

## Long-term dynamics in local host–parasite interactions linked to regional population trends

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**Abstract.** Temporal changes in the relative abundances of host–parasite populations can influence the magnitude of the effects of corresponding interspecific interactions. When parasite populations are at relatively low abundance, the negative effects on host populations may be insignificant, but when parasite abundance increases beyond critical thresholds, they can have population limiting effects on the host. Here, we used data from a 40-yr demographic study on breeding Wood Thrushes (*Hylocichla mustelina*) and avian brood parasitic Brown-headed Cowbirds (*Molothrus ater*) in the mid-Atlantic United States to disentangle host–parasite interactions. The relative abundance for these two species has changed both locally and regionally over this time period with a reduction in host abundance coincident with an increase in the parasite population. We detected a fivefold increase in Brown-headed Cowbird parasitism rates of Wood Thrushes over the 40-yr time period leading to a reduction in Wood Thrush fitness (i.e., adult survival, fecundity, and recruitment). After accounting for the effects of Wood Thrush age, individual, and annual and within-season variation in reproduction, we found that Wood Thrushes exhibited increased reproductive effort (produced more nests per year) as nest parasitism rates increased. Additionally, we found that as parasitism rates increased, both Wood Thrush clutch size and fecundity declined. In conjunction with widespread habitat loss and land use change on both wintering and breeding ranges, increasing rates of Brown-headed Cowbird parasitism are reducing Wood Thrush fitness, and are likely contributing to observed regional Wood Thrush population declines. Coordinated local and regional efforts to reduce Brown-headed Cowbird populations, particularly in fragmented landscapes, may help reduce the decline for Wood Thrushes, and likely other parasitized Neotropical migratory species.

**Key words:** brood parasitism; Brown-headed Cowbird; host–parasite interactions; *Hylocichla mustelina*; *Molothrus ater*; population dynamics; Wood Thrush.

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### INTRODUCTION

Arguably, all population dynamics influenced by biotic effects result from a combination of direct and indirect interspecific interactions (Lotka 1922, Elton 1924, Volterra 1928, Gause 1935). In a reciprocal manner, species' population

dynamics can have important influences and exhibit density-dependent effects on the nature and patterns of interspecific interactions (Elton and Nicholson 1942, Hairston et al. 1960, Burdon et al. 2013). Evolutionary relationships among species can be driven by a complex series of adaptations, linking species, and constraining

variation in the observed coevolution of interspecific interactions (Darwin 1859, Ehrlich and Raven 1964, Lampert and Hastings 2016).

Host–parasite coevolution is a widely studied example of how complex interdependencies may arise and shape interspecific interactions (Anderson and May 1978, Price et al. 1980, Morand and Poulin 1998). However, despite the existence of coevolutionarily derived interspecific relationships (e.g., predator–prey, microbiomes, host–parasite), species population dynamics resulting from environmental and demographic stochasticity can influence patterns in interspecific relationships themselves (Crombie 1947, Elton 1949, Solomon 1949, Chapman et al. 2015). Additionally, changes in population dynamics and related interspecific interactions can have differential influences across spatial scales (Krebs 1966, Wiens 1989, Ricklefs 2015, Penczykowski et al. 2016). For example, at large spatial scales, drivers of species-level population trends can give rise to unique regional interspecific interactions, which are in part dependent on relative population densities of locally interacting species (Hanski and Henttonen 1996, Laine and Hanski 2006).

The ecology and evolution of conspecific brood parasitism in birds have been well studied (Hamilton and Orians 1965, Payne 1977, Mason 1986, Kilpatrick 2002, Soler 2014) and provide a model system for testing existing and developing new hypotheses related to host–parasite dynamics (Lyon and Eadie 2008). Previous research on a generalist avian brood parasite, the Brown-headed Cowbird (*Molothrus ater*; hereafter “cowbird”), has primarily explored the potential negative effects of brood parasitism on community and population dynamics of host species (Mayfield 1977, Brittingham and Temple 1983, Robinson et al. 1995, De Groot and Smith 2001). In extreme cases, involving the endangered Kirtland’s warbler (*Setophaga kirtlandii*) and Black-capped Vireo (*Vireo atricapilla*), brood parasitism has been shown to limit populations and cowbird removal programs have proven to be an effective management strategy to restore host populations (Siegle and Ahlers 2004, Kostecke et al. 2005). While it has become generally accepted that avian brood parasites, like the cowbird, have negative effects on host populations by lowering fecundity, reducing

nestling growth, and, in some cases, nestling survival (Robinson et al. 1995, Lichtenstein and Sealy 1998, Smith et al. 2002, Grim 2006), few studies have examined the effects of large-scale population patterns of host and parasite species on host–parasite dynamics. Hence, increasing parasitism rates on host species throughout the cowbird’s range (Hoover and Brittingham 1993, Hoover et al. 1995, Stoklosa et al. 2014) have been suggested to likely be a driver of host–parasite interactions at both local and regional scales, but it is challenging to disentangle these interactions and directly measure host fitness consequences as the density of the parasite changes.

To understand how large-scale population trends can influence local host–parasite interactions, we studied the dynamics of host–parasite interactions over a 40-yr period between the Wood Thrush (*Hylocichla mustelina*) and cowbirds. Range-wide and regional population trend estimates from Breeding Bird Survey (BBS) data (Sauer et al. 2012) indicate that over the past 40 yr, Wood Thrushes have declined and cowbirds have increased. Observed population declines of breeding Wood Thrushes in the mid-Atlantic United States have closely followed range-wide declines (Roth and Johnson 1993, Weinberg and Roth 1998) while cowbird parasitism rates of breeding Wood Thrushes are five times greater than they were in the mid-1970s (this study). Unlike some host species that have evolved defensive behaviors (e.g., egg rejection) to brood parasitism (Lyon et al. 2015, Medina and Langmore 2015), the Wood Thrush readily accepts cowbird eggs providing us with the unique ability to evaluate the effects of large-scale population trends in Wood Thrushes and cowbirds without the potentially confounding factors that arise due to defensive behavioral adaptations.

The specific objectives of our study were to test for correlations between increased cowbird parasitism rates and Wood Thrush fitness (annual population growth rate, adult survival, fecundity, recruitment, and immigration). Additionally, to understand how individual Wood Thrushes may be limited by cowbirds, while accounting for variation due to female age (and age-related differences in fecundity) and time of breeding, we tested whether annual breeding effort (nests per female), clutch size

(i.e., number of Wood Thrush eggs laid per nest), and fledglings per brood differed in relation to cowbird parasitism intensity.

## METHODS

### Study area

We conducted this study within a 16.6-ha forest fragment (hereafter “Ecology Woods”; 39°39'44.15" N, 75°44'39.60" W) on the University of Delaware campus, where the ongoing long-term demographic study of breeding Wood Thrushes occurs in Newark, Delaware, United States (Roth and Johnson 1993). Ecology Woods falls on the boundary of the Piedmont plateau and Atlantic Coastal Plain physiographic regions (Fenneman and Johnson 1946) and is characterized by low rolling hills and clay soils within the White Clay Creek watershed. Tulip Poplar (*Liriodendron tulipifera*), Red Maple (*Acer rubrum*), Sweetgum (*Liquidambar styraciflua*), Red Oak (*Quercus rubra*), White Oak (*Quercus alba*), Pignut Hickory (*Carya glabra*), and American Beech (*Fagus grandifolia*) are the dominant tree species, whereas dominant understory shrub species include Spicebush (*Lindera benzoin*), Sweet Pepperbush (*Clethra alnifolia*), Southern Arrowwood (*Viburnum dentatum*), Green Briar (*Smilax rotundifolia*), and Multiflora Rose (*Rosa multiflora*).

### Regional species population trends

We used the trend analysis form to fit hierarchical models (Link and Sauer 2002) to BBS data for the Wood Thrush and cowbird from 1973 to 2013 within the New England/mid-Atlantic Coast region to compare relative host and parasite regional population trends. We visualized and compared modeled linear trends of annual trend indices (i.e., scaled abundance estimates per BBS route) and 95% credibility intervals between both species. In a previous regional analysis of Wood Thrush parasitism rates by cowbirds, Hoover and Brittingham (1993) used BBS data to assess the relative proportion of Wood Thrush to cowbird abundances in 20 states in the mid-western and eastern United States. Over the past 20 yr, both the relative proportion of Wood Thrushes to cowbirds has decreased within the mid-Atlantic region and parasitism rates have increased lending further support to the increase in magnitude of

potentially population-limiting effects due to host–parasite interactions.

### Long-term demographic data collection

We collected long-term demographic data over a 40-yr period (1973–2013) on breeding Wood Thrushes, that included information from 2592 marked individuals and 1692 nests within Ecology Woods. We discovered and monitored active Wood Thrush nests every 2–3 d (Martin and Geupel 1993) and recorded the numbers of Wood Thrush and cowbird eggs and nestlings present during each nest check, along with nest fates and likely cause of failure when possible. We captured and marked adult Wood Thrushes using mist nets (36 mm mesh size), and 6- to 10-d-old nestlings by hand extraction from nests (Federal Bird Banding permit #: 23475) between 6 May and 15 August 1973–2013. All captured Wood Thrushes were fitted with aluminum U.S. Geological Service bands, and adults were given unique color-band combinations to enable future resighting. To test for a correlation between cowbird parasitism rate and years, we used beta regression and a subsequent likelihood ratio test in the R packages “betareg” (Cribari-Neto and Zeileis 2010) and “lmtree” (Zeileis and Hothorn 2002), respectively.

### Integrated population model

We estimated Wood Thrush annual adult survival, recruitment, fecundity, and immigration using an age-structured and female-based integrated population model (IPM; Brooks et al. 2004, Abadi et al. 2010, Schaub et al. 2012, 2013). We used observations of cowbird parasitism on Wood Thrush nests in Ecology Woods from 1974 to 2013, along with annual mean estimates from the IPM model to fit regression models linking cowbird parasitism rates (i.e., mean proportion of parasitized nests) with IPM-estimated Wood Thrush demographic parameters.

The model assumed that (1) individuals reach sexual maturity and were considered breeding adults at 1 yr old; (2) counts of individuals were from annual prebreeding censuses; and (3) time dependence of all vital rates (Kéry and Schaub 2012). Within the IPM, we used mark–recapture history data from adult ( $n = 388$ ) and juvenile ( $n = 1892$ ) Wood Thrushes, annual count data of adults within Ecology Woods, the annual number of broods sampled, and number of fledglings

per brood. We used the package “R2WinBUGS” (Sturtz et al. 2005) in R and WinBUGS (version 1.4.3; Lunn et al. 2000) to run the IPM. The IPM used joint-likelihood estimation to estimate annual adult and juvenile survival probabilities and immigration rates with a Cormack–Jolly–Seber model, population size, annual growth rates ( $\lambda$ ), and fecundity (see Appendix S1 for specification of the IPM in the BUGS language).

### Fecundity and parasitism of Wood Thrushes

To investigate whether and how Wood Thrush fitness was related to changes in cowbird parasitism over time, we used information from breeding female Wood Thrushes ( $n = 324$ ) and unique nests ( $n = 1387$ ) sampled between 1974 and 2013 in Ecology Woods. We calculated the proportion of parasitized nests by dividing the number of nests with at least one cowbird egg laid by the total number of nests per female per year. Hoover and Brittingham (1993) estimated regional parasitism rates that ranged between 11% and 48%, and within our study area, we have observed a fivefold increase in parasitism rates since that time. We used three measures of Wood Thrush fitness including breeding effort (defined as number of nests per female per season), clutch size per nest, and fecundity (i.e., fledglings per female per nest) and related these measures to cowbird parasitism rates while accounting for age and seasonal (month) variation in breeding. We used the “lmer” package (Bates et al. 2014) in R to fit linear mixed-effects models with individual and year included as random effects, and test for relationships between annual breeding effort, clutch size, and fecundity and cowbird parasitism rate (i.e., the proportion of parasitized nests per female per year), additionally including all interactions. We then performed subsequent parametric bootstrapping tests using the “pbkrtest” package (Halekoh and Højsgaard 2014) in R, or in cases where model convergence issues were encountered, standard likelihood ratio tests, to evaluate significance of relationships. We used the open-source statistical software R version 3.2.2 (R Development Core Team 2015) for all statistical tests, we present means ( $\pm$ SE), unless otherwise stated. All data were tested for departures from normality using Shapiro–Wilk tests, examination of quantile–quantile plots, and visual

evaluation of homoscedasticity (Zar 2010). We set alpha to 0.10 for all tests.

## RESULTS

### Regional trends and local effects

Wood Thrush ( $-2.93/\text{yr}$ ) and cowbird ( $0.54/\text{yr}$ ) population trends were inversely related within the New England/Mid-Atlantic region from 1974 to 2013 (Fig. 1). The proportion of cowbird-parasitized Wood Thrush nests (mean  $\pm$  SD) was five times greater in the last decade of the study from 2002 to 2012 ( $0.65 \pm 0.16$ ) than in the first decade of the study from 1974 to 1984 ( $0.13 \pm 0.14$ ) and was positively related to years ( $\chi^2 = 22.3$ ,  $df = 3$ ,  $P < 0.001$ ; Fig. 2). The increase in cowbird parasitism rates was negatively related to all aspects of Wood Thrush fitness (Table 1): population size ( $F = 23.8$ ,  $df = 1$ ,  $37$ ,  $P < 0.001$ ; Fig. 3A), annual growth rate ( $\lambda$ ) ( $F = 4.31$ ,  $df = 1$ ,  $37$ ,  $P < 0.05$ ; Fig. 3B), apparent adult survival probability ( $\chi^2 = 80.1$ ,  $df = 3$ ,  $P < 0.01$ ; Fig. 3C), recruitment ( $\chi^2 = 142.7$ ,  $df = 3$ ,  $P < 0.1$ ; Fig. 3D), fecundity ( $F = 6.56$ ,  $df = 1$ ,  $37$ ,  $P < 0.05$ ; Fig. 3E), and immigration rate ( $\chi^2 = 113.6$ ,  $df = 3$ ,  $P < 0.1$ ; Fig. 1F). Overall estimates of annual demographic parameters from

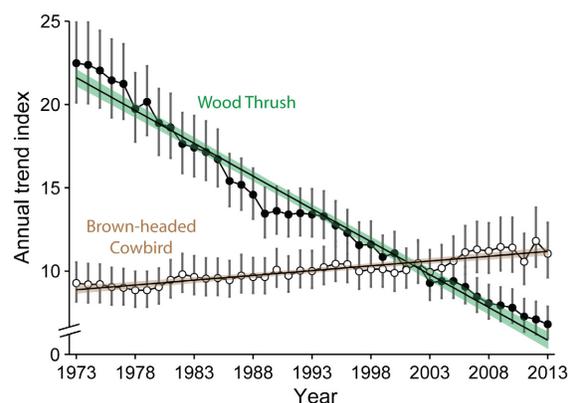


Fig. 1. Linear model fits of Breeding Bird Survey data (Sauer et al. 2012) showing inversely related trends of Wood Thrush (filled circles) and Brown-headed Cowbird (open circles) populations in the New England/Mid-Atlantic region. Gray error bars indicate 95% credible intervals, and black lines and green and light brown polygons indicate linear model fits with SEs, for Wood Thrush and Brown-headed Cowbirds, respectively.

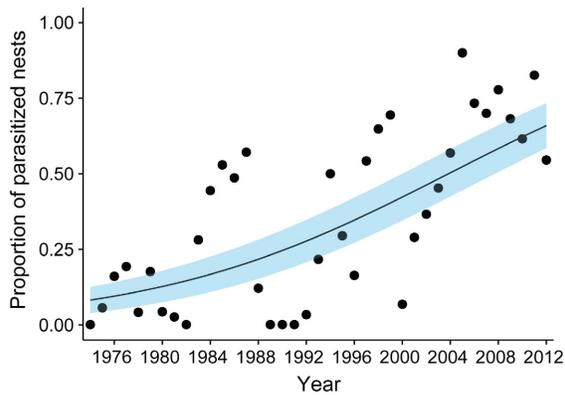


Fig. 2. Beta regression model (mean  $\pm$  95% CIs) showing the long-term increase in the proportion of Brown-headed Cowbird-parasitized nests of breeding Wood Thrushes in Ecology Woods in Newark, Delaware, United States.

the IPM for breeding female Wood Thrushes in Ecology Woods from 1974 to 2012 resulted in an average population estimate of  $18.2 \pm 1.02$  (Fig. 4A). The estimate of annual growth rate ( $\lambda$ ) was  $1.00 \pm 0.02$  (Fig. 4B). The estimated apparent survival probability was  $0.50 \pm 0.01$  for adult (Fig. 4C) and  $0.06 \pm 0.001$  for juvenile Wood Thrushes (Fig. 4D). We estimated that female Wood Thrushes produced  $1.12 \pm 0.05$  fledglings per year (Fig. 4E). Average annual immigration rates were  $0.44 \pm 0.002$  (Fig. 4F).

#### Reproduction and parasitism of Wood Thrushes

For female Wood Thrushes, mean age was  $2.26 \pm 0.04$  yr, mean clutch size was  $2.69 \pm 0.03$ , and mean fecundity was  $1.22 \pm 0.04$ . Both the number of Wood Thrush eggs laid and fledglings

per nest ranged from 0 to 5. On average, cowbirds laid  $0.37 \pm 0.02$  eggs (range 0–6) and fledged  $0.11 \pm 0.01$  offspring (range 0–2) per nest.

Cowbird parasitism was positively related to Wood Thrush breeding effort (PBtest: likelihood ratio test statistic = 6.56, nsim = 1000,  $P < 0.1$ ) and Wood thrush age groups (PBtest: likelihood ratio test statistic = 37.75, nsim = 1000,  $P < 0.001$ ; Fig. 5A). We also found a significant interaction between cowbird parasitism and Wood Thrush age groups (PBtest: likelihood ratio test statistic = 6.39, nsim = 1000,  $P < 0.05$ ; Fig. 5A).

We found clutch size was negatively related to both cowbird parasitism rates (PBtest: likelihood ratio test statistic = 14.71, nsim = 1000,  $P = 0.1$ ; Fig. 5B) and to months (LRT:  $\chi^2 = 176.7$ , df = 12,  $P < 0.001$ ; Fig. 5B). However, we found no relationship between clutch size and age group (PBtest: likelihood ratio test statistic = 18.43, nsim = 1000,  $P = 0.12$ ; Fig. 5B). Additionally, we found no interaction effects among cowbird parasitism, age group, and month (PBtest: likelihood ratio test statistic = 16.36, nsim = 1000,  $P < 0.1$ ; Fig. 5C).

Wood Thrush fecundity was negatively related to cowbird parasitism (PBtest: likelihood ratio test statistic = 14.71, nsim = 1000,  $P = 0.1$ ; Fig. 5C). We found no relationship between cowbird parasitism and age group (PBtest: likelihood ratio test statistic = 12.63, nsim = 1000,  $P = 0.39$ ; Fig. 5C) or month (PBtest: likelihood ratio test statistic = 15.30, nsim = 1000,  $P = 0.25$ ; Fig. 5C). Furthermore, we found no interactive effects among cowbird parasitism rates, age group, and month on Wood Thrush fecundity (PBtest: likelihood ratio test statistic = 10.13, nsim = 1000,  $P = 0.60$ ; Fig. 5C).

Table 1. Corresponding linear equations, correlation coefficients ( $R^2$ ), test statistics, degrees of freedom (df), and  $P$ -values shown for linear mixed-effects and beta regression ( $\dagger$ ) models showing relationships between Brown-headed Cowbird (BHCO) parasitism rate and Wood Thrush IPM-derived population parameter estimates.

| Model                                      | Equation                           | $R^2$ | Test statistic | df    | $P$        |
|--|------------------------------------|-------|----------------|-------|------------|
| Pop. estimate ~ BHCO parasitism            | $y = -14.2x + 23.2$                | 0.38  | $F = 23.8$     | 1, 37 | $< 0.0001$ |
| Lambda ~ BHCO parasitism                   | $y = -0.14x + 1.05$                | 0.08  | $F = 4.31$     | 1, 37 | $< 0.05$   |
| Adult survival ~ BHCO parasitism $\dagger$ | $\text{logit}(y) = -0.24x + 0.06$  | 0.22  | $z = -3.3$     | 3     | $< 0.001$  |
| Recruitment ~ BHCO parasitism $\dagger$    | $\text{logit}(y) = -0.11x - 2.70$  | 0.07  | $z = -1.71$    | 3     | $< 0.10$   |
| Fecundity ~ BHCO parasitism                | $y = -0.41x + 1.26$                | 0.13  | $F = 6.56$     | 1, 37 | $< 0.05$   |
| Immigration ~ BHCO parasitism $\dagger$    | $\text{logit}(y) = -0.05x - 0.242$ | 0.07  | $z = -1.74$    | 3     | $< 0.10$   |

$\dagger$  Beta regression linear models.

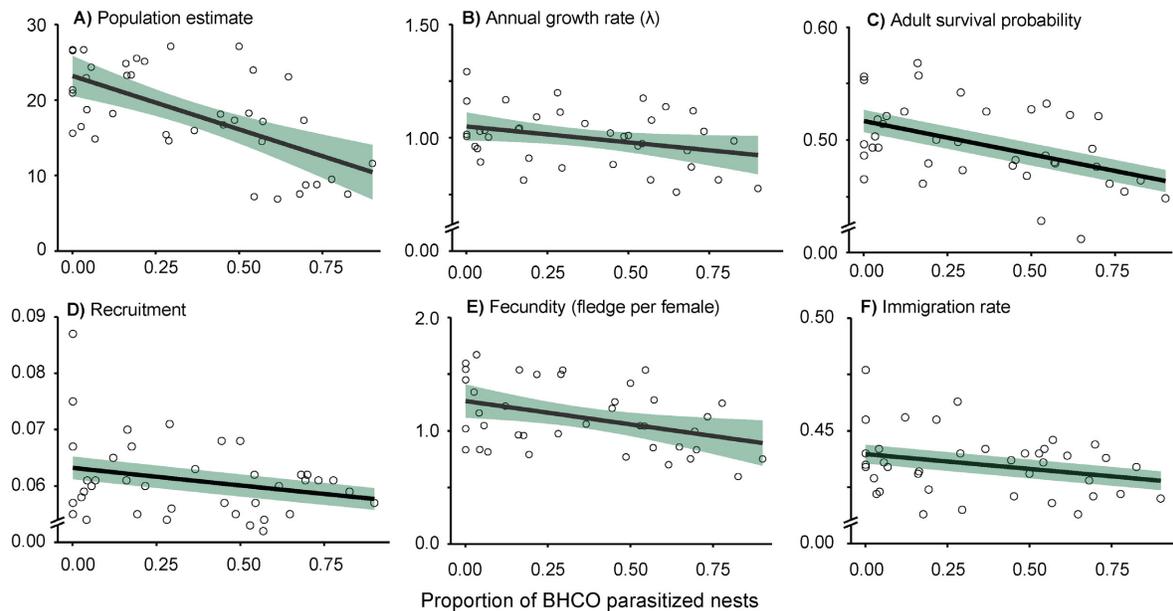


Fig. 3. Linear models showing relationships between the proportion of Brown-headed Cowbird-parasitized nests ( $x$ -axis) and (A) population estimate, (B) annual growth rate ( $\lambda$ ), (C) adult survival probability, (D) recruitment, (E) fecundity (fledglings per female), and (F) immigration rate. Plots showing model-predicted means (black line) and SEs (green polygon) are significantly correlated ( $\alpha = 0.10$ ).

## DISCUSSION

We documented how effects of increased rates of cowbird parasitism over 40 yr are negatively related to a suite of demographic parameters of a breeding population of Wood Thrushes within a small forest fragment set within an urban landscape. In light of increasing rates of cowbird parasitism, likely resulting from inversely related host (Wood Thrush) and parasite (cowbird) population trends in the mid-Atlantic region of the United States, we show how within our study area, Wood Thrushes incurred greater reproductive costs related to breeding effort (i.e., produced more nests per season), had reduced clutch sizes, and had fewer fledglings per brood. In addition to these net reproductive costs to Wood Thrushes, we found negative correlations between cowbird parasitism rates and all aspects of Wood Thrush demographics (population size, annual growth rate [ $\lambda$ ], fecundity, adult survival, recruitment, and immigration rate), indicating that when cowbird parasitism increases, they can have negative effects on both reproductive and demographic parameters that are biologically meaningful.

Beyond finding significant relationships between main effects of cowbird parasitism on Wood thrush breeding effort, clutch size, and fecundity, we uncovered novel interaction effects between parasitism rate and age group on the number of nests produced per season. Female Wood Thrushes reach peak productivity at 3–4 yr (Brown and Roth 2002), and it was during these peak productive years that we found the greatest reproductive costs related to cowbird parasitism incurred by individual females. When comparing average reproductive costs among age groups in relation to increasing parasitism rates, we observed that 3- to 4-yr-old Wood Thrushes had a greater reduction in fecundity while simultaneously incurring greater increases in breeding effort compared to other age groups. These findings suggest that there is a critical life-history relationship driving observed net reproductive costs associated with brood parasitism. Reduced host fecundity has been well demonstrated (Brittingham and Temple 1983, Pease and Grzybowski 1995, Louder and Schelsky 2014). Intuitively, reductions in host nestlings per brood can result from host egg or nestling destruction by female cowbirds (Scott et al. 1992, Sealy

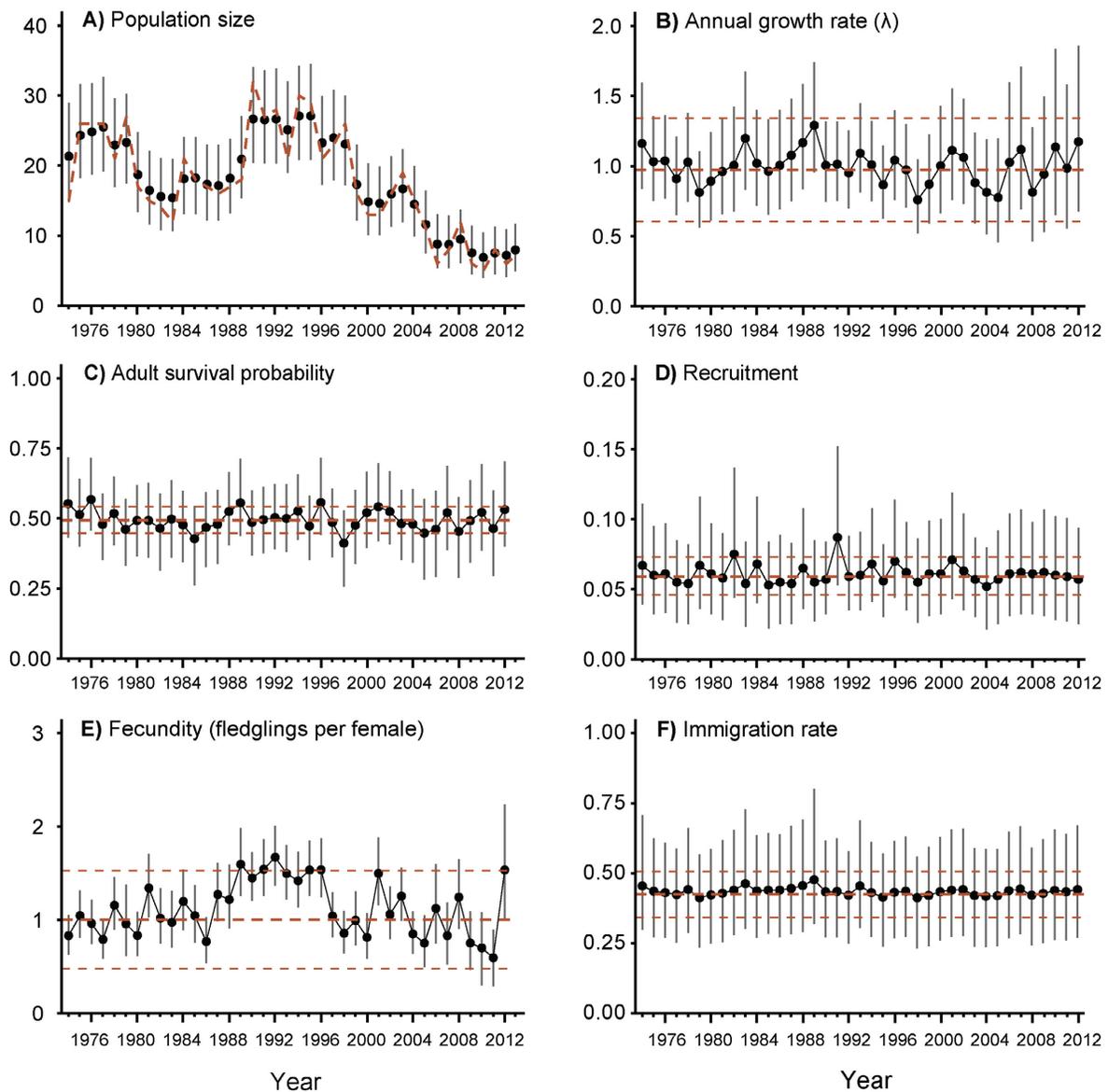


Fig. 4. Estimates of population demographic parameters for Wood Thrushes from 1974 to 2012 showing (A) population size and raw counts (orange dashed line), (B) annual growth rate ( $\lambda$ ), (C) adult survival probability, (D) recruitment, (E) fecundity (fledglings per female), and (F) immigration rate. Within all plots, annual means (black circles) and 95% credible intervals (CI; gray bars) are shown, and for (B–F), orange dashed lines indicate overall means and 95% CIs.

1994, Granfors et al. 2001), as was occasionally observed in our study.

Mechanisms resulting in negative correlations of brood parasitism with adult survival probability may be related to elevated energetic costs incurred from both increased nest and brood production (this study) and increased provisioning

flights by host parents (Hauber 2003). These effects may be magnified as the number of parasite offspring increases per brood. More research is needed to understand how variation in clutch size, identity of parasitic nestling parents, and how intraparasite competition may influence host population ecology and demographic patterns. The

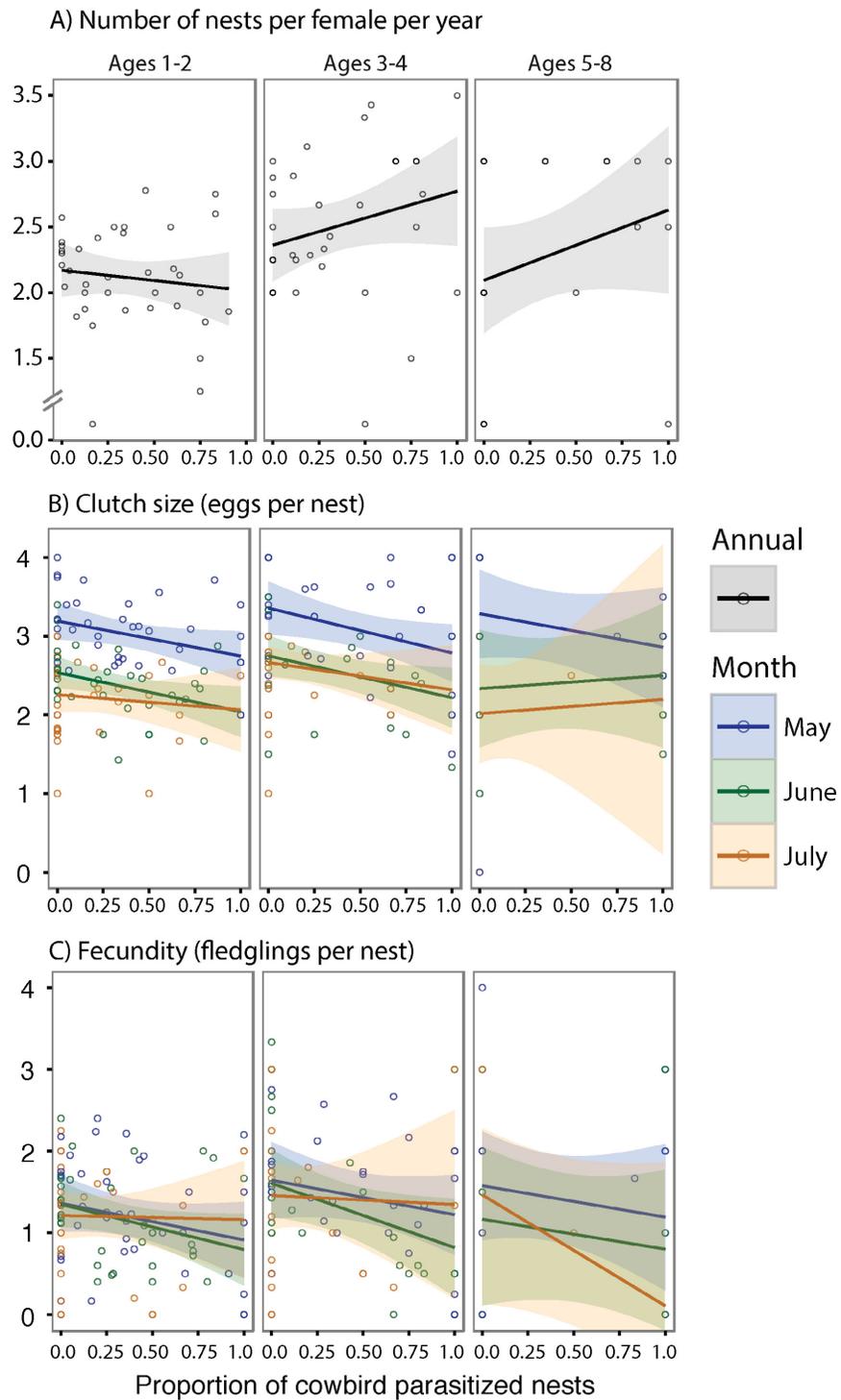


Fig. 5. Linear mixed-effects model results showing effects of Brown-headed Cowbird (BHCO) parasitism rates among female age groups on (A) number of nests per female per year (black lines). Effects of BHCO parasitism on (B) mean clutch size (eggs per nest) and (C) mean fecundity (fledglings per nest) are additionally shown among age groups and months (colored lines). Model-predicted means and 95% CIs are shown.

negative relationship we found between brood parasitism rate and host recruitment could be explained by competition between host and parasite nestlings for high-quality food and nutrients. For instance, Ladin et al. (2015) determined that Wood Thrush nestling diet and nutrition is related to cowbird parasitism, which may potentially lead to negative effects for nestling development and subsequently juvenile survival and recruitment. Indeed, patterns in negative correlations that we found are likely also due to larger-scale processes related to annual survivorship such as loss of wintering, breeding, and migratory stopover habitat.

In contrast to previous research that has sought to understand how cowbird parasitism may be causing population declines in host species (Brittingham and Temple 1983, Trail and Baptista 1993, Robinson et al. 1995), our intention in this study was to highlight how regional population trends can indirectly lead to increases in cowbird parasitism rates at local scales where coincident host and parasite population trends are inversely related. We think this represents a valuable shift in thinking about the nature of how brood parasitism affects host populations. Unlike more extreme cases where cowbird parasitism can limit endangered host species with small populations (e.g., Kirtland's Warbler), it may not be reasonable to assume broad theoretical avian brood parasite models when considering more widely distributed species that typically show geographic variation in both abundance and parasitism rates throughout the breeding range (Hoover and Brittingham 1993, Etterson et al. 2014). Our findings demonstrate how coincident host and brood parasite population dynamics across scales can lead to locally explicit negative effects on host populations. Future studies should consider host-choice decisions of brood parasites and design manipulations to test for age effects (in both host and parasitic species), to better understand ecological aspects of avian host-parasite interactions. For example, Louder (2015) found that host-choice decisions made by cowbirds parasitizing Prothonotary Warblers (*Protonotaria citrea*) were related to within- and between-season cowbird reproductive success, and interestingly, not to host nest success.

There are clear beneficial implications for disentangling how both (large-scale and region-specific) relative host-parasite population trends and direct (individual-based fecundity, survival,

etc.) effects of avian brood parasitism can influence the population dynamics and the evolution of brood parasitism and defensive host adaptations. By accounting for effects of population dynamics on parasitism rates, in tandem with continued research on the direct effects of brood parasitism on host species ecology and evolution (e.g., Kilner et al. 2004, Ruiz-Rodriguez et al. 2009, Pappas et al. 2010), we can gain important insight into broader spatial, ecological, and evolutionary patterns that might, in turn, enhance conservation strategies, where applicable (Smith 2006).

Recent research on full-annual-cycle population models (Hostetler et al. 2015) and carry-over effects between wintering and breeding periods on reproduction (Norris and Marra 2007, Harrison and Blount 2011) has suggested that large-scale population dynamics are likely related to limiting factors throughout the annual cycle. Increasingly, research on migratory movements of individuals using archival light-level geolocators (Stutchbury et al. 2009, McKinnon et al. 2013) and miniaturized global positioning system technologies (Hallworth and Marra 2015) is elucidating breeding, wintering, and migratory habitat use of birds (Stanley et al. 2015). These studies, while in their infancy, will likely be integral in determining season-specific limiting factors for migratory species. Taylor and Stutchbury (2015) developed a network model suggesting how habitat loss in core wintering areas may be related to observed large-scale population declines. However, it remains unclear how interactions between habitat quality on winter grounds and associated carryover effects (McKinnon et al. 2015) coupled with limiting factors on the breeding grounds, including negative effects of cowbird parasitism we have demonstrated, may ultimately limit populations. In addition to improved knowledge on migratory connectivity, full-annual-cycle population models require accurate demographic data, which are largely absent for many species, and have proven challenging to collect over long time periods and across large spatial scales. The long-term demographic data and population parameter estimates we present here represent the longest ongoing demographic study of Wood Thrushes. Given the location of our study area, the concomitant degree of forest habitat loss, increased urbanization, and increasing cowbird parasitism

rates within the mid-Atlantic United States, these data are uniquely suited for incorporation in the parameterization of full-annual-cycle population models (Hostetler et al. 2015) and metapopulation models (Moilanen and Hanski 1998, Cavanaugh et al. 2014) that could be used to evaluate drivers of suggested regional source–sink dynamics for the Wood Thrush (Tittler et al. 2006).

Our findings show that local long-term host–parasite interactions are driven by regional-scale population trends that may have population-limiting effects on the host. As we move toward an improved understanding of interspecific relationships that incorporate interseasonal carryover effects (Harrison and Blount 2011) through the application of full-annual-cycle population models (Hostetler et al. 2015), long-term data informing both patterns in demographic parameters and interspecific (e.g., host–parasite) interactions among species will be an important step forward.

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