REPRODUCTIVE SUCCESS OF A GENERALIST BROOD PARASITE PREDICTS THE RATE OF PARASITISM IN THE SUBSEQUENT YEAR

BY

AMBER N. ALBORES

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2013

Urbana, Illinois

Advisers:

Adjunct Assistant Professor Jeffrey Hoover
Adjunct Assistant Professor Wendy Schelsky

ABSTRACT

Brown-headed cowbirds (*Molothrus ater*) rely solely on hosts to raise their young. Although cowbirds parasitize 200+ species, recent evidence suggests that females avoid unsuitable hosts that either reject parasitic eggs or provide incompatible parental care. Female cowbirds may be able to improve their own reproductive success with information pertaining to the fledging success of cowbird or host offspring. This, in turn, could influence the laying decisions and host choices of cowbirds in subsequent years. To determine whether host reproductive success and/or cowbird reproductive success in the previous year affect the likelihood of cowbird parasitism, we examined nesting data for a highly suitable host, the prothonotary warbler (*Protonotaria citrea*). We recorded parasitism status (yes or no), number of cowbird eggs, and the number of host and cowbird fledglings for 3848 warbler nests from 1994-2010 in southern Illinois. Data were analyzed using a generalized linear mixed model (GLMM) with binomial distribution. We accounted for variation in site, nest box, identity of female warbler, and year in our analysis as random effects and included month and the parasitism rate in the previous year as covariates. From one year to the next, the probability of parasitism for a given site increased with cowbird reproductive success and tended to decrease with prothonotary warbler reproductive success even after controlling for the ambient rate of parasitism in the previous breeding season. This is the first study to suggest that the fledging success of cowbirds increases future host use by female cowbirds.

ACKNOWLEDGEMENTS

We thank numerous field assistants who collected data over many years. We also thank Patrick Weatherhead, Jeffrey Brawn, Matthew McKim-Louder, and the University of Illinois Bird Lab for their constructive comments and discussions. Funding for this research was provided by the United States Fish and Wildlife Service, the Illinois Department of Natural Resources, and The Nature Conservancy in Illinois. Finally, we are grateful for logistical support from the Illinois Natural History Survey of the Prairie Research Institute, Cypress Creek National Wildlife Refuge, and the Cache River State Natural Area.

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INTRODUCTION

Obligate avian brood parasites evade nest building, egg incubation, and offspring provisioning by laying eggs in the nests of other species. This behavior is costly for the host species whose reproductive output is diminished (Rothstein 1990; Robinson et al. 1995; Ortega 1998; Lorenzana and Sealy 1999; Hoover 2003c). Interestingly, the reproductive success of brood parasites varies greatly and depends on the host species parasitized (Brooke and Davies 1987; Soler et al. 1995; Scott and Lemon 1996; Rutila et al. 2002; Mermoz and Reboreda 2003; Grim et al. 2011; Trnka et al. 2012). While the parental investment of brood parasites is assumed to cease once the egg is laid, evidence of parasitic females monitoring the fate of their reproductive effort is accumulating (Soler et al. 1995; Arcese et al. 1996; Hoover and Robinson 2007). Females may therefore collect information that influences their future parasitism decisions.

The ability of brood parasites to track their own reproductive output could increase individual fitness if they learn to specialize on high quality hosts. The screaming cowbird (*Molothrus rufoaxillarius*), a host specialist, is thought to preferentially parasitize the bay-winged cowbird (*Agelaioides badius*) because this host provides higher reproductive success than alternative hosts within the community (De Marsico and Reboreda 2008). The brown-headed cowbird (*M. ater*) is an extreme host generalist that parasitizes a suite of hosts within diverse avian communities in many habitats throughout North America (Lowther 1993; Robinson et al. 1993; Davies 2010). These potential hosts differ considerably in their response to cowbird eggs and in their ability to raise cowbird offspring (Mason 1986; Wiley 1988), setting the stage for selection favoring individual female brown-headed cowbirds that use hosts of higher quality in the community.

The quality of potential hosts of brown-headed cowbirds (cowbirds hereafter) largely depends on the likelihood that a particular host species can recognize and reject parasitic eggs, or is in some way incompatible with raising a parasitic egg/chick. Rejecters may thwart raising parasitic young by means of egg ejection, nest desertion, or egg burial (Rothstein 1975). Also, the incubation period, nestling diet, and nestling size of many host species is incompatible with that needed to successfully rear cowbird offspring (Middleton 1977). Evidence of cowbirds avoiding incompatible hosts through non-random host use has been documented in several populations (Alderson et al. 1999; Hahn et al. 1999; Woolfenden et al. 2004; Strausberger and Ashley 2005). During the breeding season and across years, cowbirds preferentially laid eggs in the nests of dickcissels (*Spiza americana*), a species that successfully fledges cowbird young, over other available hosts at Konza Prairie Biological Station (Rivers et al. 2010). Cowbirds have also been shown to select higher quality individuals within a single host population in order to maximize their reproductive output (Grant and Sealy 2002). While cowbirds may be very general in their use of hosts over their geographic distribution, some cowbird populations and/or individual females could focus on relatively few host species depending on which hosts are best at raising parasitic young.

Microsatellite DNA markers have confirmed the presence of host specialization among some individual females within cowbird populations (Alderson et al. 1999; Woolfenden et al. 2003; Strausberger and Ashley 2005). Radio telemetry and genetic studies also indicate high breeding site and home range (primary egg-laying area) fidelity between years (Dufty 1982; Hahn et al. 1999). Cowbird females also monitor host nest contents both before and after parasitism to time the laying of eggs and ensure their acceptance by the host (Hoover and Robinson 2007). Evidence of host preference, in combination with host nest monitoring and site fidelity within cowbird populations, suggests cowbirds could use their own reproductive experience or that of their hosts to improve future breeding decisions.

In this study, we used a long-term nesting dataset from a highly suitable host to investigate factors influencing cowbird parasitism at the population level across years. As a high quality host, the prothonotary warbler (*Protonotaria citrea*; warbler hereafter) accepts cowbird eggs and has an incubation period ideal for cowbird eggs (approximately 12 days) (Petit 1999). Cowbird young are competitive for provisioned food because they are larger than warbler young throughout the nestling and fledgling stage. Warbler young are fed an insectivorous diet by both parents (Hoover and Reetz 2006), which is compatible with the diet required to raise cowbird young. Nest predation is the main factor limiting the warblers' reproductive output (Hoover 2003a) and reduces the success of warbler and cowbird eggs/chicks similarly (Hoover 2003c). Extensive predator proofing of warbler nest boxes on some sites in some years has created considerable variation in rates of nest predation for warblers over time (Hoover 2003a). However, annual and spatial variation in food availability and nest ectoparasites (i.e. blowflies, genus *Protocalliphora*) within warbler nests has sometimes uncoupled the probability of host and cowbird young surviving until fledging (W. Schelsky, personal communication). Cowbird reproductive output has also varied with the intentional removal of parasitic eggs from some warbler nest boxes in some years as the result of concurrent studies within the study system. With this unique dataset, we test whether the reproductive output of warblers and/or cowbirds on a site during a breeding season subsequently influences the probability of cowbird parasitism in the following year.

To determine whether host or parasite reproductive output in one year subsequently influences the rate of cowbird parasitism in the following year we controlled for year, month, site, nest box, and warbler female identity in the season of the parasitism event, and the rate of parasitism on a site in the previous year. Because cowbirds may be responding to current and/or past conditions when selecting hosts to parasitize, warbler density on a site in the current year and the average warbler and cowbird reproductive output from a given site in the previous year were used as predictors of the probability of parasitism. We included warbler density because in some studies host density influenced rates of brood parasitism (Barber and Martin 1997; Woolfenden et al. 2004; Stokke et al. 2007). Because fledging of cowbirds is a better indicator of host quality than fledging of host offspring, we hypothesized that female cowbirds are monitoring and responding to cowbird fledging success rather than the fledging success of the host to improve parasitism decisions in future breeding seasons. Therefore, we predicted that as more cowbird young fledge per warbler nest on a site, the following year's rate of cowbird parasitism for warblers on that site should increase, whereas the number of warbler fledglings per nesting attempt on a site should have relatively little influence on the rate of future cowbird parasitism.

METHODS

Study site and species

The study was conducted over a 17-year period (1994 to 2010) in the Cache River Watershed in southern Illinois, United States. The Cache River meanders 176 km to the Ohio River through 91% of the state's forested wetland and swamp habitat. Study sites were located in agriculturally fragmented patches of forested sloughs and floodplains with bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps, within a 192-km^2 portion of the watershed.

Agricultural development and timber harvesting in the Cache during the 1900s provided ideal foraging locations for brown-headed cowbird populations expanding east into the Midwest (Robinson et al. 1999). During the breeding season, female cowbirds travel daily from feeding areas in mowed grasses, pastures, and row-crop agriculture to breeding sites in bottomland forests where they parasitize the nests of a variety of host species. One such host, the prothonotary warbler, is a Neotropical migratory songbird that is territorial and socially monogamous (Petit 1999). These warblers nest in secondary cavities within forested wetlands and swamps and their use of nest boxes provides easy access to nests for monitoring cowbird parasitism status and nesting success. Despite a high rate of cowbird parasitism, the warblers are typically double-brooded and often capable of raising both cowbird and host nestlings in each nesting attempt (Hoover 2003c; Hoover and Robinson 2007). The warblers are a relatively high quality host compared to the other 12 host species that are commonly parasitized by cowbirds within the study area (J. Hoover, personal communication) and can raise up to three cowbird young in one nesting attempt (Hoover 2003b).

Data collection

Each year we set up and monitored approximately 1000 warbler nest boxes across 21 sites (individual patches of suitable breeding habitat for warblers separated by more than 1 km of non-suitable habitat). Nest boxes were made from modified 1.9 L beverage cartons (Fleming and Petit 1986) and placed on trees about 1.7 m above the ground in suitable habitat. Nest boxes were spaced an average of 50 m apart, and openings in boxes were made to be the average diameter (44 mm) of warbler nests in natural cavities allowing cowbird access to each nest. Study sites where the opening size of nest boxes was reduced to exclude parasitism by cowbirds were not included in our analyses. From 1999 to 2010, we removed an estimated 20-100% of cowbird eggs from approximately two thirds of study sites each year. We monitored boxes every 3-5 days from late April to early August 1994-2010. The status of each nesting attempt was recorded, including the number of warbler and cowbird eggs, nestlings, and fledglings as well as the number of cowbird eggs that were removed. We considered nestlings to have fledged if they reached 10-11 days of age and the nest was empty and intact on the subsequent visit. Additional evidence of fledging included the presence of trampled droppings in the nest, alarm calls from adults, and observations of appropriately-aged fledglings in the territory. The fate of each nesting attempt was known and recorded throughout each breeding season.

Statistical analyses

The probability of cowbird parasitism, a binary response variable, was analyzed using a generalized linear mixed model (GLMM) with Laplace approximation of the log likelihood (Bolker et al. 2009) and an identity link function (GLIMMIX; SAS 9.2). To account for variation associated with year, site, nest box identity, and female warbler identity, we included each as a random variable. For female warbler identity, we included a subset of nests where the female warbler identity was unknown (21% of all nesting attempts). These nests were always those that failed or were abandoned early in the nesting cycle and eliminating these from our dataset would have significantly reduced the variation in both the cowbird and host reproductive success variables. We also included month (April-July) as a categorical variable to account for the seasonal decline in cowbird parasitism known to occur in our study system (Hoover et al. 2006). In order to control for landscape-level effects of cowbird parasitism in our analyses, such that high parasitism in one year leads to high or higher parasitism in the next because of the configuration of forest habitat and cowbird foraging areas (Goguen and Matthews 2000; Hoover and Hauber 2007), we included the ambient parasitism rate from each site from the previous year (number of warbler nests parasitized/number of warbler nesting attempts per site). We included warbler density (number of females/hectare/site) to investigate if a current condition such as the density of a quality host predicts the probability of cowbird parasitism in the same year. Cowbird egg removal in the previous year (cowbird eggs removed/cowbird eggs laid/site) was included in our analyses because the removal of a portion of the parasitic eggs on certain sites in some years may influence future parasitism rates by altering the reproductive output of both cowbirds and warblers. Finally, to test whether host or cowbird reproductive success best predicted cowbird parasitism in the subsequent year, we included warbler reproductive success for the previous year (number of warblers fledged/number of warbler nesting attempts/site), and cowbird reproductive success for the previous year (number of cowbirds fledged/number of warbler nesting attempts/site).

We used Akaike's information criterion, corrected for small sample size (AIC_C), to identify the model that best explained cowbird parasitism rates for the prothonotary warbler (Burnham and Anderson 2002). We assembled a set of *a priori* candidate models based on our hypotheses and analyzed them using SAS 9.2 (SAS Institute, Inc., Cary, NC, USA). Each model included month to control for the seasonal decline in parasitism and ambient rate of parasitism in the previous year to control for landscape-level effects on parasitism. We did not include correlated explanatory variables ($r > 0.50$) in the same model to reduce any effects of collinearity among variables. The only variables to violate this assumption were cowbird egg removal and cowbird reproductive success both from the previous year ($r = 0.51$). In this case we moved forward with cowbird reproductive success from the previous year in our *a priori* models because this variable encapsulated the variation associated with cowbird egg removal and all other ecological factors that contribute to cowbird reproductive success. In addition, we removed cowbird eggs only during a subset of all of the years included in our analyses. The models were ranked in order of their AIC_C values, with the highest explanatory value given to models with the lowest AIC_C values and highest Akaike weight (w_i). To determine whether cowbird egg removal or cowbird reproductive success from the previous year better explained parasitism rates we compared the top ranked model that contained cowbird reproductive success to the same model replacing cowbird success with cowbird egg removal. Parameter estimates, standard errors, and 95% CI are based on model averages. All descriptive variables are presented as means ± SD unless otherwise indicated.

We also investigated whether there was any indication that female cowbirds focused their current parasitism on particular female warblers or nest boxes for those nest boxes that successfully fledged a cowbird in the previous year. To determine this we used a reduced dataset to compare parasitism status (yes, no) among three categories of nests for first nesting attempts within a given year. These categories of nests were: 1) same female warbler in same nest box as the previous year, 2) same female using a different nest box than the previous year but still in the study site, and 3) new female in a nest box that had fledged a cowbird in the previous year. If female cowbirds focused on particular female warblers that had successfully raised a cowbird in the previous year, then categories 1 and 2 should have higher rates of parasitism than category 3. If instead female cowbirds focused on particular nest boxes that had fledged a cowbird in the previous year, then categories 2 and 3 should have higher rates of parasitism than category 1. We used a chi-square test to compare the frequency of parasitism among the three categories of nests.

RESULTS

Of the 3848 warbler nests included in our analyses, 2240 (58%) were parasitized by brown-headed cowbirds. Parasitized warbler nests received an average of 1.73 ± 0.52 cowbird eggs, with 0.24 ± 0.25 cowbird young fledging from parasitized nests. Overall, 39% of warbler nesting attempts successfully fledged cowbird and/or host young between 1994 and 2010. Female cowbirds laid 3885 eggs in warbler nests, of which 18% survived to fledge.

The top ranked model predicting the probability of parasitism for prothonotary warblers included month (M), parasitism rate in the previous year (PPR), warbler reproductive success in the previous year (PWS), and cowbird reproductive success in the previous year (PCS)(Model 1; Table 1). The sum of weights (*w*i) for all models that included cowbird reproductive success in the previous year was 0.80 indicating that this variable was one of the most important ones tested (Table 2). Month was included in all the models and the probability of parasitism decreased seasonally from 92% in April to 11% in July (Figure 1). The rate of parasitism in the previous year was also included in all the models and as expected was positively correlated with parasitism in the current year (Figure 2). Cowbird parasitism of warblers increased with an increase in cowbird fledging success in the previous year, and ranged from 51% when there was little or no cowbird fledging success the previous year to 70% when cowbird fledging success the previous year was high (nearly one cowbird fledged per nesting attempt; Figure 3).

Warbler reproductive output (PWS) was included in two of the top three models and therefore, may be an important predictor of parasitism rate (*w*i = 0.68). In contrast to cowbird reproductive success, warbler reproductive success was negatively related to the probability of parasitism and the model averaged 95% CI of the β estimate overlapped zero. This suggests that PWS may have little overall influence on parasitism rates. Although warbler density (*w*i = 0.30) was included in the second top model (Model 2; Table 1), the ΔAICc = 1.67 and model averaged 95% CI of the β estimates bounded zero, indicating that warbler density added little to explain variation in the data given the other variables tested. Because cowbird egg removal was correlated with cowbird reproductive success (r = 0.51), we substituted cowbird egg removal into the top-ranked model. This model was not well supported and the removal of cowbird eggs did a poorer job than cowbird reproductive success to explain variation in the probability of parasitism as it was ranked lower than the top model (ΔAICc = 0.22) and the 95% CI of the β estimates bounded zero (UCL = 0.140, LCL = -0.818). The analysis of female warblers and nest boxes that fledged a cowbird in the previous year and their parasitism status in the subsequent year indicated no significant difference in parasitism status among the three categories of nesting attempts (X^2 = 0.715, n= 915, d.f. = 2, p = 0.699; Category 1 = 61%, Category 2 = 57%, Category 3 rate = 59%).

DISCUSSION

The probability of parasitism for prothonotary warblers increased with cowbird reproductive success in the previous year, even after controlling for other factors (previous parasitism rate and month) known to be important in our study system. This result suggests that host use by cowbird females is not merely a function of forest fragmentation and landscape use by cowbirds, but rather that female cowbirds may attempt to maximize reproductive success through active host choice. However, it is unclear if the observed correlation between cowbird reproductive success in one year and parasitism rate in the next is the result of adult cowbird females using breeding information from one year to make future breeding decisions or, alternatively, the local recruitment of cowbird offspring.

Female cowbirds may draw upon their own breeding experience or that of other cowbird females to make future host-use decisions because the fitness of brood parasites depends on the ability of the host to rear parasitic young. By using their own reproductive success (i.e. private information), the success of conspecifics (i.e. public information), or both, females could potentially increase their reproductive output across years by targeting productive sites and hosts. The use of private and public information in future breeding decisions has been widely investigated in non-parasitic passerines (Doligez et al. 2002; Hoover 2003a; Danchin et al. 2004), but data are limited for brood parasitic species. The use of private information could lead to greater host specificity within individual females as they hone their ability to choose host species that are better able to fledge parasitic young during several consecutive breeding seasons. Furthermore, females could collect public information regarding the breeding habitat, nest type, or other natural history characteristics of hosts that successfully rear cowbird offspring (Mahler et al. 2007). This may lead to the immigration of adult female cowbirds into habitat patches where warblers are breeding, thereby increasing the number of cowbirds and, consequently, the probability of parasitism for warblers.

Parasitism of warblers may increase with cowbird fledging success in the previous year because juvenile cowbirds may be site or host faithful and return to their natal location and/or host species to breed in subsequent years. Therefore, local recruitment of cowbird offspring alone could account for the rise in parasitism with increasing cowbird reproductive success. Juveniles may preferentially parasitize the species that raised them by imprinting on the host species itself (Brooke and Davies 1987; Payne and Payne 1998; Payne et al. 2000), on the nest characteristics of that species (Kattan 1997; Mahler et al. 2007), or on the habitat it was raised in (Teuschl et al. 1998). A cavity nesting passerine, the prothonotary warbler could offer cowbirds a unique nestling experience and search image compared to other available species in the host community. However, while adult brood parasites display both seasonal (Soler et al. 1995; Hoover and Robinson 2007; Langmore et al. 2007) and between-year (Dufty 1982; Raim 2000) breeding site fidelity, natal philopatry for cowbirds is considered rare (Alderson et al. 1999; Hauber et al. 2012). Therefore, the observed increase in the probability of parasitism with cowbird reproductive success is not likely explained by the local recruitment of cowbird offspring alone. In fact, only 1 (<<1%) of the approximately 610 cowbird nestlings that were banded and fledged from prothonotary warbler nest boxes in our study system has been captured in a later breeding season (M. McKim-Louder, personal communication), suggesting that local recruitment for cowbird juveniles in our system is rare and not the cause of our observed increase in the rate of cowbird parasitism.

One might expect cowbirds generally to parasitize hosts that experience low rates of nest predation and high fledging success of host young, particularly if cowbirds are able to assess that the presence of many host fledglings on a site is a function of low rates of nest predation. Low rates of nest predation associated with these hosts could lead to reduced cowbird nestling mortality and aid in bolstering existing cowbird populations. Conversely, our results indicate that warbler reproductive output is not a good predictor of cowbird parasitism in the subsequent breeding season. This suggests that, in our system, the fledging of host young is not the best information used in host selection by female cowbirds; however, it may be useful for cowbirds in some habitats with exceedingly high rates of nest predation for most host species (Winfree et al. 2006).

Warbler density in the current year was examined as a potential predictor of cowbird parasitism to investigate if female cowbirds parasitize warblers based on their availability (Woolfenden et al. 2004), instead of their ability to fledge cowbird young. While warbler density was not a good predictor of parasitism and had little influence in our study system, evidence exists for common cuckoos (*Cuculus canorus)* (Stokke et al. 2007) and Horsfield's bronze cuckoos (*Chrysococcyx basalis)* (Brooker and Brooker 2003), both host specialists. In both cases, cuckoos avoid specific host populations with host densities below a certain threshold. Alternatively, for generalist parasites, landscape features can override the effects of host density. In plumbeous vireos (*Vireo plumbeus*), for example, brown-headed cowbird parasitism was related to proximity to parasite feeding areas but not to host density (Goguen and Mathews 2000). Woolfenden et al. (2004) reported that host density was a predictor of parasitism by cowbirds for yellow warblers (*Dendroica petechia*) and red-winged blackbirds (*Agelaius phoenecius*), but was not a factor for the most frequently parasitized and highest value host, the song sparrow (*Melospiza melodia*). The influence of host density on patterns of parasitism may vary depending on the host specificity of the brood parasite and/or the quality of the host species parasitized. The rate of cowbird parasitism for prothonotary warblers could fluctuate in response to changes in the availability of alternative hosts, but we did not measure changes in the densities or rates of cowbird parasitism of other hosts during the course of this study. Nevertheless, it is difficult to imagine how the availability of alternative hosts in the current year could fluctuate in parallel with cowbird reproductive success in a way that would undermine the effect of PCS on cowbird parasitism of the warblers.

Our results suggest that the rate of parasitism for a high quality host was best predicted by brown-headed cowbird reproductive success in the previous year. This implies cowbird females are likely monitoring cowbird reproductive output to make future breeding decisions. One or a combination of factors may result in the increased rate of parasitism for warblers observed during this study, and it remains to be determined whether this pattern is being driven more by greater host specificity among local cowbird females returning to the same breeding areas across years, the immigration of adult female cowbirds into warbler breeding areas, or local recruitment of cowbird offspring produced by the warblers. Female cowbirds do not preferentially parasitize particular female warblers or nest boxes that fledged a cowbird in the previous year. This result suggests that cowbird females in our study system are not necessarily tracking individual female warblers or nest boxes across years, but may be tracking cowbird production by this host species at the scale of female cowbird egg-laying ranges within a study site (which encompass several warbler territories) or the entire study site. Female cowbirds likely are using some combination of private and public information, associated with their and other female cowbird's success with this particular host, to modify their egg-laying decisions and host specificity from one breeding season to the next.

Evidence of a generalist brood parasite using breeding information across years to enhance reproductive output provides new insights into the evolution of host specificity in obligate brood parasites. Efforts to manage parasite populations for threatened or endangered host species could possibly reduce the fledging success of parasitic young to curb parasitism attempts in subsequent years; however, this should be used with caution because new individuals can immigrate into and continually replace the experienced cowbird population. Future experimental research involving genetic analyses should help to determine the roles of private and public information in female cowbird host-use decisions and whether increases in parasitism are associated with repeated parasitism from known individuals versus an influx of new or young cowbird females.

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TABLES AND FIGURES

Table 1. Model selection to estimate probability of parasitism of prothonotary warblers, *Protonotaria citrea*, by brown-headed cowbirds, *Molothrus ater*, in southern Illinois, USA, 1994-2010.

No.	Model	AIC_C	ΔAIC_C	w_i	*K*	-2LL
1	M+PPR+PWS+PCS	4196.84	0.00	0.40	9	3780.77
2	M+PPR+PWS+PCS+Wdensity	4198.51	1.67	0.18	10	3778.28
3	M+PPR+PCS	4198.72	1.88	0.16	8	3770.41
4	M+PPR	4200.26	3.42	0.07	7	3779.78
5	M+PPR+PWS	4200.39	3.55	0.07	8	3770.29
6	M+PPR+PCS+Wdensity	4200.73	3.89	0.06	9	3773.06
7	M+PPR+PWS+Wdensity	4201.74	4.90	0.03	9	3776.34
8	M+PPR+Wdensity	4202.15	5.31	0.03	8	3771.04

M, month incubation of nesting attempt initiated (April-July); PPR, ambient rate of parasitism per site in previous year; PWS, number of warblers fledge per warbler nesting attempt per site in the previous year; PCS, number of cowbirds fledged per warbler nesting attempt per site in the previous year; Wdensity, density of warblers in a given site in the current year; AIC_C, Akaike's information criterion corrected for small sample size; $\Delta_i = AIC_{C(i)} - AIC_{C(min)}$; w_i, Akaike weight; *K*, number of explanatory parameters in the model; -2LL, -2 log-likelihood.

Table 2. Average parameter estimates with standard errors and parameter likelihood are shown for all models.

No.	Int	M	PPR	PWS	PCS	Wdensity
1	8.003 (0.521)	-1.525 (0.078)	1.233 (0.380)	-0.174 (0.087)	1.319 (0.553)	
2	7.944 (0.531)	-1.527 (0.078)	1.202 (0.384)	-0.188 (0.091)	1.287 (0.556)	0.051 (0.088)
3	7.667 (0.493)	-1.530 (0.078)	1.577 (0.341)		1.020 (0.540)	
4	7.787 (0.496)	-1.531 (0.078)	1.694 (0.338)			
5	8.036 (0.530)	-1.528 (0.078)	1.486 (0.369)	-0.116 (0.084)		
6	7.666 (0.513)	-1.530 (0.078)	1.577 (0.341)		1.019 (0.548)	0.001 (0.084)
7	7.925 (0.539)	-1.530 (0.078)	1.434 (0.375)	-0.139 (0.089)		0.072 (0.089)
8	7.735 (0.519)	-1.532 (0.078)	1.690 (0.338)			0.029 (0.084)
Model Averaged Parameter Estimates						
β	7.83	-1.53	1.37	-0.17	1.23	-0.04
β LCL	6.86	-1.68	0.57	-0.35	0.12	-0.13
β UCL	8.79	-1.37	2.17	0.01	2.34	0.23
Sum of w_i				0.68	0.80	0.30

Int, intercept; M, month; PPR, ambient rate of parasitism per site in previous year; PWS, number of warblers fledged per warbler nesting attempt per site in the previous year; PCS, number of cowbirds fledged per warbler nesting attempt per site in the previous year; Wdensity, density of warblers in a given site in the current year; Sum of w_i, sum of Akaike weight.

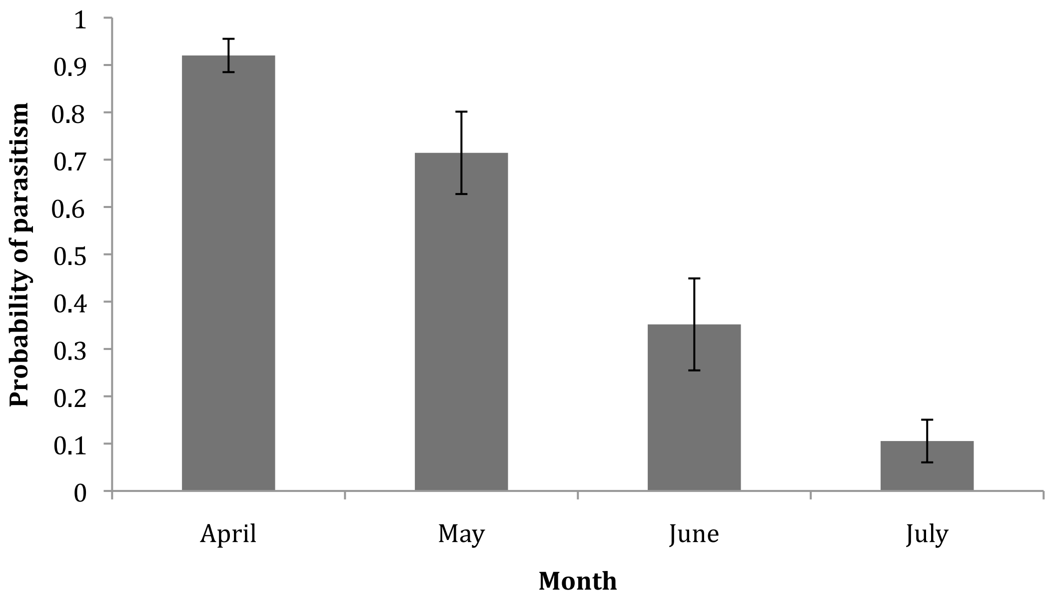

Figure 1. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds for prothonotary warblers by month, 1994-2010.

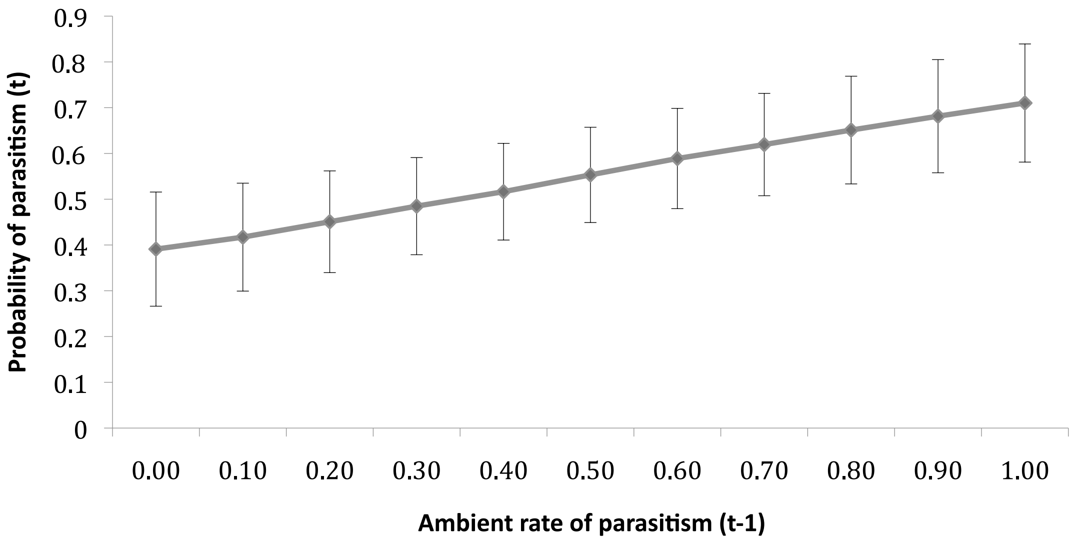

Figure 2. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds in year (t) for prothonotary warblers based on ambient parasitism in previous year (t-1), 1994-2010.

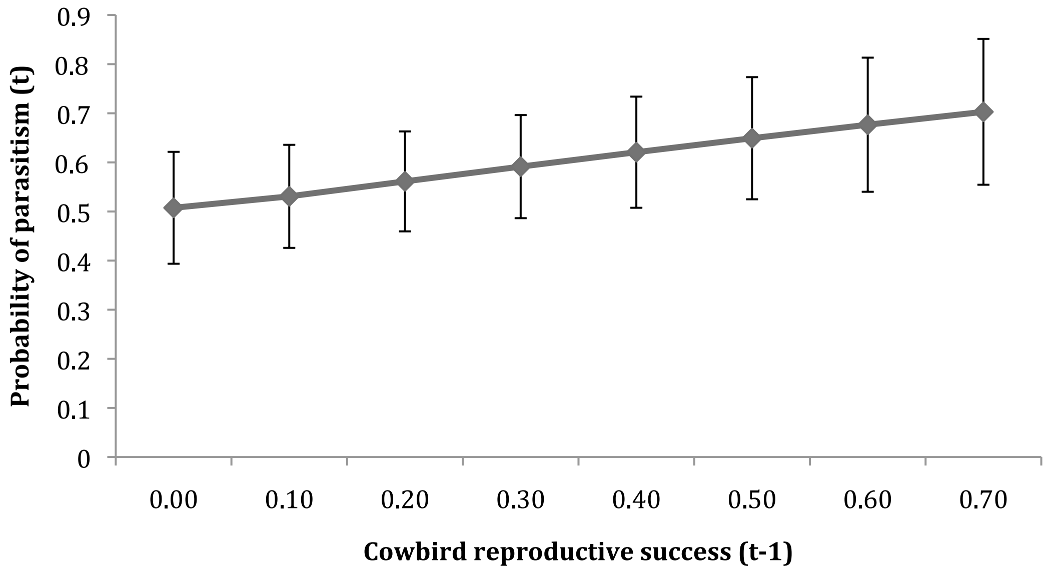

Figure 3. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds in year (t) for prothonotary warblers based on cowbird reproductive success in previous year (t-1), 1994-2010.