Short communication

No evidence for a negative effect of conspecific brood parasitism on annual survival of female Prothonotary Warblers

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Species that provide intensive parental care could suffer fitness costs associated with conspecific brood parasitism. Here we evaluate the effect of conspecific brood parasitism on apparent annual survival probability of female Prothonotary Warblers *Protonotaria citrea* using a multistate model with imperfect state assignment analysed in a hierarchical Bayesian framework. We found no difference in annual survival probability between host and non-host females. These findings agree with previous work in that there seems to be little apparent cost of conspecific brood parasitism to female Warblers in this system.

Keywords: capture–recapture, conspecific brood parasitism, multi-event model.

Conspecific brood parasitism (CBP) is a relatively widespread avian behaviour in which a female lays an egg in the nest of a conspecific and provides no subsequent parental care. This behaviour is most common in species with precocial young (Yom-tov 2001) and has been shown to have little to no cost to the hosts in those systems (Dugger & Blums 2001, Lyon & Eadie 2008). However, CBP has also been documented in altricial species that require intensive parental care and in these cases may be more costly due to the added energetic investment in young post-laying (Lyon 1993).

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Here we investigate differences in annual survival between host and non-host female Prothonotary Warblers *Protonotaria citrea*, a cavity-nesting warbler. Previous work in this system showed that ~25% of broods contained at least one parasitic nestling (Tucker *et al.* 2016). Although host females fledged both fewer biological offspring and more total offspring than non-hosts, we found no evidence for an effect of CBP on average annual reproductive success of females over a 5-year period. However, Tucker *et al.* (2016) did not investigate the potential effect of CBP on host female survival. We expected that hosts may have a reduced annual survival probability due to the increased effort of brooding and provisioning additional and unrelated nestlings, and here we test this prediction using a multistate mark–recapture model.

We could not conclusively determine CBP status for every brood but did not want to limit our survival analysis to only those females for which we could confirm host status. Therefore we used a multistate model that allowed for imperfect state assignment (Conn & Cooch 2009). This framework allowed us to include information about those females detected as breeding that could not be conclusively determined to be a host or non-host. This type of model has been applied to a range of situations when the underlying biological state is of interest but can be difficult to determine with certainty for some individuals, e.g. breeding or disease status (Barbraud & Weimerskirch 2012, Gimenez *et al.* 2012, Desprez *et al.* 2013, Sanz-Aguilar *et al.* 2015). This modelling framework allowed us to test for differences in annual survival between host and non-host females using all available data for marked females, avoiding potential bias from estimating survival for only those females for which host status was known.

METHODS

We monitored 65 nestboxes for breeding Prothonotary Warblers near Richmond, Virginia, USA, from 2009 to 2013. We captured females at the nestbox during incubation and ringed them with an aluminium leg ring as well as a unique three-colour combination of plastic leg rings. We collected blood samples via brachial venipuncture and aged adults based on plumage following Pyle (1997). Numerical age was known for females first captured in their first or second year. For females first captured as adults, numerical age at first encounter was assigned as follows: after-hatch year birds = 1.5 (≥1 year old), after-second year = 2.5 (≥2 years old). We ringed and collected blood samples from nestlings 6–8 days after hatching.

Molecular laboratory methods and maternal exclusion analyses are described in detail by Tucker *et al.* (2016). Briefly, we genotyped all individuals at six microsatellite loci and performed maternal exclusion analysis using

Cervus (Kalinowski *et al.* 2007, Lemons *et al.* 2014). Any nestling whose social mother had a log-likelihood (LOD) score less than the 95% confidence cutoff value for exclusion was considered parasitic. Any female with at least one parasitic nestling in a season was considered a host, and females for which LOD scores with all putative offspring in a season were greater than the 95% LOD cutoff were considered non-hosts. In our study, state assignment was only possible if: (1) blood samples were obtained for the female and the complete brood of nestlings, and (2) sufficient PCR-amplification of microsatellite loci occurred such that we could compare the female with all putative offspring at least three loci. Any female breeding in the study area for which we could not confirm host or non-host status was assigned to an 'unknown' state.

We used a multistate model with imperfect state assignment to estimate apparent annual survival probabilities (Conn & Cooch 2009). Capture histories representing detections and states were created for all females in our study area from 2009 to 2013. For example, the hypothetical capture history NU0H0 would represent a female that was a non-host in year 1, present and breeding with unknown host status in year 2, not detected in year 3, a host in year 4 and not detected in year 5.

Survival probabilities and transitions between host and non-host state were modelled in a hierarchical Bayesian framework. The underlying state process can be defined as a matrix in which the rows represent an individual's state in year t and columns represent state in year $t + 1$ (host, non-host or dead):

$$\begin{bmatrix} \phi^H(1 - \psi^{HN}) & \phi^H \psi^{HN} & 1 - \phi^H \\ \phi^N \psi^{NH} & \phi^N(1 - \psi^{NH}) & 1 - \phi^N \\ 0 & 0 & 1 \end{bmatrix}$$

where ϕ^H represents the probability that a bird that is alive and a host in year t survives until year $t + 1$, and ψ^{HN} represents the probability that a bird that is a host in year t transitions to being a non-host in year $t + 1$, given that it has survived. The observation process can be defined as a matrix in which the rows represent an individual's true state and columns represent possible observed states (host, non-host, unknown or not seen).

$$\begin{bmatrix} p\delta & 0 & p(1 - \delta) & 1 - p \\ 0 & p\delta & p(1 - \delta) & 1 - p \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

where p represents the probability of detecting a bird given that it is alive and in the study area, and δ is the probability of assigning a bird to a state (host or non-host), given that it is detected. For birds first encountered in an unknown state, we used a mixture parameter π to probabilistically determine whether that individual was a host or non-host following Conn and Cooch (2009).

To assess potential temporal variation in survival (ϕ) and detection (p) probabilities, we initially fit four models representing time-varying and time-constant detection and survival and compared them using the deviance information criteria (DIC; Spiegelhalter *et al.* 2002), with lower DIC indicating more support. The model with both time-constant survival and detection received the most support (Table 1), so that model structure was used to draw further inference about survival probability. We used indicator variable selection (Hooten & Hobbs 2015) to assess the relative importance of three potential drivers of individual annual survival: host state, female age and number of nestlings raised in a given year. Each β coefficient was defined as the product of a binary indicator variable ω_i and a regression coefficient θ_i:

$$\omega_i \sim \text{Bernoulli}\,(0.5)$$
$$\theta_i \sim \text{Normal}(0, \sigma_\beta)$$
$$\beta_i = \omega_i * \theta_i$$

The indicator variable is a Bernoulli random variable that effectively switches covariates 'on' or 'off' at each Markov chain Monte Carlo (MCMC) iteration. If the covariate is an important predictor, the indicator variable will be equal to 1 in a high proportion of MCMC iterations; the posterior mean of ω_i can therefore be interpreted as the variable inclusion probability. The effect of these covariates on survival was modelled with a logit link:

$$\text{logit}(\phi_{i,t}) = \mu + \beta^{host} * \text{host}_{i,t} + \beta^{age} * \text{age}_{i,t}$$
$$+ \beta^{nest} * \text{nestlings}_{i,t} + \varepsilon_t$$

$$\varepsilon \sim Normal(0, \sigma^2)$$

where μ was the baseline survival probability, β_t^{year} is the effect of year t, β^{host} is the effect of being a host,

Table 1. Results of the model selection process for time-constant or time-varying detection (p) and survival (ϕ) probabilities. A t subscript indicates a time-varying parameter; no subscript indicates a time-constant parameter. All other model parameters ($\psi^{NH}, \psi^{HN}, \delta, \pi$) were modelled as time-constant (see text). Lower DIC indicates more model support. Due to potential issues with estimation of model complexity (pD) used to calculate DIC for complex hierarchical models (Celeux *et al.* 2006), we also calculated penalized deviance based on the known number of parameters.

Model	Number of parameters (k)	Deviance	DIC	Deviance + 2k
ϕp	6	569.67	856.95	581.67
$\phi_t p$	9	570.95	860.39	588.95
ϕp_t	9	579.66	883.16	597.66
$\phi_t p_t$	11	578.25	971.40	602.25

and β^{age} and β^{nest} are the effects of female age and number of nestlings raised in a season, respectively. We also included a term to capture residual temporal variance (ε_t). Age and nestling covariates were scaled and centred for analysis.

The focus of this analysis was to investigate evidence for an effect of CBP on female survival and therefore we kept the parameterization of the other model parameters (ψ, p, δ, π) constant. Previous analyses indicated that the proportion of broods with CBP in the population did not vary significantly over time (Tucker *et al.* 2016), so we modelled the transitions between states (ψ) and the probability of being a host given that state is unknown at initial capture (π) as time-constant. We modelled the assignment probability (δ) as constant both between groups and across years, as field sampling effort and methods were constant across the study period and assignment should not be influenced by host/non-host status. We used uniform (0, 1) priors for transition probabilities (ψ), initial mixture probability (π), assignment probability (δ) and detection probability (p).

This model follows the typical assumptions of multi-state mark–recapture models (cf. Kéry & Schaub 2012): we assume no un-modelled heterogeneity in survival or recapture among individuals, no false positive detections and no loss of rings throughout the study. Additionally, we assume that the females first detected in an unknown state are a random mixture of hosts and non-hosts and that temporary emigration from the study area is random and therefore captured in the detection process. Posterior distributions of parameter estimates for the hierarchical model were sampled using JAGS and the jagsUI package for R (Plummer 2003, Kellner 2015, R Core Team 2016). Model code is available in the Supporting Information (Data S1). We ran four MCMC chains of 60 000 iterations each and discarded the first 10 000 as burn-in values. Convergence was assessed via visual inspection of traceplots and use of the Gelman–Rubin convergence diagnostic (considered converged if $R < 1.1$). Parameter estimates are presented as means and 95% credible intervals (CRI) of the posterior distributions.

Goodness-of-fit tests have not been developed for multi-event models (Pradel *et al.* 2005), so we assessed goodness-of-fit by pooling all detections, resulting in capture histories comprising solely detections and non-detections, regardless of state. These pooled data were used to assess goodness-of-fit for the Cormack–Jolly–Seber (CJS) model using the R2ucare package for R (Choquet *et al.* 2009). This is considered a conservative approach to assessing potential overdispersion in the data because it does not account for multiple states or state uncertainty (Lagrange *et al.* 2014, Souchay *et al.* 2014, Sanz-Aguilar *et al.* 2015) but can still identify potential violation of core model assumptions.

RESULTS

We included capture histories for 225 individual females in this analysis; the numbers of females detected each year in each state are provided in Table 2. Average age of breeding females in a given year was 3.4 years. The overall goodness-of-fit test for the pooled capture histories was not statistically significant ($\chi^2 = 10.56$, df = 6, $P = 0.103$), indicating adequate fit of the CJS model.

None of the covariates we included was a strong predictor of individual annual survival probability. Both female age and number of nestlings were unimportant (posterior mean: $\omega_{age} = 0.118$, $\omega_{nestlings} = 0.147$). Host state had the highest inclusion probability with posterior mean of $\omega_{host} = 0.318$, but we found no difference in survival probability between hosts and non-hosts (Fig. 1; $\phi^N = 0.473$, 95% CRI 0.297, 0.659; $\phi^H = 0.510$, 95% CRI 0.320, 0.745). Detection probability was high (Table 3; $p = 0.898$, 95% CRI 0.802, 0.964) but our limited ability to assign host/non-host state was reflected in the estimate of δ (0.517, 95% CRI 0.465, 0.570). Transition probabilities between states indicate a low probability of transitioning from a non-host to host ($\psi^{NH} = 0.165$, 95% CRI 0.080, 0.275) and therefore a higher probability of remaining as a non-host in the next year ($\psi^{NN} = 1 - \psi^{NH} = 0.835$). The estimates of transition probabilities from the host state also indicate a lower probability of transitioning to non-host than of remaining a host in the next year ($\psi^{HN} = 0.392$, 95% CRI 0.209, 0.593, $\psi^{HH} = 1 - \psi^{HN} = 0.608$). Our estimate of π indicates a probability of 0.726 (CRI 0.637, 0.807) that a breeding female first encountered in an unknown state is a non-host.

DISCUSSION

Apparent annual survival probability did not differ between host and non-host female Prothonotary Warblers, indicating that CBP does not impose a survival cost on females in this system. Our findings agree with both previous work in this system and other studies in finding little to no costs of CBP to adults, despite the energetic investment of parental care for altricial

Table 2. Numbers of host, non-host and unknown state Prothonotary Warbler females captured each year while breeding in 65 nestboxes near Richmond, VA, USA. These represent repeated observations of 225 individual females.

State	2009	2010	2011	2012	2013
Non-host	3	31	29	31	33
Host	1	8	12	17	15
Unknown	79	26	17	24	22
Total	83	65	58	72	70
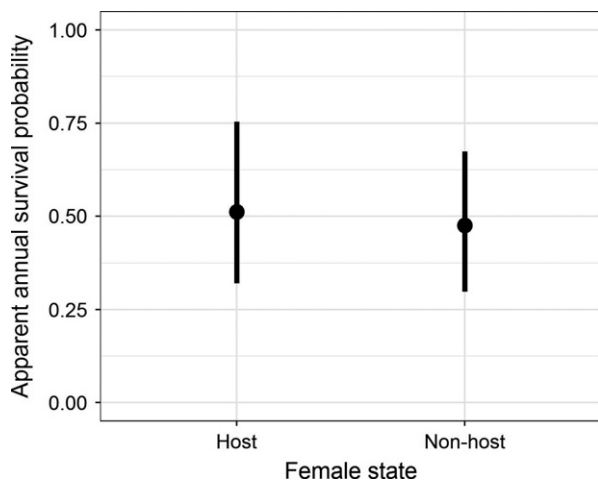
Figure 1. Estimated annual apparent survival probability for host and non-host female Prothonotary Warblers. Points represent posterior means and error bars are 95% credible intervals.

Table 3. Parameter estimates from a multi-event model used to estimate female apparent annual survival. The superscripts N and H represent state-specific parameter estimates for non-hosts and hosts, respectively. The parameter σ represents residual temporal variance around survival estimates on the linear scale. All other parameters are defined in the text.

Parameter	Posterior mean	Posterior sd	95% CRI
p	0.898	0.042	0.802, 0.964
δ	0.517	0.027	0.465, 0.570
π	0.726	0.043	0.637, 0.807
Ψ^{HN}	0.392	0.099	0.209, 0.593
Ψ^{NH}	0.165	0.051	0.080, 0.275
Φ^{N}	0.473	0.089	0.297, 0.659
Φ^{H}	0.510	0.105	0.320, 0.745
σ	0.665	0.428	0.244, 1.725

nestlings (Lyon & Eadie 2008). Studies investigating potential costs of CBP in precocial systems have largely found no evidence for an effect of CBP on host fitness (Lank *et al.* 1990, Rohwer & Heusmann 1991, Dugger & Blums 2001). Fewer studies have investigated costs to adults in altricial systems. Brown and Brown (1997) found that host American Cliff Swallows *Petrochelidon pyrrhonota* had decreased annual survival probabilities; however, they concluded that overall costs of CBP were minimal in that system as well. In general, there is little evidence for a direct cost of CBP to adults; if there is a cost of CBP to hosts, it seems to manifest in reduced hatching or survival probability of host offspring (Semel *et al.* 1988, Lyon 1993, Nielson *et al.* 2006).

Using a model with imperfect state assignment allowed us to include information about females with unknown host status by probabilistically assigning their true underlying state. The focus of this analysis was to evaluate the potential effect of CBP on host female survival probability, and therefore we deemed it outside the scope of this study to explore ecological drivers and patterns in other model parameters, including transition and assignment probabilities. Future work, with more years of data, could explore temporal variation and ecological drivers of transitions between host and non-host state as well as potential predictors of assignment probability (δ), including clutch size and the number of clutches laid in a season.

Estimates of transition probabilities between host and non-host states suggest that both hosts and non-hosts are more likely to remain in their current state than to transition in the next year. These results lend support to the hypothesis that observations of apparent CBP in this system may be driven by nestbox takeover during the laying period. Other studies with Wood Ducks *Aix sponsa* (Semel & Sherman 2001) and Common Eiders *Somateria mollissima* (Waldeck & Andersson 2006) have shown that CBP and nestbox takeover can be difficult to discriminate. We have observed complete burial of eggs under new nests in our study area (~5–7% of clutches) and it is possible that takeover events could result in the incorporation of the previous female's eggs into the new clutch, leading to apparent CBP. In this scenario, the apparent host female is the one that successfully evicts the previous female and takes over the nestbox. If a female's individual traits determine whether she takes over another nestbox, we would expect that behaviour to remain relatively fixed over time (Sih *et al.* 2004), resulting in repeated observations of a given female as an apparent host. Additionally, we would expect apparent hosts to be dominant, potentially higher quality individuals which could mitigate potential costs of raising unrelated nestlings. Our findings that females are more likely to remain in their current state than transition indicate that female personality and/or quality may play important roles in driving nestbox takeover and apparent CBP in this system.

Further study is needed to understand the behaviours that underlie our observations. Future studies using video observations and/or radio frequency identification (RFID) technology to monitor individual interactions at nestboxes during the egg-laying period as well as albumin fingerprinting of buried eggs to identify the female responsible for laying them will help to unravel whether CBP, nestbox takeover or both are occurring in this species. After such studies in Common Eiders, Andersson *et al.* (2015) recently described their behaviour as complex and involving a range of behaviours from parasitism and nest takeover to kin selection favouring acceptance of eggs from related individuals. A range of such behaviours may also be occurring in cavity-nesting songbirds with a high degree of parental care and is a rich area for future study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. R and JAGS model code used to fit multi-state model with imperfect state assignment.