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RESEARCH ARTICLE

Local conspecific density does not influence reproductive output in a secondary cavity-nesting songbird

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ABSTRACT

Density dependence is a conceptual cornerstone of avian population biology and, in territorial songbirds, past research has emphasized interactions among food limitation, density, and reproduction. Documenting the importance of density effects is central to understanding how selective forces shape life histories and population dynamics. During the 2008–2011 breeding seasons, we nearly doubled overall conspecific breeding densities on study sites, and manipulated nest box spacing to increase local breeding densities (defined as the number of pairs breeding within 200 m of a pair's nest) of a secondary cavity-nesting songbird, the Prothonotary Warbler (*Protonotaria citrea*). Our primary objective was to test for effects of food limitation, as mediated by conspecific local densities, on measures of productivity. We monitored breeding pairs and recorded the total number of fledglings produced along with several components of reproductive output (clutch size, hatching success, nestling survival, and probability of attempting a second brood), rates of nestling provisioning, and nestling body condition prior to fledging. We predicted that if the availability of food were affected by local densities, then one or more of these parameters measuring reproduction would be affected negatively. We did not detect an effect of local density on total reproductive output or its components despite our vast range of local densities (1–27 pairs; i.e. 0.16–2.23 pairs ha⁻¹). Further, we also did not detect differences in nestling provisioning rates and nestling body condition relative to local density. By breeding in a productive ecosystem rich in food resources, these warblers appear to avoid reduced reproductive output when breeding in high densities. Whereas density-dependent food limitation may commonly reduce reproductive output in many species, the ecological circumstances underlying when it does not occur merit further investigation and may provide new insights into what is driving territoriality and what are the primary factors affecting individual fitness.

Keywords: conspecific density, density dependence, food limitation, hatching success, nestling body condition, nestling provisioning, Prothonotary Warbler, reproductive output

La densidad local de individuos conespecíficos no influencia el rendimiento reproductivo en un ave canora que anida en cavidades secundarias

RESUMEN

El concepto de denso-dependencia es central para la biología poblacional de las aves y, en las aves canoras territoriales, las investigaciones pasadas han enfatizado las interacciones entre la limitación de alimentos, la densidad y la reproducción. Documentar la importancia de los efectos de la densidad es central para entender como las fuerzas selectivas moldean las historias de vida y las dinámicas poblacionales. Durante las estaciones reproductivas de 2008 a 2011, casi duplicamos las densidades totales de individuos reproductivos conespecíficos en los sitios de estudio, y manipulamos el espaciado de las cajas nido para aumentar las densidades locales de individuos reproductivos (definida como el número de parejas criando dentro de los 200 m del nido de la pareja) de *Protonotaria citrea*, un ave canora que anida en cavidades secundarias. Nuestro objetivo principal fue evaluar los efectos de la limitación de alimentos, mediada por las densidades locales de individuos conespecíficos, sobre las medidas de productividad. Monitoreamos parejas reproductivas y registramos el número total de volantones producidos junto a varios componentes del rendimiento reproductivo (tamaño de la nidada, éxito de eclosión, supervivencia de los polluelos y probabilidad de intentar una segunda camada), a las tasas de aprovisionamiento de los polluelos y a la condición corporal de los polluelos antes del emplumamiento. Predijimos que, si la disponibilidad de alimentos se viera afectada por las densidades locales, entonces uno o más de estos parámetros que miden la reproducción serían afectados negativamente. No detectamos un efecto de la densidad local en el rendimiento reproductivo total o en sus componentes a pesar de nuestro amplio rango de densidades locales (1–27 parejas; i.e. 0.16–2.23 parejas ha⁻¹). Más aún, tampoco detectamos diferencias en las tasas

de aprovisionamiento de los polluelos y en la condición corporal de los polluelos en relación a la densidad local. Al reproducirse en un ecosistema productivo rico en recursos alimenticios, estas aves parecen evitar una reducción en el rendimiento reproductivo cuando crían en altas densidades. Mientras que la limitación de alimentos dependiente de la densidad puede por lo general reducir el rendimiento reproductivo en muchas especies, las circunstancias ecológicas que subyacen cuando esto no ocurre merecen futuras investigaciones y pueden proporcionar nuevas ideas sobre lo que impulsa la territorialidad y cuáles son los factores principales que afectan la adecuación biológica de los individuos.

Palabras clave: aprovisionamiento de los polluelos, condición corporal de los polluelos, densidad conspecífica, denso-dependencia, éxito de eclosión, limitación de alimentos, *Protonotaria citrea*, rendimiento reproductivo

INTRODUCTION

Density dependence, where a factor's effect on the size or growth of a population varies with the population density, is a conceptual cornerstone of population biology (Lack 1954, Murdoch 1994, Hixon et al. 2002). There is strong evidence among many avian studies for density (i.e. crowding) effects on mating systems (rates of extra-pair paternity; McKellar et al. 2014), nest predation (Schmidt and Whelan 1999, McKellar et al. 2014, Sofaer et al. 2014), and competition for food resources (e.g., Török and Tóth 1988, Both 1998a, Rodenhouse et al. 2003, Sillett et al. 2004, Wilkin et al. 2006). In particular, reduced reproductive output resulting from density-dependent competition for food resources has been reported in several studies of territorial songbirds (e.g., Arcese and Smith 1988, Newton 1998, Sillett et al. 2004, Mallord et al. 2007, Brouwer et al. 2009) and usually occurs through some combination of changes in clutch size, hatching success, and fledging success (e.g., Kluijver 1951, Perrins 1965, Lack 1966, Alatalo and Lundberg 1984, Böth 1998a). Effects of density on food availability may not be apparent early in the nesting cycle but could manifest during the peak of breeding season food demands (i.e. the nestling stage) and be evident in nestling provisioning rates (Sillett et al. 2004) and subsequent nestling body condition (Alatalo and Lundberg 1984, Török and Tóth 1988, Both 1998b). Additionally, decreased food availability under crowded conditions could influence female condition and rates of double-brooding (i.e. initiating a second nest after successfully fledging a first nest) (Kluijver 1951, Dhondt 1977, Both 1998b, Sillett et al. 2004, Nagy and Holmes 2005) and ultimately affect population dynamics.

Along with food availability, nest predation and interspecific brood parasitism often play large roles in reducing reproductive output (e.g., Ricklefs 1969, Robinson et al. 1995, Davies 2000, Chalfoun et al. 2002, LaManna and Martin 2017). Previous research in our study system on Prothonotary Warblers (*Protonotaria citrea*), a secondary cavity-nesting species, revealed that nest failures caused by predators and reductions in reproductive output associated with brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) limited reproduction in the warblers (Hoover 2003a,b, Hoover 2006, 2009a, Hoover and Reetz 2006). However, neither nest predation nor brood parasitism were density dependent

(Hoover 2001, Louder et al. 2015). Nest predation is negatively correlated with depth of water beneath active nests (Hoover 2006, 2009a). When water levels are high or, alternatively, nest predation is experimentally reduced or eliminated, reproductive success can increase more than 4-fold (Hoover 2003a, 2006, 2009a) and many warblers raised multiple broods in a single breeding season (Hoover 2003a). High reproductive success (i.e. fledging 2 broods) results in high between-year fidelity of adults to territories (Hoover 2003a) and increased conspecific breeding densities in subsequent years on study sites (Hoover 2009a,b). Raising many fledglings also likely increases the demand on food resources (Nilsson 1994, van Noordwijk et al. 1995, Both et al. 2009). In this study, we therefore focused on determining whether the reproductive output of the warblers could be affected by competition for food when densities were increased and confounds of nest predation and cowbird nestlings were reduced as much as possible. Reducing nest predation was necessary in order to increase warbler densities over time, and reduced nest predation is comparable with other studies that have assessed whether reproductive output is affected by conspecific density and food limitation in the absence of nest predation (e.g., Alatalo and Lundberg 1984, Both 1998b, Wilkin et al. 2009, Smallegange et al. 2011, Hedblom and Söderström 2012, Serrano-Davies et al. 2017).

Over 4 breeding seasons, we experimentally increased warbler densities by predator-proofing nest boxes on study sites to increase reproductive success and subsequent between-year fidelity to breeding sites. We also manipulated nest box spacing to achieve a larger range of local conspecific breeding densities within each study site than would typically occur. The manipulated densities were not higher than what we have observed in the deepest water swamps within the study system (see the Discussion section below). We also removed cowbird eggs from warbler nests to reduce the potentially confounding effect of warblers raising cowbird nestlings (Hoover 2003b, Hoover and Reetz 2006). If food limited reproductive output when warbler densities were increased experimentally, then we expected warbler reproductive output to decrease. Specifically, we predicted that if food resources became limiting in response to increased densities, then total annual fledgling production by females would decrease with increased local densities owing to the singular or combined effects of local density on clutch size, hatching success, nestling survival, and double-brooding

attempts by females. We also predicted that increased local densities would reduce nestling provisioning rates and nestling body condition prior to fledging.

METHODS

Study Area and Focal Species

We worked within the Cache River Watershed in southern Illinois, USA, during the 2008–2011 breeding seasons. The watershed drains >1,900 km² of land into the Ohio and Mississippi rivers at the southern tip of Illinois (Demissie et al. 2008) and contains a diverse suite of habitats within an agricultural matrix. Wet forest habitats, including bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatic*) swamps, occupy ~9% of the landcover (Mankowski 1997). Local monthly weather data for April–July during 2008–2011 are provided in Appendix Table 3.

The Prothonotary Warbler (hereafter “warbler”) is a Neotropical migrant that breeds in the eastern and central U.S. (Petit 1999). The warbler is an obligate secondary cavity-nesting species that breeds over or near standing water in bottomland hardwood and swamp forests (Petit and Petit 1996). They are territorial, socially monogamous, readily accept nest boxes (Fleming and Petit 1986), and adults exhibit high site fidelity between breeding seasons, especially following years of high reproductive success (Hoover 2003a). During the breeding season, the warbler’s (adults and nestlings) diet is diverse and includes caterpillars (order Lepidoptera), flies and midges (order Diptera), spiders (class Arachnida), mayflies (order Ephemeroptera), and dragonflies (order Odonata) mostly gleaned from leaves, twigs, and branches (Petit et al. 1990a,b, Petit 1999, Dodson et al. 2016), and predominantly comes from within their breeding territory (Petit 1999).

Manipulating Local Breeding Densities

In March 2008, we established a grid-system of 170 nest boxes on each of 2 40-ha study sites that were separated by 6.5 km. These study sites were usually covered by water at the beginning of each breeding season, with differences in micro-topography leading to some areas within sites lacking standing water later in the season in some years. We divided each site into 4 10-ha subplots (2 low-density and 2 high-density nest box treatments) to control for any habitat differences (e.g., more wet or less wet areas) within sites and to promote variation in local conspecific densities. We assigned nest box density treatments to subplots at each site by using a coin toss to determine the treatment for the upper left (i.e. northwestern most) subplot, and then gave the lower right subplot the same treatment and the remaining 2 subplots (upper right and lower left) the opposite treatment. Low-density subplots had 80–100 m

spacing between boxes (a total of 18–21 boxes per subplot); high-density subplots had 35–50 m spacing between boxes (a total of 65–67 boxes per subplot). Nest boxes were placed on tree trunks ~1.7 m above ground level and had openings that were 44 mm in diameter. We eliminated nest predation (see below), resulting in high between-year site and territory fidelity of returning birds (Hoover 2003a) with settlement of new birds in areas within sites where some nest boxes were not occupied (especially high-density subplots).

Eliminating/reducing Effects of Nest Predation and Brood Parasitism

To isolate the putative effects of density-dependent food limitation on reproductive output, we eliminated nest predation and reduced the effects of brood parasitism by Brown-headed Cowbirds. Because previous work has shown that raccoons (*Procyon lotor*) are the major nest predator in this system (Hoover 2006), we placed all active nest boxes onto greased poles at least 2 m from the nearest tree to prevent access by raccoons and other ground-based predators. To reduce the many negative effects of cowbird parasitism (Hoover 2003b, Hoover and Reetz 2006), we removed cowbird eggs during early incubation. Removal of cowbird eggs was conducted under permit and the eggs were used in a separate study assigning parentage to cowbird eggs/nestlings.

Monitoring Individual Warblers and Estimating Their Reproductive Output

During 2008–2011, we captured all adult birds that were using nest boxes and banded each with a unique combination of a numbered aluminum leg band (U.S. Geological Survey) and colored plastic leg bands. We captured and/or re-sighted (for those already banded) birds to identify the individual male and female associated with each nesting attempt each year. We captured females during incubation by placing a small plastic bag over the opening of nest boxes. We captured males by placing a male decoy warbler paired with a playback of a warbler song in front of a mist-net within each male’s territory. Upon capture of adults, we measured body mass (g), wing chord length (mm), and tarsus length (mm) of each individual and determined their age (second-year [SY; i.e. 1-yr-old and entering their first breeding season] vs. after-second-year [ASY; i.e. ≥2 yr old] [see Kowalski 1986, Pyle et al. 1987]).

From late April through early August each year, we inspected nest boxes every 5–7 days to determine if and when nests were initiated. We monitored active nests in boxes every 3–7 days. We also monitored natural cavity nests when they were found, but this was a rare occurrence (i.e. only 2 warbler pairs used natural cavities on the plots across the 4 yr of the study). We recorded warbler

clutch size and parasitism status (cowbird egg present or not) during each nest check and removed any cowbird eggs at the start of or during the first few days of incubation. We also noted whether adults were present at the box or in the area and determined the identity of the adults if needed. The frequency of box- and nest-monitoring efforts allowed accurate determination of nest initiation, hatch dates (we always checked nests within 2 days of hatching), and nestling ages. On day 6, 7, or 8 post-hatching, we measured each nestling's tarsus length (mm) and body mass (to the nearest 0.01 g using a digital scale) and banded it with a numbered aluminum leg band (U.S. Geological Survey). We monitored breeding pairs after nestlings fledged to determine whether pairs made additional nesting attempts.

Estimating Nestling Provisioning Rates and Nestling Body Condition

We used video cameras to conduct 1-hr nestling provisioning observations on day 6, 7, or 8 post-hatching. All observations were made between 0700 and 1100 hours and prior to any other research activity at the nest box that day. Cameras were deployed for 80 min and placed >20 m away from an active box and hidden behind a tree to minimize any potential disturbance to the adult warblers as they flew to/from the nest. We checked nests immediately after videotaping to count the number of nestlings. We later transcribed videos, and the first and last 10 min of video were censored to eliminate any potential bias resulting from human disturbances when entering and leaving the territory. We determined the number of feeding trips made per hour by each parent and summed these values to obtain the overall provisioning rate per nestling (i.e. total number of trips/hour/nestling by both adults). We determined nestling body condition by calculating the standardized residuals from the regression of average nestling mass (g) on average nestling tarsus length (mm) per brood to correct for body size (Adams and Frederick 2009).

Estimating Local Densities

We georeferenced the location of every nest box using a Trimble Juno Global Positioning System unit (Trimble Navigation, Sunnyvale, California, USA) and transferred the coordinates into ArcGIS (ESRI, Redlands, California, USA) to quantify the distances between nest boxes. Previous work in the Cache River watershed has shown that warbler behavior is most influenced by interactions with other pairs within a 200-m radius of their own nest box. For example, ~75% of extra-pair young are sired by males who hold territories within 200 m of a cuckolded male's nest box (Schelsky 2010); breeding dispersal decisions tend to be based on conspecific interactions at this spatial scale (Schelsky 2010), and the vast majority of foraging by adults occurs within 200 m of their nest (J.

P. Hoover personal observation). Therefore, we calculated "local density" (hereafter, density) as the number of warbler pairs breeding in nest boxes within a 200-m radius of each active nest box. This measure of density is similar to that used by McKellar et al. (2014), who used paternity and telemetry data to justify their scale (also a 200-m radius) for measuring density in a population of American Redstarts (*Setophaga ruticilla*).

Statistical Analyses

We used a linear mixed model to test for the effects of density (continuous variable) on the annual reproductive output (total number of warbler fledglings produced across all nesting attempts; continuous) of individual female warblers, and clutch size (number of warbler eggs present in nest when incubation began; continuous) for individual nesting attempts. Clutch size data had a variance/mean ratio <1 resulting in underdispersion when modeled using a Poisson or negative binomial distribution, thus our data were best modeled using a normal distribution (McDonald and White 2010). Both annual reproductive output and clutch size met assumptions of normality.

To test for density effects on other components of reproductive success including hatching success (number of eggs that hatched divided by clutch size; proportion), nestling survival (number of nestlings that fledged divided by number of eggs that hatched; proportion), and probability of attempting a second brood (a female laying a new clutch of eggs within the same breeding season after producing fledglings in her first attempt; binomial, yes or no), we used generalized linear mixed models (Proc GLIMMIX; SAS Institute 2003) and specified a binomial distribution and a logit link function.

We accounted for the potential effects of year (categorical), a density \times year interaction, date (continuous), female age (categorical), and cowbird parasitism status (categorical) on annual reproductive output and its components. We included year and a density \times year interaction in all of our analyses because density-dependent effects are often conditioned by annual variation in biotic (e.g., food availability) and abiotic (e.g., weather) factors and their interaction (Higgins et al. 1997, Newton 1998, Turchin 1999, Sillett et al. 2004, Smallegange et al. 2011). We also included date because it is known to be negatively correlated with clutch sizes (Petit 1989, Blem and Blem 1992, Hoover 2001) and attempts at second broods in these warblers (Hoover 2001). Date was defined as the date incubation began for each nesting attempt for the clutch size, hatching success, and nestling survival analyses, and as the date incubation began for the first nesting attempt of a given female each year for the attempts at second broods and annual reproductive output analyses. Female age (SY or ASY) was included to account for younger females (i.e. breeding for the first time) possibly being less productive

than older females (e.g., [Perrins and McCleery 1985](#)). We included cowbird parasitism status (parasitized or not parasitized) in analyses of clutch size, hatching success, and nestling survival because the presence of cowbird eggs and/or the actions of female cowbirds can reduce these components of reproductive success, even if cowbird eggs are removed by researchers in early incubation ([Hoover 2003c](#), [Hoover and Robinson 2007](#)).

Approximately 23% of all first nesting attempts ($n = 286$) were made by females who were first detected on site during the latter half of the breeding season (on/after 10 June). We had no knowledge of whether these females had nested elsewhere before arriving on site and exploratory analyses showed that double-brooding had a significant effect on the number of young produced but that the probability of attempting a second brood dropped sharply after the beginning of June. Therefore, we omitted these late-arriving females from the analysis of annual reproductive output. We specified treatment (high- or low-density subplot) nested within site, and female identity, as random effects for all of these analyses. We used female identity as a random effect because high site fidelity led to repeated observations of some of the same females in successive years and we assumed that females rather than males or pairs had a larger influence on the reproductive output.

Prior to fitting models, we examined correlations among all fixed effects and found that none were moderately to strongly correlated ($|r| > 0.50$), which can lead to spurious parameter and variance estimates ([Freckleton 2011](#)). To determine if we had sufficient statistical power to detect differences with our data, we approximated point estimates for the standardized effect sizes of the correlation coefficient r for mixed-effect models for the 5 parameters measuring reproduction mentioned above (featured in [Table 1](#)) and density. We used equations 22–24 provided in [Nakagawa and Cuthill \(2007\)](#) and approximated r using the t -statistics from each of the corresponding mixed-effect models. Reliable methods to estimate the confidence intervals (CIs) for standardized effect sizes using non-independent data are generally lacking ([Nakagawa and Cuthill 2007](#)), thus we do not report them here. To interpret our estimates of r we employed the benchmarks for small (0.1), medium (0.3), and large (0.5) effect sizes proposed by [Cohen \(1988\)](#).

We used linear mixed models ([SAS Institute 2003](#)) to test for an effect of density on nestling provisioning rates and nestling body condition. The provisioning rate and nestling condition data met assumptions of normality. In these analyses, we again accounted for the potential effects of year, a density \times year interaction, and date. For nestling condition, we also included the number of host nestlings as a linear fixed effect to account for the influence the number of nestmates can have on nestling growth ([Podlesak and Blem](#)

TABLE 1. Results of linear and generalized linear mixed models comparing Prothonotary Warbler annual fledgling production and various components of reproductive output to local density, year, local density \times year, date, female age, and cowbird parasitism

	Clutch size ($n = 374$) ^a			Hatching success ($n = 373$) ^a			Nestling survival ($n = 373$) ^a			Probability of attempting second brood ($n = 191$) ^b			Total annual fledgling production ($n = 190$) ^b		
	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P
Local density	2.19	1,363	0.14	0.09	1,150	0.77	0.58	1,150	0.45	0.05	1,69	0.83	0.00	1,262	0.96
Year	0.08	3,363	0.97	3.64	3,150	0.01	0.85	3,150	0.47	1.28	3,69	0.29	1.21	3,243	0.31
Local density \times year	0.18	3,363	0.91	2.08	3,150	0.11	0.15	3,150	0.93	0.57	3,69	0.64	1.09	3,245	0.35
Date	35.59	1,363	<0.01	1.33	1,150	0.25	81.47	1,150	<0.01	29.06	1,69	<0.01	79.55	1,273	<0.01
Female age	2.42	1,363	0.12	0.06	1,150	0.81	0.32	1,150	0.57	2.23	1,69	0.14	0.62	1,271	0.43
Cowbird parasitism	1.50	1,363	0.22	19.49	1,150	<0.01	5.45	1,150	0.02	—	—	—	—	—	—

^a n = number of nests.

^b n = number of females.

2002). For both of these analyses we nested treatment within site as a random effect, and specified breeding pair identity as a random effect to account for instances where particular warbler pairs were sampled in more than one year of our study. We specified breeding pair identity rather than female identity as the random effect to incorporate the influence of male and female parental care efforts as a whole on nestling growth and development. Prior to fitting models, we examined correlations among all fixed effects and again found that none were moderately to strongly correlated ($|r| > 0.50$). Values reported in the results section are means \pm SE unless otherwise indicated, and for some fixed effects we report β (i.e. regression coefficient) and 95% CIs.

RESULTS

We collected data from 374 nesting attempts associated with 200 unique individual female and 164 unique individual male warblers. The annual numbers of unique females present on both sites combined during 2008–2011 were 62, 96, 119, and 107, respectively. Thirty-eight percent of all nesting attempts were parasitized by Brown-headed Cowbirds and there were 1.41 ± 0.06 cowbird eggs per parasitized nest. Clutch sizes were 4.28 ± 0.05 and 4.18 ± 0.04 warbler eggs for parasitized and non-parasitized nests, respectively. None of the nests were deserted following our removal of cowbird eggs. Over the 4-yr study, 36 (9.5%) of the 374 nesting attempts failed to produce a fledged warbler. These failures all occurred during the nestling phase with the vast majority (30) resulting from nestling death late in the breeding season (mid- to late-July). Four nests failed for unknown reasons, and 2 likely were depredated by raptors.

Local Densities

Our manipulation of nest box densities and reduction of nest predation had the intended effect of creating a wide range of densities over time that included 1–27 pairs of conspecifics breeding within 200 m of focal pairs (i.e. 0.16–2.23 pairs ha^{-1}). Specifically, in 2008 mean conspecific (i.e. local) density was 6.6 ± 0.2 neighbors (range: 2–10) and by 2010 it had more than doubled to 14.9 ± 0.5 neighbors (range: 1–27). In 2011, mean densities were 12.6 ± 0.6 neighbors (range: 2–23). The initial mean site-wide density values of (6.6) in 2008 and peak value (14.9) in 2010 translate to 0.61 and 1.27 pairs ha^{-1} , respectively. The starting density in 2008 (0.61 pairs ha^{-1}) was similar to warbler densities observed during earlier years on sites with no nest boxes (0.65 pairs ha^{-1} , $n = 8$ sites) (Hoover 2001).

Effects of Local Density on Reproduction

Contrary to our predictions, we did not detect differences in total annual fledgling production of individual female warblers with increased density ($\beta = -0.033$, 95%

CI = -0.125 , 0.059) (Table 1, Figure 1A). Nor did fledgling production differ by year, the density * year interaction, or female age ($\beta = -0.171$, 95% CI = -0.598 , 0.257) (Table 1). As we expected, total fledgling production did decrease with date ($\beta = -0.063$, 95% CI = -0.077 , -0.049).

We did not detect differences in clutch size relative to density ($\beta = 0.009$, 95% CI = -0.021 , 0.039) (Table 1, Figure 1B) or any other factors included in the analysis except for date ($\beta = -0.013$, 95% CI = -0.018 , -0.009), with clutch sizes decreasing later in the breeding season (Table 1). To investigate whether clutch size was affected by a date * density interaction (e.g., an effect of density was present late but not early in the breeding season), we conducted an additional analysis and did not detect an effect of the interaction ($F_{1,362} = 0.68$, $P = 0.41$). We did not detect a difference in hatching success relative to density ($\beta = -0.073$, 95% CI = -0.165 , 0.018) (Table 1, Figure 1C), but hatching success was lower for parasitized nests (parasitized = $81 \pm 0.1\%$, non-parasitized = $92 \pm 0.1\%$) (Table 1) and was different among years (2008 = $89 \pm 0.06\%$, 2009 = $86 \pm 0.02\%$, 2010 = $93 \pm 0.01\%$, 2011 = $90 \pm 0.02\%$).

We did not detect an effect of density on nestling survival ($\beta = 0.024$, 95% CI = -0.135 , 0.183) (Table 1, Figure 1D), but nestling survival decreased with date ($\beta = -0.084$, 95% CI = -0.102 , -0.065). Nestling survival was also slightly lower in nests that had been parasitized by cowbirds (parasitized = $96 \pm 0.03\%$, non-parasitized = $98 \pm 0.01\%$). An additional analysis did not detect an effect of a date * density interaction on nestling survival ($F_{1,149} = 0.1$, $P = 0.84$). We did not detect differences in the probability of female warblers attempting second broods relative to density ($\beta = 0.092$, 95% CI = -0.087 , 0.271) (Figure 1E) or any of the other factors except for date ($\beta = -0.189$, 95% CI = -0.258 , -0.119) (Table 1), where the probability of females attempting a second brood decreased for those females initiating their first nesting attempts later in the breeding season. In our study, the standardized effect sizes (r) were -0.043 for fledgling production, 0.03 for clutch size, -0.003 for hatching success, -0.015 for nestling survival, and 0.006 for probability of second broods, which suggests weak relationships for all variables with density.

Nestling Provisioning and Body Condition

There were no detectable differences in nestling provisioning rates relative to density ($\beta = 0.110$, 95% CI = -0.024 , 0.244) or any other factor included in the analysis except for an effect of year (Table 2, Figure 2). Accordingly, we detected no differences in nestling body condition prior to fledging relative to density ($\beta = 0.025$, 95% CI = -0.020 , 0.071) (Table 2, Figure 3). Nestling body condition did differ with number of nestmates ($\beta = -0.202$, 95% CI = -0.304 , -0.099) and date ($\beta = -0.015$, 95% CI = -0.021 , -0.009) (Table 2).

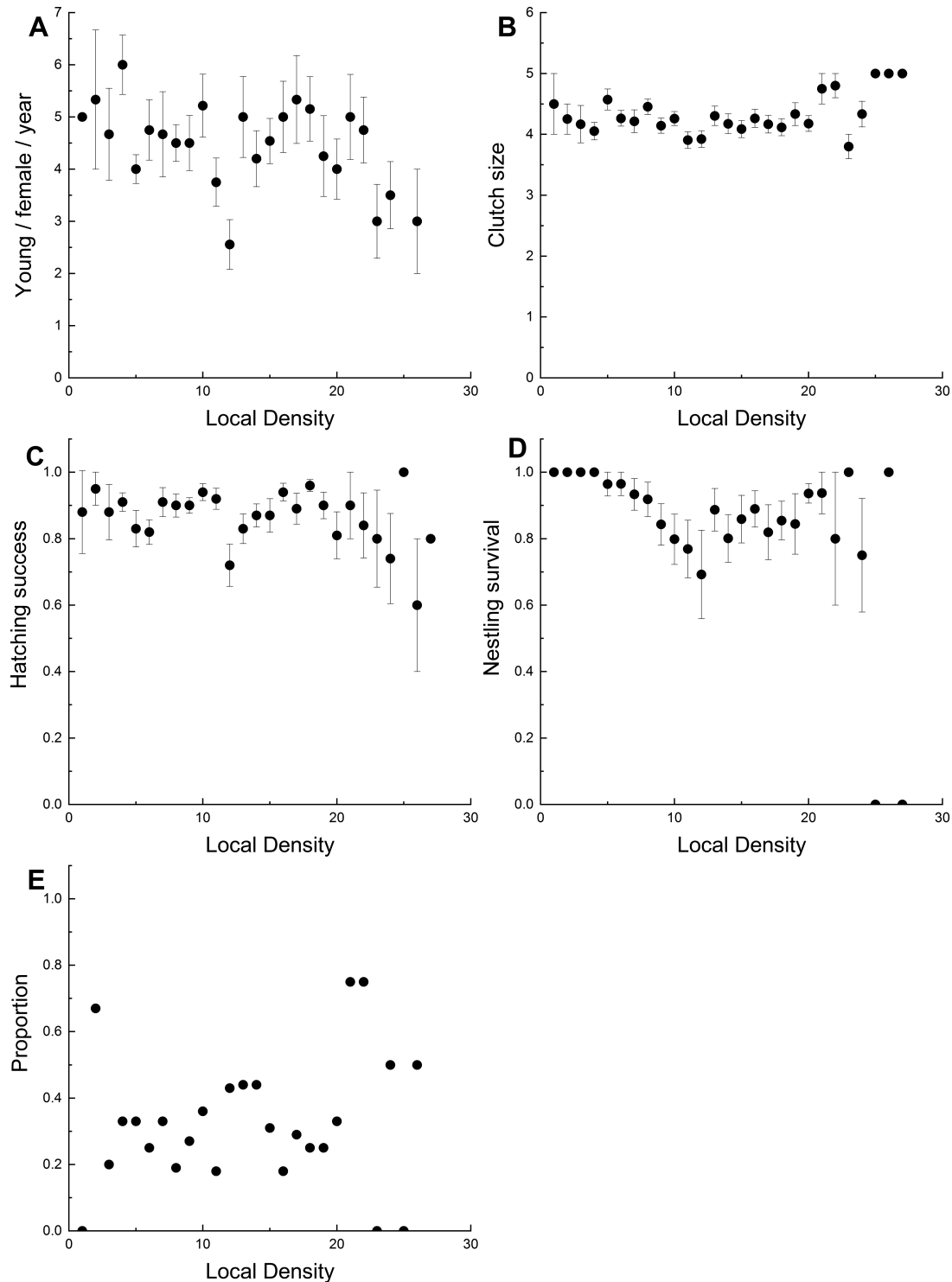
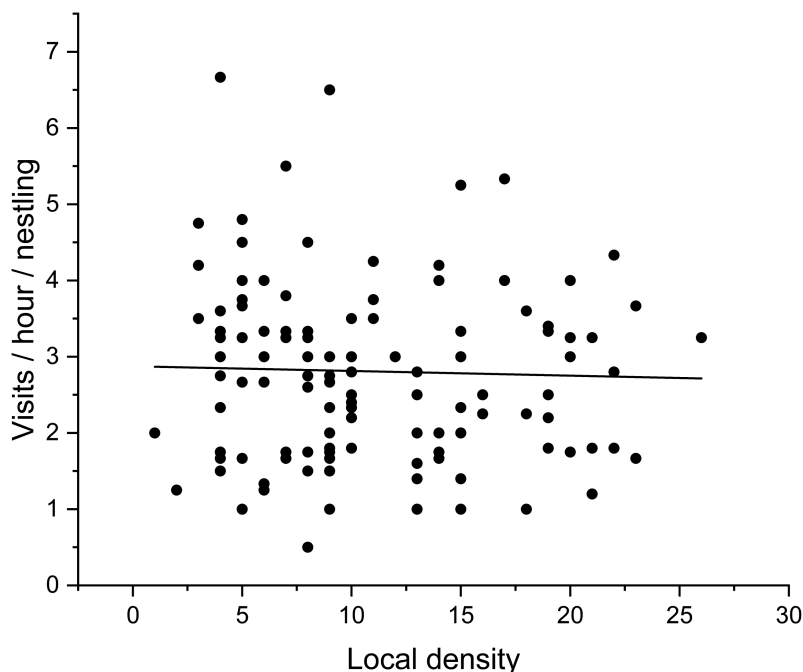


FIGURE 1. Reproduction parameters in relation to conspecific local density (the number of pairs breeding within 200 m of a pair's nest) of Prothonotary Warblers during 2008–2011 in southern Illinois. Data for **A–D** are presented as untransformed means \pm one standard error. **(A)** Total number of fledglings produced per female per year; error bars are not included for one density with a sample size of 1 female. **(B)** Clutch size; error bars are not included for densities with sample sizes of 1 nest (25 and 27) or where the response variable did not vary (26). **(C)** Hatching success including nests that were parasitized by Brown-headed Cowbirds; error bars are not included for densities with sample sizes of 1 nest (25 and 27). **(D)** Nestling survival; error bars are not included for densities with sample sizes of 1 nest (25 and 27) or where the response variable did not vary (1–4 and 26). **(E)** The proportion of females attempting a second brood; densities 1, 23, and 25 included 2, 5, and 1 female(s), respectively.

TABLE 2. Results of linear mixed models comparing Prothonotary Warbler nestling provisioning rates and nestling body condition in relation to local density, year, local density * year, date, and number of nestmates (nestling body condition analysis only)

	Nestling provisioning rates ($n = 121$) ^a			Nestling body condition ($n = 339$) ^a		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Local density	0.00	1 and 112	0.99	1.89	1 and 277	0.17
Year	2.66	3 and 112	0.05	2.25	3 and 315	0.08
Local density * year	2.20	3 and 112	0.09	1.31	3 and 312	0.27
Date	2.93	1 and 112	0.09	26.07	1 and 244	<0.01
Number of nestmates	–		–	14.95	1 and 322	<0.01

^a n = number of nests.**FIGURE 2.** Nestling provisioning rates (total feeding visits/hour/nestling) by Prothonotary Warbler adults in relation to conspecific density (the number of pairs breeding within 200 m of a pair's nest) during 2008–2011 in southern Illinois. Raw data are presented.

Nestlings with more nestmates had reduced body condition compared with those with fewer nestmates. Nestlings raised alone had the best overall body condition scores (i.e. residuals of mass regressed on tarsus length) prior to fledging ($= 0.57 \pm 0.2$) whereas nestlings raised with 4 nestmates had the poorest overall body condition ($= -0.18 \pm 0.1$). Nestling condition decreased as the breeding season progressed (i.e. date increased). A post-hoc analysis did not detect an effect of a date \times density interaction on nestling body condition ($F_{1,266} = 0.08$, $P = 0.77$).

DISCUSSION

If density-dependent food limitation reduced the warbler's reproduction via a "crowding" mechanism (e.g., Sillett et al. 2004), then we should have observed a

local density or local density \times year effect on one or more of the parameters measuring reproduction. If a "site-dependence" mechanism (i.e. average reproductive output per pair is negatively correlated with overall site-wide numbers of pairs over time; Rodenhouse et al. 1997) was operating, then there should have been a year effect on reproductive output with higher values in the first year of the study (2008) when numbers of pairs were lowest. None of these outcomes were observed and our manipulations successfully increased densities but failed to elicit density-dependent reductions in the quantity or condition of offspring produced. The high densities our manipulations achieved do occur elsewhere in this study system in permanent deep-water swamps (with and without nest boxes) where the deep water limits nest predation naturally (Hoover 2001, 2009a). We have confidence that our negative findings were robust because the standardized effect sizes for the 5 parameters measuring reproduction

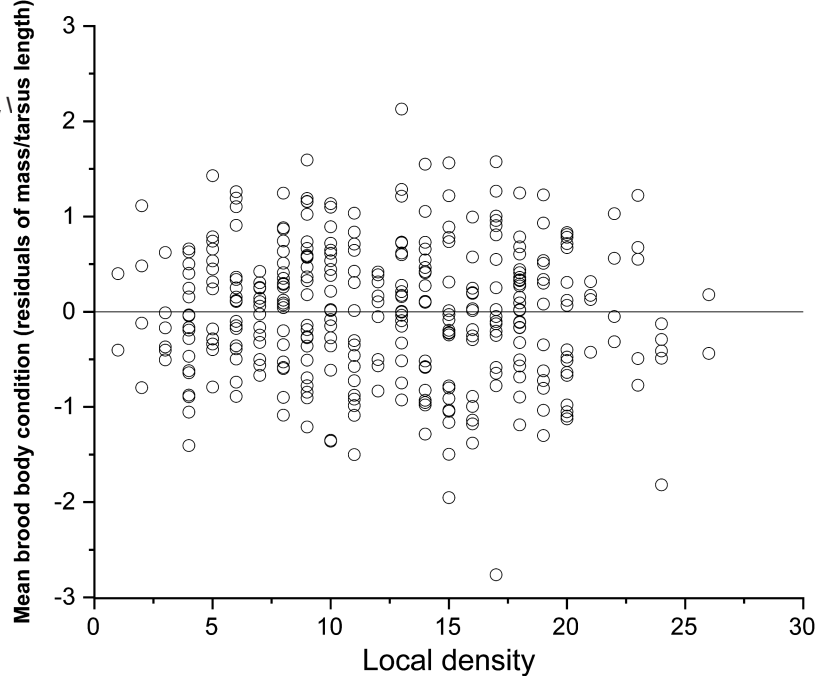


FIGURE 3. Body condition (residuals of mass [g] on tarsus [mm]) of Prothonotary Warbler nestlings in relation to conspecific density (the number of pairs breeding within 200 m of a pair's nest) during 2008–2011 in southern Illinois. Raw data are presented with each dot representing a brood.

(Table 1) were all $<|0.045|$, well below what Cohen (1988) proposed as a “conventional” value to serve as a benchmark for what is considered to be a “small” effect ($r = 0.1$). Small standardized effect sizes for all parameters measuring reproduction corroborate our conclusions of not detecting an effect of conspecific density on reproductive output, indicating that our results are not simply an artifact of sample size.

Bottomland and swamp forests, such as those in our study system, produce a diverse and abundant invertebrate biomass (Batzer et al. 2016) that continuously emerges throughout the warbler's breeding season (Petit and Petit 1996, Heinrich et al. 2013, Batzer et al. 2016, Dodson et al. 2016). This abundant and diverse invertebrate biomass in bottomland forest ecosystems likely promotes the diverse assemblage of abundant insectivorous bird species that breed in this habitat type (Sallabanks et al. 2000, Wakeley et al. 2007, Hoover 2009a). The warblers are insectivorous during the breeding season but are not highly specialized on one particular type of insect (Petit et al. 1990a,b, Petit 1999, Dodson et al. 2016). Emerging aquatic insects in bottomland forest ecosystems can subsidize the prey base of breeding insectivorous birds in general (Nakano and Murakami 2001, Baxter et al. 2005), and these warblers specifically (Petit and Petit 1996, Dodson et al. 2016), thereby making them less vulnerable to food limitation. Density-dependent food limitation during breeding seasons may be more common in species having specialized diets (Cattau et al. 2014), depending on food resources that are cyclic or temporally sporadic (Grant and Grant 1989, Karell et al. 2009), or breeding in less productive habitats (Wilkin et al. 2009, Dhondt 2010, Serrano-Davies et al. 2017).

In our study, warblers were able to provision their young enough that body condition during the latter half of the

nestling stage was not influenced by density. Several other songbird studies have documented reduced nestling mass or condition with increased density (Alatalo and Lundberg 1984, Both 1998b, Sillett et al. 2004, Wilkin et al. 2006; but see Arcese and Smith 1988, Török and Tóth 1988), but we are aware of only one previous field study that documented provisioning rates in relation to experimentally manipulated conspecific breeding densities. Sillett et al. (2004) found support for a density-dependent crowding mechanism whereby adult Black-throated Blue Warblers (*Dendroica caerulescens*) in reduced neighbor density treatments provisioned their nestlings at a greater rate and fledged heavier young than adults in control treatments during 1 yr of their study. They attributed their result to an effect of environmental conditions on the prey base (caterpillars and spiders available in the understory) of the Black-throated Blue Warblers with pairs in lower density treatments having access to more food because of reduced competition with conspecifics. By contrast, Petit and Petit (1996) and our study found no evidence for a crowding mechanism in Prothonotary Warblers, supporting the conclusion that the availability of abundant and diverse protein-rich terrestrial and aquatic insects during the breeding season may buffer these birds from negative effects of increased densities on provisioning rates, nestling condition, and reproductive output in general.

The territorial and despotic behavior of male warblers (Petit and Petit 1996) facilitates the defense of nest sites and mates (Petit 1999, Hoover 2001). Territoriality in general can limit the density of local breeding populations (e.g., Treinys et al. 2017) and reduce or prevent potential negative effects of density on reproduction (Brown 1969, Fretwell and Lucas 1970, Newton 1992). High densities of conspecifics can reduce access to food, however, by

compressing territories and increasing territorial disputes and interactions with neighbors (McCleery and Perrins 1985, Arcese and Smith 1988, Stamps 1990, Ridley et al. 2004). Although we did not estimate territory size in our study, some pairs of warblers on our study sites experienced high densities and presumably had compressed territories as a result (see Petit and Petit 1996), but apparently not to an extent where reproductive output became limited by food. In addition, nesting within high densities may be incentivized for males with previous experience on a site because they can gain an extra-pair mating advantage (i.e. getting more extra-pair young with local females without losing paternity in their own nests; Schelsky 2010). Based on our results, this advantage would not be diminished by food-based density-dependent reductions of the reproductive output from their own and extra-pair nests and may help explain the function of territories in this species if not primarily food- and nest site-based.

Individuals better able to successfully compete for resources (e.g., older birds with prior breeding experience, birds in better condition) could choose to breed in high densities where food is more abundant, whereas those less able to compete are relegated to breed in lower densities where food is less abundant (i.e. the “ideal dominance” distribution model of Fretwell and Lucas 1970; see also Newton 1998, Pärt 2001, Kokko et al. 2004). While it is not possible to experimentally place randomly selected individuals into high and low densities, our study design and ability to account for numerous other factors in analyses should have limited the ability of differences in the quality of individuals to mask the effects of density-dependent food limitation. In addition, prior work in our study system found no correlation between male condition or age and conspecific density (Schelsky 2010), and in this current study there was also no effect of density on male condition ($F_{1,66} = 1.0, P = 0.32$) while controlling for year.

Overall, our results suggest that high densities do not decrease food availability enough to reduce reproductive output when only raising warbler nestlings. We acknowledge that by removing cowbird eggs and hence nestlings from nests we reduced the overall demand on food typically seen in our study system (Hoover and Reetz 2006), and that if cowbird nestlings had been allowed to remain, we might have seen an effect of density on warbler productivity. Our removal of cowbird eggs during early incubation did not result in any nest desertion by the warblers, and we did not observe any nest failures suggestive of female cowbird involvement. It is unlikely that the late season nest failures were the result of “farming” or “mafia” behaviors of female cowbirds (Hoover and Robinson 2007) because they occurred when warblers are unlikely to attempt to nest again and female cowbirds are unlikely to parasitize nests (Hoover et al. 2006). We did find that parasitized nests had lower hatching success than non-parasitized

nests, even after removing cowbird eggs. This is likely a result of damage to host eggs associated with female cowbirds attempting to remove warbler eggs from nests prior to parasitism, or cowbird eggs landing directly on and damaging host eggs during a parasitism event (Hoover 2003b). Hatching success also was significantly different among years but was highest during 2010 and 2011 when densities were highest and therefore not attributable to negative effects of conspecific density. It is possible that, by greatly reducing cowbird success, we altered parasitism in subsequent years on our study sites (Louder et al. 2015), which could explain the annual variation in hatching success that we found. In the future, experimental random assignment of cowbird eggs to pairs of warblers at different levels of density could test whether raising broods that included a cowbird nestling generates enough additional food demand to elicit density-dependent reductions in some parameters measuring reproduction.

Seasonal effects on reproduction (e.g., Verhulst and Nilsson 2008, O'Brien and Dawson 2013, Franks et al. 2018) and seasonal declines in parameters measuring reproduction, such as those described in our study (e.g., Hochachka 1990, Crick et al. 1993, Gladbach et al. 2010, Harriman et al. 2017), are common in birds. Clutches laid later in the breeding season were typically second nesting attempts of warbler pairs trying to produce a second brood, and reductions in clutch size with each subsequent attempt within a breeding season are typical in this species (Petit 1989, Blem and Blem 1992, Hoover 2001). Females that commence breeding later within their discrete breeding season are less likely to have time to attempt a second brood, and therefore less likely to produce as many total offspring as earlier-nesting females (this study). Nestling body condition and survival decreased later in the breeding season, and the lack of detecting a date \times density interaction suggests that a density effect on food availability late in the breeding season was not responsible. A seasonal decline in nestling survival and body condition could result if the size or number of food items per trip (i.e. load), delivered by adults provisioning nestlings, decreased later in the breeding season. Unfortunately, our videos of provisioning warblers did not provide us with enough detail to assess this possibility. If provisioned food loads had decreased seasonally, we again would expect density to possibly become important later in the breeding season, but it did not. The presence of hematophagous blowflies (*Protophthora* spp.) is another factor that could explain seasonal declines in nestling condition and survival, particularly for those nests later in the season where no nestlings survived. Blowflies are a common parasite in bird nests (Sabrosky et al. 1989), they can have detrimental effects on nestlings (Puchala 2004, Simon et al. 2004), and the intensity of blowfly infestations can increase seasonally (Roby et al. 1992). This explanation is plausible, because during

other work in this study system we have observed blowfly (*Protophormia metallica*) larvae and pupae in warbler nests and have noted a tendency for blowfly loads (number of pupal cases per nestling per brood) to increase with date (unpublished data). One additional explanation is that hot summer temperatures later in the breeding season may have had adverse effects on nestlings. One recent study found that experimental warming of clutches of eggs resulted in reduced begging by the subsequent nestlings (Mueller et al. 2019). If this occurred, then provisioning rates could be reduced later in the season when temperatures are highest if reduced begging by nestlings promoted reduced provisioning by adults. Provisioning rates tended to decrease seasonally, but not significantly. Regardless, a negative effect of heat on nestling body condition and survival could occur regardless of warbler density and may be a fruitful direction for future research into seasonal effects on these parameters.

Despite our lack of evidence for a negative effect of density on reproductive output in this experimental system, it is generally accepted that density-dependent processes work to regulate populations (Turchin 1999). Further, multiple mechanisms likely interact to regulate populations (Krebs 2002, Rodenhouse et al. 2003). For migratory songbirds in particular, factors influencing them on stopover and wintering grounds may carry over to the breeding season, and integration of long-term monitoring efforts across the annual cycle can help elucidate delayed density dependence and carry-over effects important in population dynamics (Beckerman et al. 2002, Ratikainen et al. 2008, Hostetler et al. 2015, Marra et al. 2015). For the warblers in our system, future work to evaluate the impact of conspecific density on other demographic parameters such as adult and juvenile annual survival is also warranted. Finally, it would be valuable to document how food (i.e. insect) abundance varies over space and time to better understand how birds breeding in productive habitats like bottomland and swamp forests might be buffered from the negative effects of density on reproduction. Whereas reproductive output may be reduced by density-dependent food limitation in many species, the ecological circumstances underlying when it does not occur may provide important insights into what is driving territoriality and what are the primary factors affecting individual fitness.

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Ethics statement: This research was conducted in compliance with Animal Research Protocols 07040, 07224, 10011, 10013, and 10173 (each approved by the Institutional Animal Care and Use Committee of the University of Illinois at Urbana-Champaign), USFWS Permit number MB815400-1, and U.S. Geological Survey Banding Permit number 06507.

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Data depository: Analyses reported in this article can be reproduced using the data found at the Illinois Data Bank https://doi.org/10.13012/B2IDB-6382488_V1

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APPENDIX TABLE 3. Total monthly precipitation (mm) and average daily minimum, maximum, and average temperature (°C) for the city of Carbondale in southern Illinois during the Prothonotary Warbler breeding season, 2008–2011. Thirty-year climatological averages (1981–2010) are also shown

	Total precipitation					Minimum temperature					Maximum temperature					Average daily temperature				
	April	May	June	July	Mean	April	May	June	July	Mean	April	May	June	July	Mean	April	May	June	July	Mean
2008	na ^a	159	31	202	131	na	11.6	18.9	19.4	16.6	na	23.3	30.6	31.2	28.4	na	17.4	24.8	25.3	22.5
2009	198	91	69	158	129	7.7	13.5	19.4	18.8	14.9	19.4	24.8	30.8	28.9	26.0	13.6	19.2	25.2	23.9	20.4
2010	98	96	86	38	80	10.1	15.1	21.1	21.7	17.0	23.4	25.8	32.2	33.1	28.6	16.7	20.4	26.7	27.4	22.8
2011	343	178	0	102	156	9.6	13.2	18.1	22.3	15.8	21.6	23.8	30.3	34.0	27.4	15.6	18.6	24.2	28.2	21.6
30-yr av	105	131	101	91	107	7.3	13.1	17.8	19.9	14.5	19.7	24.9	29.7	31.4	26.4	13.5	19.0	23.7	25.7	20.5

^a Data from the Carbondale weather station were not available for April 2008.