

INDIRECT EFFECTS OF A COMPETITOR ON LIFE HISTORY AND REPRODUCTIVE
TRAITS IN A CAVITY NESTING BIRD

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requirements for the degree of Master of Science in Biology

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ABSTRACT

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Research on life history evolution in birds has revealed both direct and indirect effects of predation. Increased levels of nest predation favor reproductive behaviors that reduce the threat of predators on offspring or allow parents to bet hedge for future reproductive attempts. In this study, I investigate whether the presence of a competitor, the house wren (*Troglodytes aedon*), results in similar indirect effects on life history and reproductive behaviors of Carolina chickadees (*Poecile carolinensis*). House wrens compete for nesting cavities and will kill Carolina chickadee eggs and nestlings. I monitored nest boxes in Western North Carolina where exposure to house wrens varies. I surveyed house wren presence at active Carolina chickadee nests and measured clutch size and mass, incubation, provisioning rates, nestling growth rates, development, and fledging success of chickadees. House wren takeover accounted for 35% of nesting failures, more than any other cause of failure in our study. I found smaller clutch sizes in areas where house wrens were present. However, I did not detect any effects of house wren presence on chickadee egg size, incubation, provisioning, growth, or development. These results

suggest that house wren presence affects a narrow range of life history traits early in the nesting period, possibly because this is when house wrens are the biggest threat. Reducing clutch size may be a strategy used by Carolina chickadees to decrease reproductive investment in an environment where early nest failure is probable, allowing adults to reserve energy for survival to the next breeding season.

INTRODUCTION

One important question in the study of evolutionary biology concerns the factors that shape life history, the suite of evolved characteristics and strategies that directly influence an organism's fitness (Ricklefs and Wikelski 2002). In avian biology, early life history studies focused on the relative importance of food limitation and predation on clutch size variation within and among species (Moreau 1944, Lack 1947 and 1948, Skutch 1949). Mounting research has shown that nest predation is a primary cause of nest failure and thus a major factor influencing selection of traits and phenotypic plasticity (Lima 1987, Albano 1992, Martin 1995, Martin 2002). Recent work has focused on how threat of predation indirectly affects clutch size (Eggers et al. 2006), incubation behavior (Chalfoun and Martin 2010), parental provisioning (Pretelli et al. 2016), nestling growth and development (Hua et al. 2014) and reproductive success (Zanette et al. 2011). However, some avian populations experience interference competition for nest sites, not predation, as the primary cause of reproductive failure (Birch 1990, Kennedy and White 1996, Doherty and Grubb 2002, Deng and Zhang 2016). In this study, I address how presence of a competitor may also have indirect effects on life history.

Studies on nest competition and usurpation have focused on direct effects, such as impacts on reproductive success and population demography (Ingold 1989, Eguchi et al. 2013) or the ultimate causes of usurpation, such as habitat loss (Doherty and Grubb 2002, Kronland 2007). Some work has also investigated how competitors influence specific behaviors including nest location choice (Prokop 2004), nesting phenology (Ingold 1989, Wieb 2003), egg covering (White and Kennedy 1997), and mate feeding during incubation (Ghalambor and Martin 2000). But the primary focus of these studies has not been on indirect effects of competitor presence on reproductive behaviors over all stages of the breeding attempt. Competitors, like predators, can

be a threat to the nest; for example, house wrens are aggressive competitors for cavity space and will kill and expel eggs, and sometimes nestlings, in an established nest (Belles-Isles and Picman 1986, Quinn and Holroyd 1989, Finch 1990, Pribil and Picman 1991). Thus, competitor presence may have indirect effects on life history and reproductive traits. Unlike predators, competitors may pose a more limited or stage-specific threat to the nest. For example, while some predators are a threat to both the parents and the nest, interference competitors may only be a threat to the nest (Ghalambor and Martin 2000). Furthermore, competitors may only pose a threat during the egg stage and not the nestling stage (Eguchi et al. 2013).

Studies that focus on the indirect effects of predator presence may provide a guideline for predicting how nesting birds will respond to the presence of an interference competitor during different stages of the breeding attempt. Increased threat of predation can influence clutch size in a brood size dependent way: a smaller brood will not be as noisy or require as many feeding trips that might attract predators and laying fewer eggs decreases the egg laying period before incubation starts and thus decreases the length of time eggs are at risk (Skutch 1949). Life history theory also predicts that trade-offs between current and future reproduction should result in a strategy to reduce investment in the current, risky breeding attempt by reducing clutch size (Slagsvold 1982, 1984). Experimental evidence supports life history predictions and shows that increasing the threat of predation leads to smaller clutch sizes (Doligez and Clobert 2003, Eggers et al. 2006, Travers et al. 2010, Zann et al. 2011, Hua 2014). Species or populations that experience greater predation have also evolved smaller clutch sizes (Martin 1995 and 2002, Ferretti et al. 2005, Olsen et al. 2008). Additionally, if a smaller clutch size allows more breeding attempts, a bet-hedging strategy spreads out the risk of failure from predation over multiple nesting attempts and can maximize annual fecundity by increasing the probability that at least

one brood will fledge (Farnsworth and Simmons 2001, Olsen et al. 2008, Zanette et al. 2011). Interestingly, reduced investment in eggs may not be reflected in clutch size, but instead in reduced egg size and clutch mass (Fontaine and Martin 2006).

Nest predation has been invoked to explain variation in incubation behavior including incubation rhythm, the average length of time the incubating parent spends on or off the nest (termed on- and off- bouts, respectively), and incubation attentiveness, the total percentage of time the incubating parent spends on the nest. Species that experience increased predation have longer on and off bouts, presumably to decrease activity at the nest that may attract predators (Conway and Martin 2000). Experimental and correlational evidence from single species studies also show higher threat of predation is associated with longer off bouts (Ferretti et al. 2005, Massaro et al. 2008, Chalfoun and Martin 2010). Off bout length is important to consider because increased time off the nest can result in offspring costs such as decreased embryo mass, reduced residual yolk, and reduced growth efficiency (Olson et al. 2006). Increased threat of predation is associated with greater incubation attentiveness (Fontaine and Martin 2006, LaManna and Martin 2016) because increased parental effort in egg warming can speed up egg development and lead to earlier hatching and shorter incubation periods, and thus a decrease in time that eggs are exposed to predation (Martin et al. 2015, LaManna and Martin 2016).

Increased threat of predation is associated with a decrease in both total (Ghalambor and Martin 2001, Fontaine and Martin 2006, Eggers et al. 2008, Zanette et al. 2011, Sofaer et al. 2012, Yoon et al. 2016) and per nestling (Chalfoun and Martin 2010, Pretelli et. al. 2016) provisioning rates. As originally proposed by Skutch (1949), these patterns can be explained by an advantageous decrease in parental activity around the nest in the presence of visual predators that may be using this feeding activity as a cue to find the nest.

Both incubation behavior and provisioning behavior have consequences for how quickly offspring grow and develop, and thus how long they spend in each phase of development (i.e. incubation period and nestling period). With increased predation risk, it is advantageous to shorten these developmental periods when offspring are at risk. As mentioned above, some studies have found that greater nest attentiveness is associated with shorter incubation periods under high predation risk (Martin et al. 2015, LaManna and Martin 2016). Increased threat of predation is also associated with a shorter nestling stage both among species (Remes and Martin 2002) and within a species (Hua et al. 2014, Yoon et al. 2016).

Decreased nestling provisioning is associated with slower growth rates and smaller, poorer quality nestlings (Scheuerlein et al. 2006, Thomson et al. 2006, Zanette et al. 2011) which is significant because fledgling size upon leaving the nest is a predictor of survival and competitive ability (Coslovsky and Richner 2011). Interestingly, over evolutionary time, species or populations that evolved under high predation risk are expected to evolve the ability to develop faster (Remes and Martin 2002, Olsen et al. 2008), even with lower per nestling provisioning rates, which suggests an evolutionary strategy that prioritizes resource allocation to growth of traits that allow nestlings to leave the nest with possible tradeoffs elsewhere (Martin et al. 2011).

Changes in this suite of life history characteristics (clutch size, incubation behavior, feeding rate, and growth and development) in response to predator presence have fitness consequences, even in the absence of a direct predation event. For example, Zanette et al. (2011) reported a 40% decrease in success due to smaller clutch sizes, a smaller percentage of eggs hatching, and a smaller percentage of nestlings fledging, even though predation was excluded from the study system.

In this study, I hypothesize that presence of a nest site competitor will have indirect effects on the life history traits of a cavity nesting bird because, like predators, competitors are a threat to the nest. In Western North Carolina, Carolina chickadees (*Poecile carolinensis*) and house wrens (*Troglodytes aedon*), both obligate cavity nesters, overlap and compete for limited nest sites. Ballentine (unpublished data) has observed in a nest box study that the primary cause of nest failure for Carolina chickadees can be attributed to damage by house wrens. House wrens are aggressive interference competitors that compete for nesting space by destroying nests of other birds (Belles-Isles and Picman 1986, Quinn and Holroyd 1989, Finch 1990, Pribil and Picman 1991, Kattan 2016). They compete for multiple cavities each season because they build many “dummy” nests (cavities filled with sticks but without an actual nest cup and not actively used by the female) in addition to the primary nest (Alworth 1996, Dubois and Getty 2003). Multiple nests may be attractive to females; for example, male buff-breasted wrens build multiple “dormitory nests” that are used for roosting and may indicate parental quality of the male (Gill and Stuchbury 2005). However, this idea has little other empirical support and has been contested by many (Metz 1991, Dubois and Getty 2003). Another hypothesis posits that multiple dummy nests serve to reduce the efficiency of predator search images by increasing the ratio of empty nests to full nests (Finch 1990). Sometimes house wrens destroy a nest without building their own, which may reflect competition for food or competition for predator free space (Simons and Simons 1990) because decreased nest density has been shown to decrease predation (Martin and Martin 2001).

I monitored Carolina chickadee nests in boxes to compare life history traits of chickadees naturally exposed to house wren threat to those that are not. Specifically, I tested the following predictions:

- 1) Investment in clutch: Compared with those unexposed to house wrens, Carolina chickadees in the presence of house wrens have reduced clutch investment via
 - a. Reduced clutch size or
 - b. Reduced egg size
- 2) Incubation: Compared with those unexposed to house wrens, Carolina chickadees exposed to house wrens have
 - a. Increased length of incubation off bouts and
 - b. Increased incubation attentiveness
- 3) Provisioning: Carolina chickadees in the presence of house wrens reduce nestling provisioning trips compared to chickadees unexposed to house wrens.
- 4) Growth and Development: Compared with those unexposed to house wrens, Carolina chickadees in the presence of house wrens
 - a. Have shorter incubation and nestling stages
 - b. Have reduced growth rates
 - c. Produce smaller nestlings
- 5) Success: Carolina chickadees in the presence of house wrens will have reduced reproductive success, even in the absence of nest takeovers, compared to chickadees not exposed to house wrens.

METHODS

Species Descriptions

Carolina chickadees are small passerines (9-12 g) that inhabit coniferous, deciduous, and mixed forests, open woodlands, and increasingly suburban areas (Mostrum et al. 2002, Figure 1). Carolina chickadees are year-round residents in the southeastern United States ranging from north Florida to Pennsylvania and Ohio and west to Texas (Mostrum et al. 2002). Carolina chickadees are not threatened, but populations have been declining in recent decades (Mostrum et al. 2002, Sauer et al. 2014). Although these birds are omnivorous, their diet is mainly composed of arthropods gleaned from foliage, with the exception of over winter when up to half of the diet is plant matter (Mostrum et al. 2002). Carolina chickadees are cavity nesters and will readily use nest boxes (Mostrum et al. 2002). Carolina chickadees do not migrate and associate with flocks over the winter. Prior to nesting, dominant males establish nesting sites with females in the flock's territory, whereas subordinate males leave the territory and often nest in suboptimal sites or do not nest at all for the season (Mostrum et al. 2002). Chickadees form socially and sexually monogamous pairs that may last for more than one season (Mostrum et al. 2002). Nest construction begins approximately 20 days before the first egg is laid and is composed of a base of moss finished with a cup made from animal hair and plant fiber (Mostrum et al. 2002). Egg laying typically occurs daily in the morning and incubation by females begins after the last egg is laid (Mostrum et al. 2002). Females are the sole incubators of the eggs although both sexes provision the nestlings (Mostrum et al. 2002). Incubation lasts between 12 and 15 days and fledging occurs between 16 and 19 days after hatching (Mostrum et al. 2002). Predators of adult chickadees are mostly avian predators including sharp-shinned hawks (*Accipiter striatus*) and cooper's hawks (*Accipiter cooperii*). Nest predators include small

mammals such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), flying squirrels (*Glaucomys volans*) and cats (*Felis catus*) as well as rat snakes (*Pantherophis obsoletus*) (Mostrum et al. 2002). Mean lifetime is 1.1 years after the January post hatching (Mostrum et al. 2002).



Figure 1. Carolina chickadee *Poecile carolinensis* (Audubon.org)

House wrens are also small passerines (10-12 g) that occupy open woodlands and thrive in suburban and urban areas (Johnson 2014, Figure 2). These birds have an extensive geographic range; in North America, house wrens migrate from their breeding range in the United States and Canada to their winter range in the southern-most U.S. states and Mexico for the winter (Johnson 2014). House wren presence is expanding in North Carolina (Sauer et al. 2014) and house wrens nested in areas where they were previously undetected (personal observation). House wrens glean arthropods from shrubs and low bushes year-round (Johnson 2014). House wrens are also cavity nesters and nest in boxes as well as many other man-made structures (Johnson 2014). As discussed above, house wrens are aggressive nest site competitors and often claim multiple nesting sites.



Figure 2. House wren *Troglodytes aedon* (Audubon.org)

Study Areas

Nest boxes used for this study were dispersed across Macon and Jackson Counties, North Carolina. The Highlands Plateau Audubon Society established and have maintained 165 boxes for multiple years that are used by both Carolina chickadees and house wrens. I established fifty additional boxes during winter 2016-2017. Boxes were placed in habitats ranging from woodlands to suburban areas and ranged in elevation from 593 meters to 1261 meters above sea level. All boxes were built identically with external dimensions of 5.5 cm length x 5.5 cm width x 29 cm height. However, due to a previous study some boxes have entrance holes of 4.5 cm in diameter while others have holes of 3.5 cm in diameter. While some studies have found that hole size influences success (Morosinotto et al. 2013), I did not find an association between hole size and whether or not a nest fledged any young (chi square test of independence: $\chi^2=0$, $df=1$, $p=1$), so hole size was not taken into account in analyses. Spacing of the boxes varied across the study area. Due to a previous study, some boxes were set up in pairs, with a minimum distance of 15 meters between two boxes.

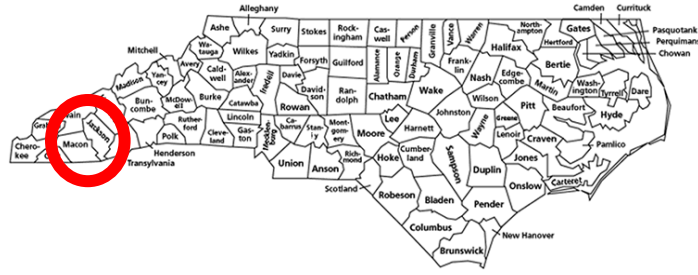


Figure 3. The research area included Macon County and Jackson County, neighboring counties in Western North Carolina where nest boxes were distributed.

House Wren Surveys

House wren surveys were conducted weekly starting in mid-March 2017, well before the predicted return of house wrens from wintering habitat. The first house wren was detected on April 14th. For each survey, I stood approximately five meters from the nest box to observe for visual and auditory cues of house wren presence for five minutes. All surveys were conducted between 7 am and noon when avian activity is highest and most obvious. I collected data on house wren presence as well as abundance and distance from the nest box. Surveys ended in early May after all Carolina chickadee nests were initiated, with the exception of two renesting attempts.

Data Collection in the Field

Starting at the end of February 2017 boxes were checked once a week, well before Carolina chickadee nest building began. Once I observed any moss in a box, I increased my observations of that box to two to three times a week to determine the first egg date. I assumed that chickadees laid one egg a day in the morning until the clutch was complete (Mostrum et al.

2002). Therefore, if I found a nest with more than one egg, I back counted to determine the day that the first egg was laid. It was noted whether or not eggs were buried in the cup prior to incubation (as noted in White and Kennedy 1997). Once clutches were complete, I measured clutch mass using an electronic scale and then calculated average egg mass per clutch.

Before clutch completion I installed two Thermochron iButtons (Maxim Integrated, San Jose, CA) in the nest box to determine onset of incubation and incubation rhythm as done by others (Cooper and Mills 2005, Hartman and Oring 2006). iButtons are an effective way to monitor nests full time without disturbing the nests and iButtons do not affect nest survival, hatching success, or abandonment (Hartman and Oring 2006). I placed one iButton in the moss just below the nest cup to measure approximate incubation temperatures and another in the corner of the nest box to measure ambient temperatures in the nest box. I set the iButtons to record temperature every five minutes and at this setting the iButtons had enough storage for six days of data. Therefore, I returned to the nests one to two times during incubation to download data and reset the iButtons. I removed iButtons after hatching.

To determine hatch date (day 0), I visited nests every day around the estimated hatch date by assuming incubation started after the last egg was laid and lasted 12 days (Mostrum et al. 2002). Throughout the nestling period I visited nests every 2-3 days and weighed nestlings together using an electronic scale to determine brood mass and average nestling mass per brood.

On the morning of day 7, 8, or 9 after hatching, I installed LawMate cameras (Annandale, VA) to capture nestling provisioning footage. The cameras were small with approximate dimensions of 3.5 cm length x 2 cm width x 0.5 cm height. I attached cameras to the top, inside of the nest box above the cup, with Velcro. Velcro strips were installed in the boxes before the nesting season to reduce disturbance and novel objects when installing the camera. Cameras

were connected by wire to a battery pack and memory storage device that were attached either underneath or behind the nest box. I left cameras in the boxes for a minimum of four hours before removing them.

On day 12 of the nestling stage I weighed nestlings individually and measured wing length and tail length (with a 15cm wing rule) and tarsus length (with SPI 150mm calipers). On this day, I also reinstalled iButtons using the same methods as mentioned above (one nest iButton and one ambient iButton) to determine fledge date.

Incubation and iButton Analysis

I analyzed iButton data with Raven Pro 1.4 (Cornell Lab of Ornithology). First, I downloaded iButton data and compiled Microsoft Excel (Redmond, WA) files with the following columns: Date, Time, Temperature from Nest iButton, Temperature from Ambient iButton. I then converted files using Rhythm (Cooper and Mills 2005), a program that selects off-bouts based on a set of parameters and allows Raven to display the incubation data as a time series with the selected off bouts (Cooper and Mills 2005). I used two sets of parameters in Rhythm, one with high sensitivity and one with low sensitivity. Because iButtons were often moved around in the nest by the female, some iButtons were buried deep in the cup while others were exposed at the surface. In order to detect temperature changes I used high sensitivity parameters with buried iButtons and low sensitivity parameters with exposed iButtons (Table S1). Some nests have missing data due to equipment failure or lost iButtons. I still included these nests in the analysis using the data I was able to collect.

Raven allowed me to look at incubation nest temperature data as a time series (Figure 4). The drop in the nest temperatures represented the beginning of an off-bout when the female left

the nest (Cooper and Mills 2005). I performed a visual inspection to ensure that all off bouts selected by Rhythm were true off bouts. For example, the program often selects the entire night time as an off-bout, so I manually deleted or fixed any off bouts that occurred before sunrise or after sunset in order to look at off bouts during the day only (Cooper and Mills 2005).

In order to calculate average off bout for a given nest, I combined all iButton data for the duration of the nest's incubation or the duration of available data and averaged all the off bouts. I always excluded the off bout directly following iButton installment because this may not be a true reflection of incubation rhythm but rather of response to human disturbance.

In order to calculate nest attentiveness, I first calculated the complete number of daytime minutes, defined as when the female left the nest for her first off bout until she returned from her last off bout. Next, I found the total number of minutes between those times that the female was on the nest (total on bout minutes = total daytime minutes – total off bout minutes). Attentiveness was recorded as the percentage of on bout minutes in total daytime minutes (attentiveness = total on bout minutes / total daytime minutes).

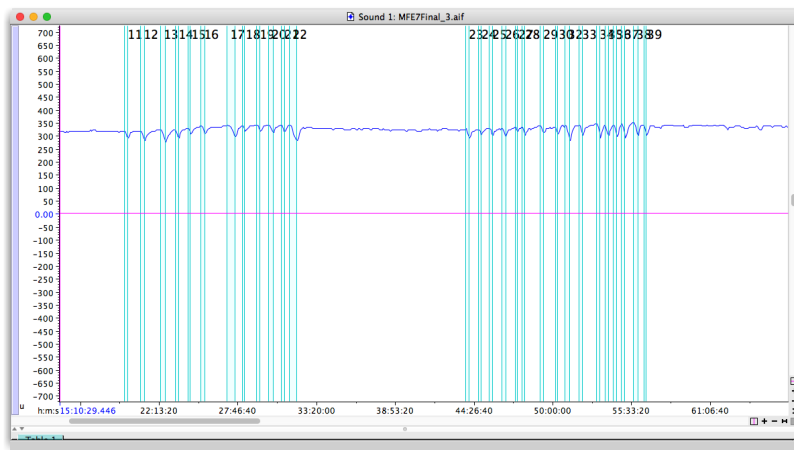


Figure 4. iButton Analysis. Screen shot from Raven showing incubation temperatures as a time series with selected off bouts in blue.

Provisioning and Video Analysis

I obtained adequate video data from 50 chickadee nests; some boxes were excluded because the video failed before enough footage was captured (memory filled up or camera fell down) or video footage was too dark to score. While some authors have shown that one hour of video is adequate to estimate feeding rate (Lendvai et al. 2015), I noticed enough variation in my data that I decided to look at four hours, which was the maximum I was able to capture for most boxes. Seven videos were scored for a six-hour segment (8:30 am to 2:30 pm) to determine if there was a pattern in provisioning rates in this time frame. There was no pattern in provisioning rates (Table A1) so all video footage used for analysis was a continuous four-hour segment that falls between 8:30 am and 2:30 pm on days 7-9 of the nestling stage. Videos that did not meet these criteria were excluded. I scored the videos for number of parental trips to the nest. It was not always possible to ensure that the parents were carrying food because of light or camera angle so I included all trips; it has been shown that parental visits are an adequate estimate of food delivery (McCarty 2002).

Growth Rate Calculation

I calculated three different measurements of growth rate. First, I calculated an overall linear growth rate from the first day of measurement (days 0-2 for most nests) up to day 10 (but may have been days 7, 8, or 9 for some nests). After day 10, growth begins to level off (visual inspection) and thus may bias the estimated linear rate for the period of fastest growth. I also calculated an early linear growth rate (the first day of measurement up to day 4 or 5) and a late linear growth rate (from day 5 or 6 up to day 8, 9, or 10).

Statistical Analysis

I performed statistical analysis in R version 3.3.2 (R Core Team 2016). The presence of house wrens was scored as a binary variable for all predictions. All predictions were analyzed with general linear models using the `lm()` function from base R unless otherwise noted. All data were checked for adherence to assumptions and transformed as needed. Clutch size and egg size models had house wren presence as the predictor variable and first egg date (as a Julian date value) and elevation as covariates. Both elevation (Badyaev 1997, Badyaev and Ghalambor 2001) and date of laying (Verhulst et al. 1995) influence life history strategies including clutch size and egg size. For the egg size model, clutch size was also included as a covariate. Mean offspring length and nest attentiveness models also had house wren presence as the predictor variable and first egg date and elevation as covariates. First egg date and elevation are included as covariates as proxies for temperature which can influence incubation behavior (Arida et al. 2010).

Both total and per nestling feeding rate models had house wren presence as the predictor variable and brood size as a covariate. Nestling age had no effect on total ($F_{1,47}=1.4658$, $p=0.2319$) or per nestling ($F_{1,47}=0.7292$, $p=0.3974$) provisioning rates and video start time had no effect on total ($F_{1,47}=1.49295$, $p=0.1712$) or per nestling ($F_{1,47}=1.1133$, $p=0.2967$) provisioning rates so these variables were not included in provisioning models. Both incubation stage length and nestling stage length were analyzed with house wren as the predictor variable and elevation and date as covariates (Badyaev 1997). Incubation stage length also included attentiveness as a covariate (Martin 2015, LaManna and Martin 2016). All three models of linear growth rate (full, early, and late) had house wren as the predictor variable. All linear rates were log transformed to better fit model assumptions.

All three body measurements of day 12 nestlings (mass, wing length, tail length) were correlated so I averaged each measurement for each box and analyzed them together using a MANOVA with the `manova()` function in base R with house wren presence as the predictor variable. I then analyzed each measurement separately with linear mixed models using function `lme()` from package `nlme` (Pinheiro et al. 2018). House wren presence was the predictor variable and box was a random factor.

Chi square tests of independence using the `chisq.test()` function were used to test the association between house wren presence and egg burying as well as house wren presence and nest abandonment. Nest success was first analyzed as a binary measure (success means at least one nestling fledged) in relation to house wren presence with a chi square test of independence. Next, only data from nests that had any eggs were analyzed for hatch success with house wren as the predictor variable and average off bout and attentiveness as covariates. Hatch percent was arcsine transformed to better meet assumptions. Finally, only data from those nests that fledged any young were considered in order to test only for indirect effects on success (i.e. it excluded all nests that were abandoned or destroyed by house wrens). This success model included number of fledglings with house wren presence as the predictor variable.

RESULTS

Nesting Attempts

I monitored 108 nesting attempts throughout the breeding season. An attempt was defined as a nest built with a cup (i.e. abandonment before completing the nest was not considered). Fifty-three nests were successful, defined as at least one nestling fledging from the nest. The other 55 attempts were failures, although 5-6 pairs went on to renest (one may have been a second brood). Nineteen nest failures were due to house wren destruction (18 during the laying or incubation stages and 1 during the nestling stage), 18 failures were due to abandonments (2 before egg laying, 12 during laying or incubation stages, and 4 during nestling stage), 14 failures were due to predation (5 during laying or incubation stages and 9 during the nestling stage), and 4 failures were due to other causes including bears (2), humans (1) and 1 eastern bluebird (*Sialia sialis*) takeover before eggs were laid.

Clutch Investment

Chickadees in the presence of house wrens laid smaller clutches ($\bar{x} = 5.00$ eggs \pm 0.15 SE, n=28) than chickadees unexposed to house wrens ($\bar{x} = 5.47$ eggs \pm 0.12, n= 59, $F_{1,82}=6.37$, $p=0.0136$, Figure 5, Table B1).



Figure 5. House wren presence is associated with a smaller clutch sizes in Carolina chickadees (n=87, $F_{1,82}=6.37$, $p=0.0136$). Data are presented as mean \pm SE.

Egg size did not differ between nests exposed to house wrens ($\bar{x} = 1.02\text{g} \pm 0.02$, $n = 28$) and those unexposed house wrens ($\bar{x} = 1.02\text{g} \pm 0.01$, $n = 58$, $F_{1,80}=2.37$, $p=0.1278$, Figure 6, Table B2). There was an effect of clutch size ($F_{1,80}=11.97$, $p < 0.01$) and first egg date ($F_{1,80}=4.80$, $p = 0.0313$) on egg size. However, the relationship was not strong with either clutch size ($r^2 = .08641$) or first egg date ($r^2 = .0373$).

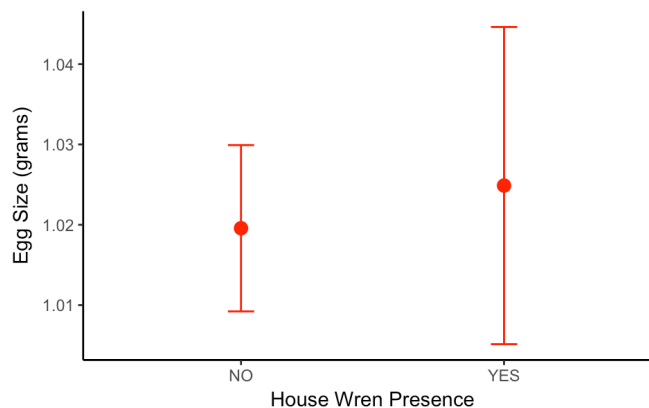


Figure 6. House wren presence is not associated with mean egg size (n=86, $F_{1,80}=2.37$, $p=0.1278$). Data are presented as mean \pm SE.

Egg burying behavior did not differ between chickadees exposed to house wrens and those not exposed to house wrens ($\chi^2=0.4878$, $df = 1$, $p =0.4849$). In the presence of house wrens 11 clutches were buried and 12 were not, while in the absence of house wrens 27 clutches were buried while 18 were not.

Incubation Rhythm

Mean off-bout length did not differ between nests in the presence of house wrens ($\bar{x} = 19.06$ minutes ± 1.56 , $n=27$) and nests unexposed to house wrens ($\bar{x} = 17.64$ minutes ± 0.69 , $n=56$, $F_{1,77}= 1.47$, $p = 0.2293$, Figure 7, Table B3).

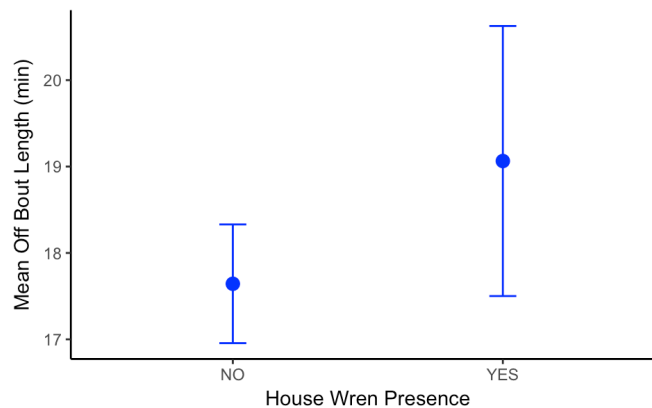


Figure 7. House wren presence is not associated with mean off-bout length ($n=83$, $F_{1,77}=1.47$, $p=0.2293$). Data are presented as mean \pm SE.

Incubation attentiveness also did not differ between nests in the presence of house wrens ($\bar{x} = 61.50\% \pm 1.65$, $n=27$) and nests unexposed to house wrens ($\bar{x} = 63.88\% \pm 0.73$, $n=56$, $F_{1,77}= 1.77$, $p = 0.1868$, Figure 8, Table B4).

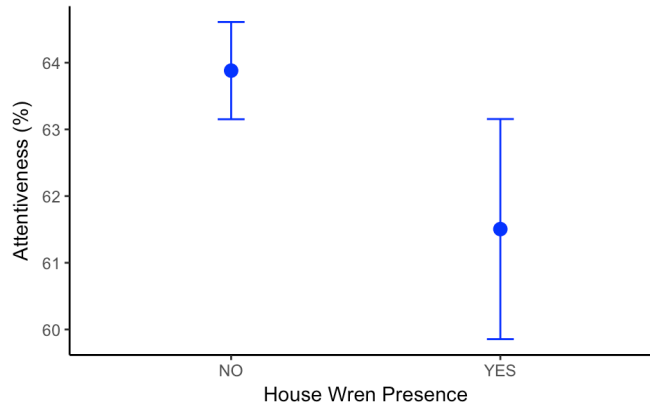


Figure 8. House wren presence is not associated with incubation attentiveness ($n=83$, $F_{1,77}=1.77$, $p=0.1868$). Data are presented as mean \pm SE.

For both average off-bout length and attentiveness, chickadees in the presence of house wrens showed much more variation than those that were unexposed (Figure 7 and Figure 8). Chickadees in the presence of house wrens showed larger standard deviation in average off bout length (8.12 versus 5.14) and attentiveness (8.57 versus 5.46). The difference in variance of attentiveness between chickadees exposed and unexposed to house wrens was significant (Levene's test: $F_{1,81}= 4.87$, $p=0.0302$).

Provisioning Behavior

There was no difference in total provisioning rate between nests in the presence of house wrens ($\bar{x} = 14.02$ trips/hour \pm 1.01, $n=14$) and nests not in the presence of house wrens ($\bar{x} = 14.94$ trips/hour \pm 1.14, $n=36$, $F_{1,47}=0.20$, $p=0.6548$, Figure 9a, Table B5). Similarly, the per nestling feeding rate did not differ between nests in the presence of house wrens ($\bar{x} = 4.20$ trips/nestling/hour \pm 0.39, $n = 14$) and nests not in the presence of house wrens ($\bar{x} = 3.55$ trips/nestling/hour \pm 0.23, $n = 36$, $F_{1,47}= 1.09$, $p = 0.3029$, Figure 9b, Table B6). There was an

effect of nestling number on both total provisioning ($F_{1,47}= 31.23, p < .001, r^2=.3994$, Figure 10a) and on per nestling provisioning ($F_{1,47}= 6.54, p = .0138, r^2=.1404$, Figure 10b).

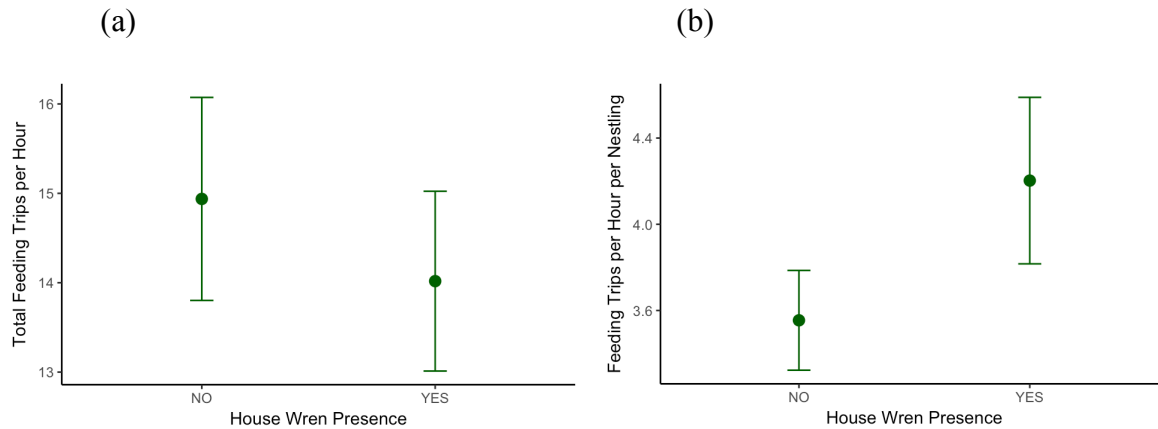


Figure 9. House wren presence is not associated with (a) total feeding trips per hour ($n=50, F_{1,47}=0.20, p=0.6548$) or (b) per nestling feeding trips per hour ($n=50, F_{1,47}= 1.09, p = 0.3029$). Data is presented as mean \pm SE.

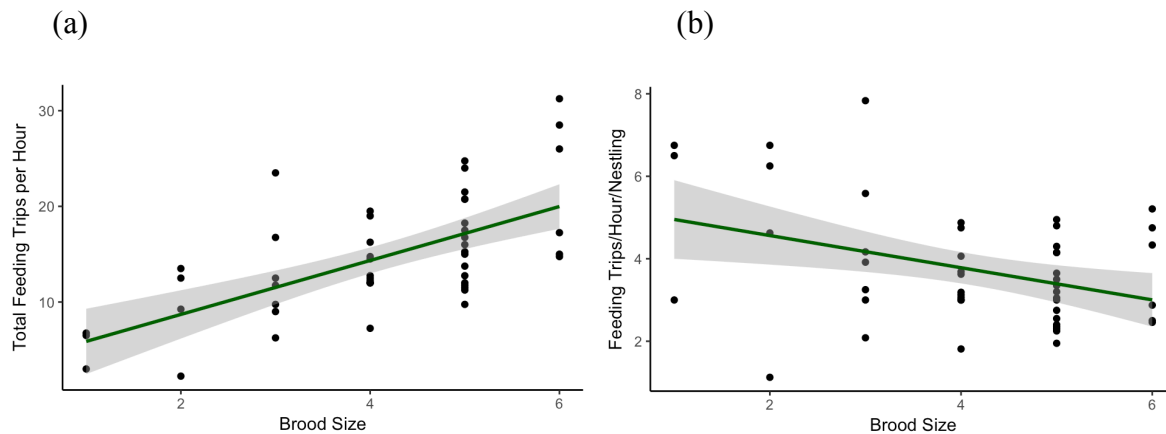


Figure 10. (a) Total feeding trips per hour is associated with brood size ($r^2=0.3994$). (b) Per nestling feeding trips per hour is associated with brood size ($r^2=0.1404$). Graphs show regression lines \pm 95% confidence intervals.

Stage Lengths

The length of the incubation stage did not differ between nests in the presence of house wrens ($\bar{x} = 13.69$ days \pm 0.31, $n = 13$) and nests not in the presence of house wrens ($\bar{x} = 13.33$ days \pm 0.18, $n=40$, $F_{1,44}=0.25$, $p = 0.6194$, Figure 11a, Table B7). Similarly, the length of the nestling stage did not differ between nests in the presence of house wrens ($\bar{x} = 16.89$ days \pm 0.42, $n = 9$) and nests not in the presence of house wrens ($\bar{x} = 16.96$ days \pm 0.21, $n=35$, $F_{1,40} = 0.19$, $p = 0.664$, Figure 11b, Table B8).

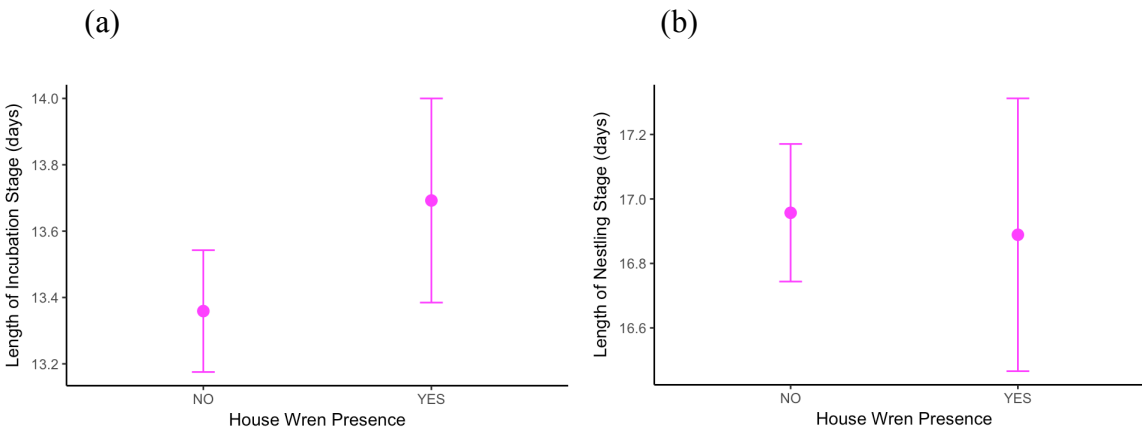


Figure 11. House wren presence is not associated with (a) length of incubation stage ($n=53$, $F_{1,44}=0.25$, $p = 0.6194$) or (b) or length of nestling stage ($n=44$, $F_{1,40} = 0.19$, $p = 0.664$). Data are presented as mean \pm SE.

Growth Rates

The overall growth rates of chickadee nestlings in the presence of house wrens ($\bar{x} = 0.79$ g/day \pm 0.03, $n=17$) did not differ from those unexposed to house wrens ($\bar{x} = 0.78$ g/day \pm 0.02, $n=49$, $F_{1,64} = 0.03$, $p= 0.8636$, Figure 12a, Table B9). Early growth rates did not differ between nests in the presence of house wrens ($\bar{x} = 0.67$ g/day \pm 0.05, $n=15$) and nests unexposed to house wrens ($\bar{x} = 0.71 \pm$ 0.03, $n=48$, $F_{1,61} = 1.13$, $p= 0.2928$, Figure 12b, Table B10). Finally, late

growth rates also did not differ between nests in the presence of house wrens ($\bar{x} = 0.80 \pm 0.05$, $n=17$) and nests not in the presence of house wrens ($\bar{x} = 0.79 \pm 0.03$, $n=48$, $F_{1,63} = 0.03$, $p=0.8628$, Figure 12c, Table B11).

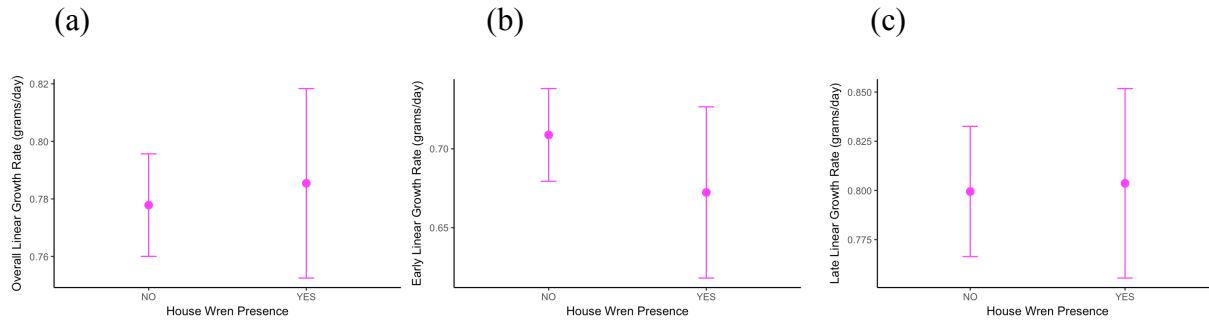


Figure 12. House wren presence is not associated with three measures of growth rate: (a) Overall growth rate ($n=66$, $F_{1,64} = 0.03$, $p = 0.8636$); (b) Early growth rate ($n=49$, $F_{1,61} = 1.13$, $p = 0.2928$); (c) Late growth rate ($n=65$, $F_{1,63} = 0.03$, $p = 0.8628$). Data are presented as mean \pm SE.

Nestling Measurements

There was no difference in a multivariate measure of average body size in nestlings from nests exposed house wrens and those not exposed to house wrens ($n=55$, $F_{1,38}=0.59$, $p=.6222$, Table B12). Day 12 mass of nestlings did not differ between nestlings in the presence of house wrens ($\bar{x} = 8.53\text{g} \pm 0.16$, $n=44$) and nestlings not in the presence of house wrens ($\bar{x} = 8.99\text{ g} \pm 0.06$, $n=164$, $\chi^2=1.39$, $df=1$, $p=0.238$, Figure 13a, Table B13). Wing length of nestlings on day 12 was similar between nestlings in the presence of house wrens ($\bar{x} = 32.74\text{ mm} \pm 0.49$, $n=44$) and nestlings not in the presence of house wrens ($\bar{x} = 34.69\text{ mm} \pm 0.26$, $n=164$, $\chi^2=3.35$, $df=1$, $p = 0.0671$, Figure 13b, Table B14). Finally, day 12 tail length did not differ between nestlings in

the presence of house wrens ($\bar{x} = 12.09 \text{ mm} \pm 0.49$, $n=35$) and nestlings not in the presence of house wrens ($\bar{x} = 14.29 \text{ mm} \pm 0.29$, $n=116$, $\chi^2=2.42$, $df=1$, $p = 0.1201$, Figure 13c, Table B15).

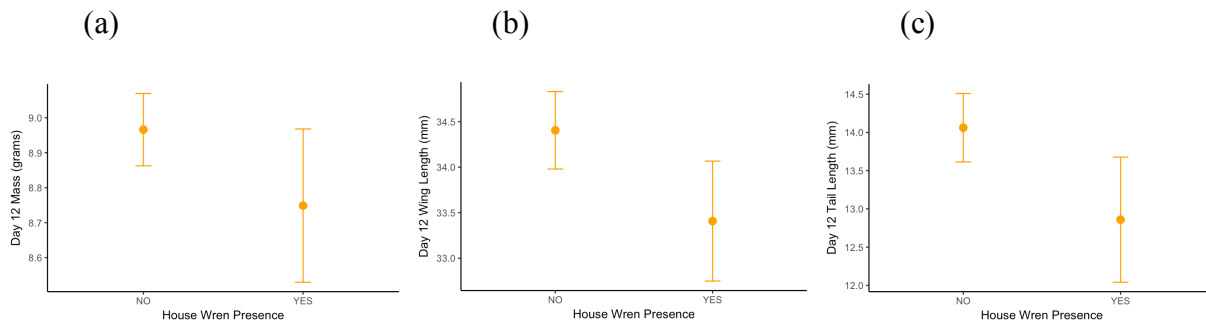


Figure 13. House wren presence is not associated with three measures of nestling size on day 12: (a) mass ($n=208$, $\chi^2=1.39$, $df=1$, $p=0.238$); (b) wing length ($n=208$, $\chi^2=3.35$, $df=1$, $p = 0.671$); (c) tail length ($n=151$, $\chi^2=2.42$, $df=1$, $p = 0.1201$). Data are presented as mean \pm SE.

Success

For overall chickadee success, I found that whether or not a nest was successful was dependent on house wren presence ($\chi^2=7.62$, $df = 1$, $p = 0.0058$). However, I did not detect an indirect effect of house wren presence on fledgling success; there was no difference in number of fledglings from successful nests between nests in the presence of house wrens ($\bar{x} = 3.36$ fledglings ± 0.47 , $n=11$) and those not in the presence of house wrens ($\bar{x} = 4.05$ fledglings ± 0.22 , $n= 39$, $F_{1,48}= 2.02$, $p = 0.1618$, Figure 14, Table B16). Percentage of the clutch that hatched did not differ between nests in the presence of house wrens ($\bar{x} =70.42 \pm 6.39$, $n=16$) and those not unexposed to house wrens ($\bar{x} = 79.35 \pm 2.99$, $n=48$, $F_{1,57}= 1.09$, $p = 0.3002$, Figure 15, Table B17). House wren presence was not a significant predictor of nest abandonment ($\chi^2=0.36$, $df=1$, $p=0.551$).

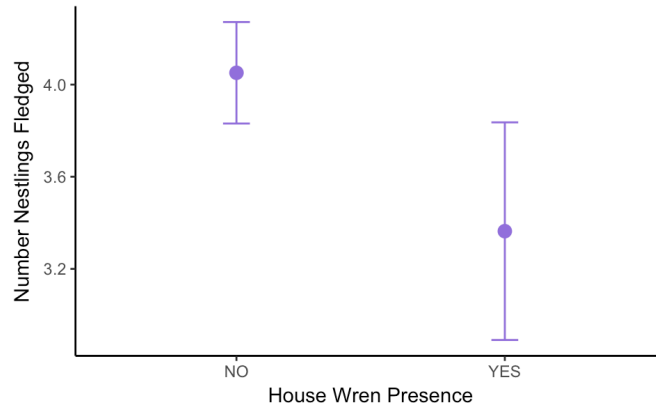


Figure 14. House wren presence is not associated with mean number of fledglings ($n=50$, $F_{1,48}=2.02$, $p=0.1618$). Data are presented as mean \pm SE.

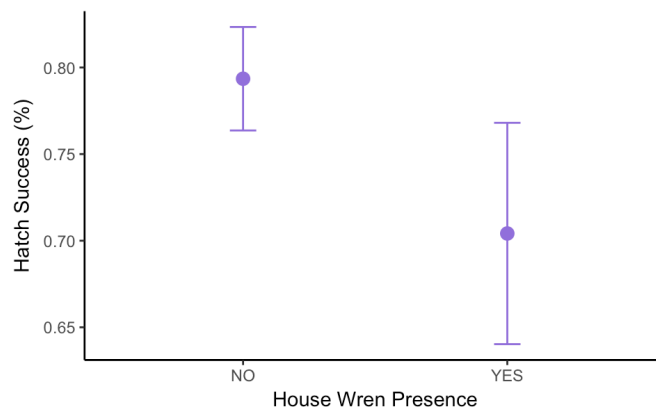


Figure 15. House wren presence is not associated with percent hatch success ($F_{1,57}=1.09$, $p=0.3002$). Data are presented as mean \pm SE.

DISCUSSION

In this study, I investigated whether the presence of house wrens in a naturally varied environment in Western North Carolina had any indirect effects on life history characteristics of Carolina chickadees in nest boxes. I found that house wrens were the primary cause of nest failure for chickadees in this study system and that beyond direct takeovers, presence of house wrens is associated with reduced chickadee investment early in the breeding attempt.

Clutch Size

I found evidence that house wren presence is associated with reduced clutch investment for chickadees via reduced clutch size. While other studies have found that some birds compensate for smaller clutch sizes with larger eggs (Zanette et al. 2011), I did not find a difference in egg sizes, which implies that females in the presence of house wrens are investing fewer resources into producing eggs. Reducing clutch size in a high-risk nesting attempt, for example, in the presence of predators, is well established in the literature (Martin 1995 and 2002, Ferretti et al. 2005, Eggers et al. 2006, Olsen et al. 2008, Zanette et al. 2011, Hua 2014). Reasons cited for clutch reduction include bet hedging to distribute the risk among multiple nesting attempts or a trade-off between current reproduction and future reproduction. Because Carolina chickadees are single brooded in this study area and rarely renest, it is likely that by reducing clutch sizes chickadees are trading off for increased adult survival to the next breeding season. Similarly, Julliard et al. (1997) found clutch size reduction in great tits after exposure to predators and because of the long-term nature of the study, researchers were able to track individual adult survival and found evidence that larger clutch sizes are associated with decreased adult survival. The mechanisms for this cost of reproduction are becoming better

understood; for example, reproductive effort can accelerate senescence via oxidative stress (Wiersma et al. 2004), hormonal regulation, or immune function (Harshman and Zera 2006). Increased adult survival may mean that chickadees have higher reproductive success over their lifetimes even with reduced clutches in the current attempt.

Incubation

I was surprised to find that average off bout length (average length of time the female is off the nest when she leaves, Figure 7) was not associated with house wren presence because the incubation stage is when the nests were most vulnerable to house wren destruction (18 of the 19 failures due to house wrens occurred during laying or incubation). Association between bout lengths and threat to the eggs due to predator presence has mixed findings in the literature; some studies have found increased incubation bout length (Conway and Martin 2000, Ferretti et al. 2005, Massaro et al. 2008, Chalfoun and Martin 2010), while others have found no change in bout length (Morosinotto et al. 2013, Basso and Richner 2015). Other studies with contrasting results have shown longer on bouts but no change in off bouts (Pretelli et al. 2016) or shorter on bouts and longer off bouts (Zanette et al. 2001). These inconsistencies may be due to differences in experimental design, such as amount of observation time or type of predator cue presented in an experiment (Zanette et al. 2001, Morosinotto 2013).

Predation studies operate on the assumption that changes in bout length occur under increased threat of predation because longer bouts decrease activity around the nest which reduces attracting predator attention (Ferretti et al. 2005, Massaro et al. 2008, Chalfoun and Martin 2010). Because house wrens are nest site competitors and not predators, they may not be using activity as a cue to find nests but looking for cavity holes, or other indicators of good

nesting sites. Thus, I may not have found an association between house wren presence and average off bout length because altering incubation rhythm is not an effective strategy under house wren threat.

Similarly, I did not find that house wren presence was associated with incubation attentiveness (the total amount of time the female is on the nest during the incubation period, Figure 8). Other studies have found that predation risk does not influence attentiveness (Morosinotto 2013, Basso and Richner 2015, Chalfoun and Martin 2010) but that other factors, such as temperature are also important predictors (Conway and Martin 2000, Ardia 2010).

The high variance in incubation behaviors in chickadees exposed to house wrens may be evidence that some, but not all, chickadees are responding to the threat of house wrens. Many studies have found that changes in reproductive behavior in response to predation threat occur in a later brood or later season, especially in an unpredictable environment (Juliard et al. 1997, Chalfoun and Martin 2010). It is possible that some individual chickadees or populations of chickadees do not have previous exposure to house wrens because house wren numbers are increasing in North Carolina (Sauer et al. 2014) and during this study house wrens were observed in areas not previously seen (personal observation). Thus, it may be that individuals will change behavior to respond to house wren threat next season or that selection for changes in incubation behavior is still in the process.

If it is true that some but not all individuals are responding to the threat of house wren presence, then there is support that some chickadees are lengthening their off bouts as predicted; average off bout length in the presence of house wrens is 19.06 min versus 17.64 min. In contrast to what I predicted, there may be support that in the presence of house wrens some chickadees are decreasing their attentiveness; average attentiveness in the presence of house wrens is

61.50% versus 63.88%. This can happen if off bout lengths are increased without also increasing on bouts lengths. Some studies have found support for this behavior in the presence of predators (Ibanez-Alama and Soler 2012). These two measurements taken together (longer off bouts and lower attentiveness) show decreased parental investment in incubation which is predicted by life history theory: parents should invest less in a risky nesting attempt and invest more in themselves (i.e. more time off the nest foraging).

Provisioning

Variance in both total number of trips and per nestling trips was mostly explained by brood size (Figure 10) which shows that although parents with larger broods make more total trips to the nest, it does not quite make up for the extra mouths to feed. Provisioning data were collected on days 7-9 of the nestling period and it is likely that house wrens are not a threat to chickadees at this point in the nestling stage (Belles-Isles and Picman 1986) Therefore, there may not be pressure for parents to reduce activity around the nest, especially if house wrens do use activity as a cue.

Other factors that may help to explain variation in provisioning rate include food abundance (Eggers 2008) and size and quality of food (Pretelli et al. 2016). Predation threat, which was the largest cause of failure for nests in the nestling stage, influences provisioning rate as well (Fontaine and Martin 2006, Sofaer et al. 2012, Yoon et al. 2016). Predation threat can also influence specific patterns of nest visitation throughout the day (Eggers et al. 2004) as well as how parents provision food among nestlings within the brood (Moks and Tilgar 2014).

Growth and Development

Incubation stage length was not associated with house wren presence (Figure 13a) which is consistent with incubation attentiveness not being predicted by house wren presence. There was very little variation in incubation stage lengths, so it is possible that this trait is constrained and not easily shortened because of development needs. Similarly, nestling stage length was not associated with house wren presence (Figure 13b), possibly because house wrens are not a threat to older nestlings, so there is no pressure for nestlings to leave the nest early. This is in contrast to predation studies which have found shortened nestling periods in the presence of predators which are a threat to nestlings of all ages (Hua et al. 2014, Yoon et al. 2016), so it is advantageous to shorten the risky nestling stage and leave the nest earlier.

Growth rates were not associated with house wren presence (Figure 11), which is consistent with no association between house wren presence and provisioning rates. Although not significant, day 12 measurements showed that nestlings in the presence of house wrens were on average slightly smaller than others (Figure 12). It has been found that there are factors besides provisioning rates that influence mass at time of fledging, such as stress during laying (Coslovsky and Richner 2011). Thus, it is possible that the trend observed in day 12 nestling measurements may be due to the effects of stress on the females who laid eggs in the presence of house wrens. I was unable to account for amount or quality of food which may also explain the trend in size differences.

Predation studies have found that increased threat of predation may lead to increased investment in wings at the cost of mass upon leaving the nest to enhance ability to escape predation as fledglings (Coslovski and Heinz 2011, LaManna and Martin 2016). However, unlike predators, house wrens are not a threat to new fledglings so there is no selective pressure

to develop enhanced flight ability at costs elsewhere. Accordingly, I found that all body measurements were smaller on average (although not significantly) in the presence of house wrens and did not find evidence for increased allocation to wing growth for chickadees in the presence of house wrens.

Success

House wrens had a significant direct effect on chickadee success; chickadees were more likely to be successful when not in the presence of house wrens. However, I was not able to detect an indirect effect of house wren presence on success in terms of number fledged (Figure 14), despite differences in clutch size. This inconsistency is not explained by a higher percentage of eggs hatched (Figure 15). It is possible that I was unable to detect a pattern due to a small sample size; only 11 successful nests remained in the presence of house wrens at the end of the season. There is a trend because chickadees in the presence of house wrens fledged fewer young on average than those not in the presence of house wrens (3.36 fledglings versus 4.05 fledglings).

Another explanation may be that those nests with the smallest clutch sizes in the presence of house wrens were the ones that failed. An analysis of only those nests that were successful (fledged at least one nestling) showed no significant difference in clutch size between those exposed to house wrens ($\bar{x} = 5.09 \pm 0.16$, $n=11$) and those not ($\bar{x} = 5.59 \pm 0.14$, $n=39$, $F_{1,45} = 2.9839$, $p=0.091$, Table B18). Failure to detect a pattern in clutch size may again be due to small sample sizes. Alternatively, this may suggest that female chickadees are better able to predict house wren threat and adjust clutch sizes than I was with my survey. Or, it may show that poorer quality females who are laying smaller clutches are the ones nesting in areas with the highest house wren exposure.

Conclusions

My study suggests that house wren presence has an indirect effect on Carolina chickadee life history, although this effect may be constrained to early in the breeding attempt. I found evidence for indirect effects on clutch investment and possibly incubation investment, but parental activity and investment during the nestling stage was unaffected by house wren presence. Unlike nest predators that are a threat to nests throughout the breeding attempt and into the post-fledging stage, the threat of house wrens wanes as nestlings grow bigger. Thus, this study is an interesting extension to the question of how parents respond to threats to the nest because house wrens are a stage-specific threat. This study suggests that parents can respond to stage-specific threats accordingly and do not alter their strategy throughout the entire breeding attempt.

Interesting future research in this study system would be to track individuals over multiple seasons to see if individual behavior changes depending on exposure to house wren threat. Additionally, comparing populations of chickadees that have been exposed to house wren threat for many generations to those that have not may reveal if selection has acted on any life history traits. Larger sample sizes would also help answer whether house wren presence has indirect effects on reproductive success beyond clutch size, which I was not able to detect. Additionally, manipulative experiments (with playbacks or house wren mounts) at different stages during the breeding attempt could show more precisely how and when parents are able to adjust their reproductive investment and strategies.

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APPENDIX A

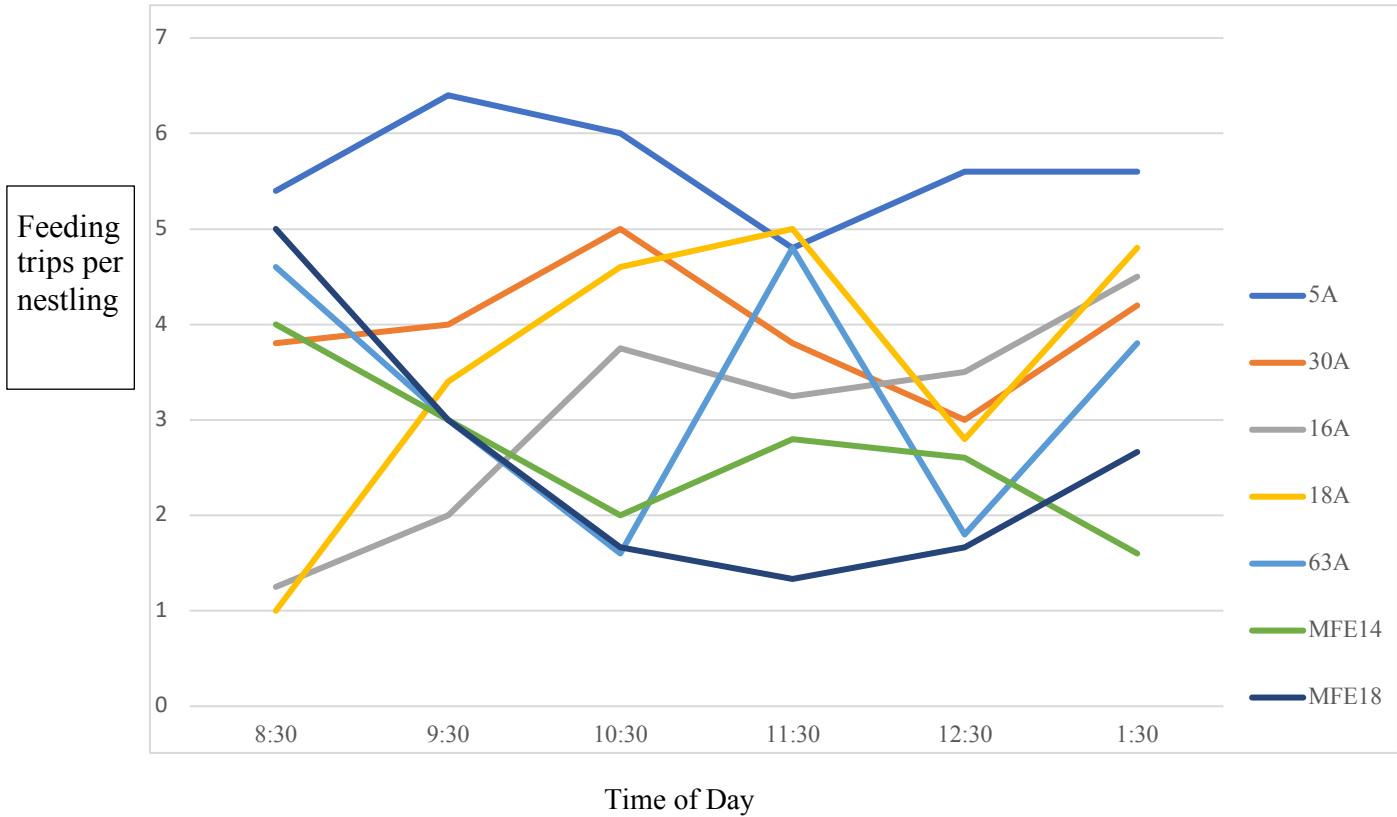


Figure A1. Preliminary video analysis. First seven videos scored for per nestling feeding trips over six hours. There was no apparent provisioning pattern throughout the time period of 8:30 am - 2:30 pm.

Table A1. iButton Parameters. High sensitivity and low sensitivity iButton parameters used in Rhythm for off bout selection. High sensitivity was used if iButtons were buried deep in the nest while low sensitivity was used when iButtons were exposed at the surface of the nest.

Parameter	High Sensitivity	Low Sensitivity
Minimum off bout duration	5 min	5 min
Minimum off bout depth	1°	2°
Minimum initial slope (cooling)	.05° min ⁻¹	.1° min ⁻¹
Timeout (cooling)	30 min	30 min
Minimum initial slope (warming)	.01° min ⁻¹	.05° min ⁻¹
Timeout (warming)	30 min	30 min
Maximum final slope (warming)	.005° min ⁻¹	.005° min ⁻¹

APPENDIX B

Table B1. Linear model results for clutch size

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	5.1933	1	6.3665	0.0136
Julian Date	1.1365	1	1.3932	0.2413
Elevation	0.6887	1	0.8442	0.3609
Residuals	66.8898	82		

Table B2. Linear model results for egg size

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.0156	1	2.3684	0.1278
Clutch Size	0.0789	1	11.9683	0.0009
Julian Date	0.0317	1	4.8042	0.0313
Elevation	0.0204	1	3.0934	0.0824
Residuals	0.5276	80		

Table B3. Linear model results for mean off bout length

Variable	Sum Sq	df	F value	Pr(<F)
HOWR Presence	57.1062	1	1.4686	0.2293
Julian Date	116.814	1	3.0041	0.0871
Elevation	35.7741	1	0.92	0.3405
Residuals	2994.17	77		

Table B4. Linear model results for incubation attentiveness

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.008	1	1.7738	0.1868
Julian Date	0.0014	1	0.3161	0.5756
Elevation	0.0019	1	0.424	0.5169
Residuals	0.3457	77		

Table B5. Linear model results for total provisioning per hour

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	4.6819	1	0.2025	0.6548
Nestling Number	722.111	1	31.2266	<0.0001
Residuals	1086.87	47		

Table B6. Linear model results for per nestling provisioning per hour

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	1.9183	1	1.0852	0.3029
Nestling Number	11.5654	1	6.5427	0.0138
Residuals	83.081	47		

Table B7. Linear model results for incubation stage length

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.3181	1	0.2503	0.6194
Elevation	0.2821	1	0.222	0.6399
Attentiveness	1.1822	1	0.9302	0.3401
Julian Date	1.0058	1	0.7914	0.3785
Residuals	55.9192	44		

Table B8. Linear model results for nestling stage length

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.2913	1	0.1916	0.664
Julian Date	2.0929	1	1.3763	0.2477
Elevation	3.179	1	2.0906	0.156
Residuals	60.826	40		

Table B9. Linear model results for overall growth rate

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.0008	1	0.0297	0.8636
Residuals	1.8843	64		

Table B10. Linear model results for early growth rate

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.2106	1	1.1261	0.2928
Residuals	11.4062	61		

Table B11. Linear model results for late growth rate

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.0026	1	0.0301	0.8628
Residuals	5.4371	63		

Table B12. MANOVA results for day 12 nestling measurements (mass, wing length, tail length)

Variable	Df	Pillai	Approx. F num	df	Den Df	Pr(>F)
HOWR Presence	1	0.047261	0.59526	3	36	0.6222
Residuals	38					

Table B13. Mixed linear effects model results for day 12 body mass

	Chisq	df	Pr>(chisq)
HOWR	1.3927	1	0.238

Table B14. Mixed linear effects model results for day 12 wing length

	Chisq	df	Pr>(chisq)
HOWR	3.3532	1	0.0671

Table B15. Mixed linear effects model results for day 12 tail length

	Chisq	df	Pr>(chisq)
HOWR	2.4166	1	0.1201

Table B16. Linear model results for success in terms of number of fledglings

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	4.0571	1	2.0192	0.1618
Residuals	96.4429	48		

Table B17. Model results for hatch success measured in percent of eggs hatched

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	0.2061	1	1.0929	0.3002
Attentiveness	0.2623	1	1.3906	0.2432
Off Bout Length	0.0019	1	0.0101	0.9201
Residuals	10.7498	57		

Table B18. Linear model results for clutch size only from successful nests

Variable	Sum Sq	df	F value	Pr(>F)
HOWR Presence	1.8969	1	2.9839	0.091
Elevation	1.0939	1	1.7208	0.1962
First Egg Date	2.6889	1	4.2298	0.0455
Residuals	28.6069	45		