whether our high fecundity estimates on the MNF are unusual is difficult to determine without additional information from other study areas.

COMPARISON OF METHODS

Although some of the above patterns of predation and parasitism were apparent from our initial analysis of the nesting data using the Mayfield method and observed parasitism levels, we were unsure as to how these factors were ultimately affecting seasonal fecundity. For example, although nesting success estimates were nearly identical for the Wood Thrush on both sites and the Worm-eating Warbler on the GWNF, the Worm-eating Warbler may be producing one fewer young per season. In addition, despite significantly lower nesting success of the Blue-headed Vireo on the MNF as compared to the Red-eyed Vireo on the MNF, their seasonal fecundity estimates were nearly the same. As a result of some of these discrepancies, using the probability of nest success (the Mayfield method) as an indicator of season-long productivity may in some instances be misleading.

The occurrence of multiple parasitism events in the Worm-eating Warbler and Blue-headed Vireo also presented problems in how the outcome of those nests would be categorized under the Mayfield method. For the Worm-eating Warbler, which never abandoned a parasitized nest (either with one or two eggs), a reduced number of host young were ultimately fledged, especially in a nest with two cowbird eggs. However, many of these nests where at least one host young fledged would be considered successful under the Mayfield method (as we have defined it). For the Blue-headed Vireo, many nests that were multiply parasitized were abandoned, allowing the female to renest immediately and potentially produce a nest of all host young. However, these abandoned nests are considered failures according to the Mayfield method. Even though other information is needed to assess the ultimate stability of both populations (see below), incorporating the differences in life history traits between these and the other species allowed us to make more meaningful comparisons as to impacts of parasitism and predation on seasonal fecundity.

CONSERVATION IMPLICATIONS

We demonstrate how species-specific differences in breeding biology, which are themselves influenced by other trade-offs in life history traits, influenced seasonal fecundity within our study area. Although there are many applications for the type of data we have collected, perhaps the most useful is within a conservation framework such as a source/sink assessment (Pulliam 1988). The ability to arrive at a reasonable estimate of seasonal fecundity, along with rates of adult and juvenile mortality is essential to ultimately determine the status of areas such as ours as a source or sink (Brawn and Robinson 1996). Furthermore, because a source for one species may be a sink for another, data for multiple species are critical for effective community-based management decisions. The data we have collected provide both useful information on the basic breeding ecology of these four Neotropical migratory bird species within this region and

one important step to make more informed management and conservation decisions about them.

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