

January 2013

Breeding Biology Of Chuck-Will's-Widows: Incubation, Brooding, And Provisioning Behavior And Characteristics Of Nest Sites

Ryan Sean O'Connor
Eastern Kentucky University

Follow this and additional works at: <https://encompass.eku.edu/etd>



Part of the [Biology Commons](#), and the [Ornithology Commons](#)

Recommended Citation

O'Connor, Ryan Sean, "Breeding Biology Of Chuck-Will's-Widows: Incubation, Brooding, And Provisioning Behavior And Characteristics Of Nest Sites" (2013). *Online Theses and Dissertations*. 115.
<https://encompass.eku.edu/etd/115>

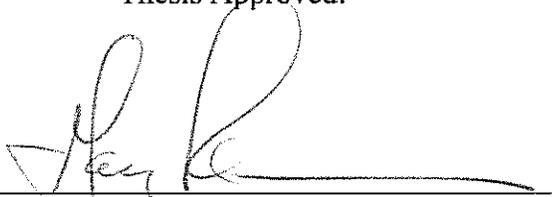
This Open Access Thesis is brought to you for free and open access by the Student Scholarship at Encompass. It has been accepted for inclusion in Online Theses and Dissertations by an authorized administrator of Encompass. For more information, please contact Linda.Sizemore@eku.edu.

BREEDING BIOLOGY OF CHUCK-WILL'S-WIDOWS: INCUBATION,
BROODING, AND PROVISIONING BEHAVIOR, AND CHARACTERISTICS OF
NEST SITES

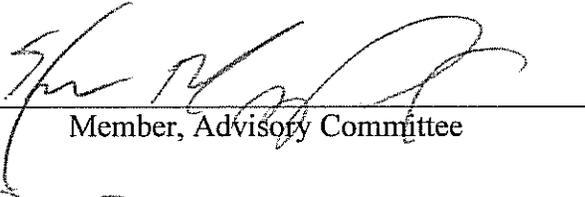
By

Ryan Sean O'Connor

Thesis Approved:



Chair, Advisory Committee



Member, Advisory Committee



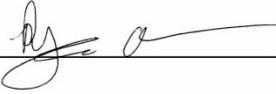
Member, Advisory Committee



Dean, Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at Eastern Kentucky University, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of the source is made. Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor, or in [his/her] absence, by the Head of Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature _____ 

Date _____ 4/1/13

BREEDING BIOLOGY OF CHUCK-WILL'S-WIDOWS: INCUBATION,
BROODING, AND PROVISIONING BEHAVIOR AND CHARACTERISTICS OF
NEST SITES

By

RYAN SEAN O'CONNOR

Bachelor of Science
Michigan State University
East Lansing, Michigan
2010

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 2013

DEDICATION

I would like to first dedicate this thesis to a good friend and mentor of sorts, Frank Roggenbuck, who first piqued my interests in birds and directed me on my current path. Lastly, and most importantly, this thesis is dedicated to my family. Without their support and encouragement, none of this would have been possible.

ACKNOWLEDGMENTS

First and foremost, I would like to thank my advisor, Dr. Gary Ritchison, whose support and guidance was invaluable. I would also like to thank my other committee members, Dr. Herman Mays, Jr., and Dr. David Brown, for their help and advice throughout this project. Additional thanks to Dr. Herman Mays, Jr., for first proposing a study of Chuck-will's-widows at the Edge of Appalachia Preserve and for providing accommodations at the field station. Special thanks to everyone at the Eulett Center for their help and for always providing assistance when needed, and to Brad McLeod and Adam Heist for help in the field. Lastly, I thank the Kentucky Academy of Science and the Kentucky Ornithological Society for financial support.

Abstract

Chuck-will's-widows (*Antrostomus carolinensis*) are cryptically colored ground-nesting nightjars that breed throughout much of the eastern United States, primarily in mixed-forest habitat. Because of their cryptic plumage and nocturnal habits, little is known about their behavior, particularly their breeding and nesting behavior. Thus, my objectives were to: (1) quantify patterns of incubation behavior (e.g., on bouts vs. off bouts) and the respective roles of males and females, (2) quantify the brooding and provisioning behavior of males and females, and, (3) compare the characteristics of nest sites and randomly selected unused sites to determine those features important in nest site selection.

My study was conducted at the Richard and Lucile Durrell Edge of Appalachia Preserve in Adams County, Ohio. During the breeding seasons of 2011 and 2012, I located six Chuck-will's-widow nests. All clutches consisted of two eggs laid on either leaf litter (N = 4) or bare ground (N = 2). Females were observed incubating more often (N = 12 observations at four nests) than males (N = 3 observations at two nests). Additionally, during 16 visits to five nests, females were flushed from nests more often (N = 14, or 87.5% of visits) than males (N = 2). Overall, the mean duration of incubation on-bouts was 442.1 min (N = 94). Incubation bouts of females were longer (mean = 274.5 min, N = 12 at four nests) than those of males (mean = 7.7 min, N = 3 at two nests). Females incubated eggs both during the day and at night whereas males were only observed incubating eggs at dusk.

Most incubation off-bouts occurred at dawn (N = 45 at six nests) and dusk (N = 48 at six nests) and averaged 35.0 min in duration (N = 104). Nightjars are visually

oriented crepuscular and nocturnal insectivores so eggs are likely left unattended at dusk and dawn so adults can forage. Off-bouts were shorter in duration during the middle (days 10 – 15) and late (days 16-21) stages of incubation than early in incubation (days 4 – 9). Changes in nest attentiveness may be related to the increased reproductive value of eggs as the incubation period progresses. Both males and females provisioned young, with eight observed visits by males and three by females. At dusk, feeding rates were highest ($P = 0.0026$) during the hour immediately after sunset and declined thereafter. Chuck-will's-widows may actively forage during the period after sunset because prey availability is higher and light levels are sufficient for effective foraging.

Most characteristics of nest sites and randomly selected unused sites were similar, but nest sites had less canopy cover (mean = 70.8%) than unused sites (mean = 92.4%). Nest sites in areas with less canopy cover may have increased light levels and thus may provide better foraging habitat for Chuck-will's-widows. In addition, a more open canopy may make it easier for adults flying to and from nest sites. Chuck-will's-widows have high aspect ratio wings and so may prefer more open canopies above nest sites to make it easier to visit and leave nests under low light conditions.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION.....	1
II. METHODS.....	3
Study site.....	3
Nest searching.....	3
Nest-site characteristics.....	6
Breeding behavior and nest fate.....	8
III. RESULTS.....	13
Breeding behavior.....	13
Development of young.....	18
Nest-site characteristics.....	18
IV. DISCUSSION.....	20
Breeding phenology.....	20
Nest sites and clutch sizes.....	21
Incubation.....	23
Brooding and feeding young.....	27
Development of young.....	29
Nest-site characteristics.....	31
LITERATURE CITED.....	33
APPENDIX.....	40

LIST OF TABLES

TABLE	PAGE
1. Mean duration (\pm SE) of on-bouts and off-bouts of adult Chuck-will's-widows during the incubation period in 2011 and 2012 at the Edge of Appalachia Preserve in Adams County, Ohio.....	41
2. Mean duration (in minutes) of on- and off-bouts of adult Chuck-will's-widows at four nests during the early (days 4 – 9), middle (days 10 – 15), and late (days 16 – 21) stages of incubation	42
3. Mean provisioning rates (visits to feed young/30 min) of three pairs of Chuck-will's-widows (males and females combined) during 2011 and 2012 at the Edge of Appalachia Nature Preserve, Adams County, Ohio.	43
4. Characteristics of young Chuck-will's-widows from the Edge of Appalachia Nature Preserve in Adams County, Ohio.....	44
5. Comparison of the characteristics of nest sites of Chuck-will's-widows and randomly selected, unused sites in southeastern Ohio.....	45

LIST OF FIGURES

FIGURE	PAGE
1. iButton placement in the ground at a Chuck-will's-widow nest.....	46
2. Aerial photograph of nest sites of Chuck-will's-widows in 2011 and 2012 at the Edge of Appalachia Preserve System, Adams County, Ohio.....	47
3. Aerial photographs of nest sites of Chuck-will's-widows in 2011 and 2012 at the Edge of Appalachia Preserve in Adams County, Ohio.	48
4. Incubation behavior of a Chuck-will's-widow on 14 May 2012.	49
5. Nest temperatures and ambient temperatures of an unsuccessful Chuck-will's-widows nest in 2011.	50
6. Movements of Chuck-will's-widow chicks from nest site for two nests from 2011.....	51
7. Plumage development of young Chuck-will's widows.....	52

Chapter I

Introduction

Nightjars and nighthawks (Family Caprimulgidae) are cryptically colored ground-nesters typically found in forest habitats (Vilella 1995). Caprimulgids are insectivorous species, mostly foraging at dusk and dawn and during nights with sufficient moonlight (Mills 1985). Because of their cryptic plumage and nocturnal habits, little is known about many aspects of their behavior and ecology, particularly their breeding and nesting behavior (Csada and Brigham 1994, Vilella 1995, Wilkinson 2009).

Chuck-will's-widows (*Antrostomus carolinensis*) are found throughout much of the eastern United States, primarily in deciduous, pine, oak-hickory, and mixed-forests (Straight and Cooper 2012). Chuck-will's-widows nest on the ground and females may (e.g., Brush 1990) or may not (e.g., Nicholson and Fowler 1997) create a nest depression. Eggs are typically laid on leaf litter, such as oak or pine, or on bare ground (Hoyt 1953, Ganier 1964, Straight and Cooper 2012). Previous studies suggest that nest sites are located in dense cover near old roads and forest edges (Imhof 1976, Peterjohn and Rice 1991) or near cedars (*Juniperus* spp.) or pines (*Pinus* spp.) in areas where those trees are present (James and Neal 1986, Palmer-Ball 1996). In contrast, Ganier (1964) reported that Chuck-will's-widows nests were not located near trees, bushes, or logs. Beyond these qualitative descriptions, little is known about the factors important in nest-site selection by Chuck-will's-widows.

Beyond a few anecdotal reports, little is known about the incubation and brooding behavior of most caprimulgids (Wilkinson 2009), including Chuck-will's-widows.

Female Chuck-will's-widows typically lay clutches of two eggs and incubation apparently starts with the laying of the first egg (Hoyt 1953). Among caprimulgids, incubation is thought to be primarily or exclusively by females (Vilella 1995), but some investigators have noted that males may occasionally incubate during the day (e.g., Berry 1979). In contrast to these patterns, Vilella (1995) found that male Puerto Rican Nightjars (*Antrostomus noctitherus*) incubated more than females. Incubation by Chuck-will's-widows is thought to be primarily by females, but some cases of male incubation have been observed (Stevenson and Anderson 1994). Studies to date indicate that male Chuck-will's-widows do not provision or otherwise care for young after hatching (Ganier 1964, Stevenson and Anderson 1994, Straight and Cooper 2012).

Clearly, additional study is needed to better understand nest-site selection and the breeding behavior of caprimulgids in general and Chuck-will's-widows specifically. Thus, during two breeding seasons, I attempted to locate as many nests of Chuck-will's-widows as possible in southeastern Ohio. My objectives were to: (1) quantify patterns of incubation behavior (e.g., duration of on-bouts vs. off-bouts) and the respective roles of males and females, (2) quantify the brooding and provisioning behavior of males and females, and, (3) compare the characteristics of nest sites and randomly selected unused sites to determine those features important in nest site selection.

Chapter II

Methods

Study site. Field work was conducted from 7 May to 1 August 2011 and 2012 at the Richard and Lucile Durrell Edge of Appalachia Preserve (hereafter, the Edge; 38°45'N, 83°27'W), Adams County, Ohio. The Edge is jointly managed by the Ohio Chapter of The Nature Conservancy and the Cincinnati Museum Center and includes 11 nature preserves encompassing over 5,665 ha. The Edge consists of mixed hardwood forests interspersed with open prairies and barren rocky outcroppings. Dominant canopy species where Chuck-will's-widows occurred included oaks (*Quercus* spp.), eastern red cedar (*Juniperus virginiana*), red maple (*Acer rubrum*), and Virginia pine (*Pinus virginiana*). Common understory plants included saplings of dominant canopy species, *Desmodium* spp., eastern redbud (*Cercis canadensis*), gray goldenrod (*Solidago nemoralis*), stiff gentian (*Gentianella quinquefolia*), and wiry witch-grass (*Panicum flexile*).

Nest searching. Chuck-will's-widows first arrive on their breeding grounds in southern Ohio, including the Edge of Appalachia Preserve, from mid- to late April and nesting typically begins in early May (C. Bedel, pers. observ.). From 7 May to 15 June 2011 and 2012, three methods were used to locate nests (i.e., where eggs were laid on litter or the ground). First, during daylight hours, I searched for nests by walking through apparently suitable nesting habitat. Based on previous accounts, Chuck-will's-widows typically nest in dense cover near old roads or forest edges, often laying eggs near the base of cedars (*Juniperus* spp.) or pines (*Pinus* spp.; Straight and Cooper 2012).

To locate potential nesting habitat throughout the preserve, I used an aerial photograph in ArcGIS (Version: 9.3, 2008) to find openings with mixed forest edges. A total of 26 areas were chosen as potential nesting habitat based on aerial photographs and locations where the Edge personnel either heard or saw Chuck-will's-widows in the past. I then visited each potentially suitable habitat and delineated a series of transects 2 m apart and walked slowly in a random cardinal direction along those transects searching for nesting adults. The number and distance of transects varied with each area depending on its size. I attempted to re-walk transects in a different random cardinal direction in each potential habitat at least twice a week. Some areas were too large to cover in one day, and therefore transects were broken up into multiple days. In addition to walking day transects, I attempted to visit each potential habitat at least once during the night to listen for singing adults and to look for the characteristic reflective eye-shine typical of nightjars.

Second, I conducted night surveys by driving sections of the preserve between 21:00 and 22:00 hrs listening for singing Chuck-will's-widows. Night surveys were concomitant with walking transects and ended on 15 June. Between 2 – 4 times a week, I surveyed a different section of road. I surveyed about 42.2 km of the approximately 80.5 km of road that runs through or adjacent to the Edge. Upon hearing singing, I stopped my car and recorded the coordinates of the singing individual (with their calls typically being audible at distances of at least 100 m; Wilkinson 2009) from the road with a GPS unit. I then placed the coordinates into ArcGIS (attempting to approximate the general location of singing adult) and noted any apparently suitable nesting habitat within a radius of 128 m from the spot of singing. Home-range sizes have not been calculated for Chuck-will's-

widows, but Vilella (1995) determined the average home range size of Puerto Rican nightjars to be 5.2 ha and a circle with a radius of 128 m encompasses an area of about 5.2 ha. If no apparently suitable habitat was located within a radius of 128 m, I located the closest apparently suitable habitat outside this range. Given the disparity in size between these two species (Chuck-will's-widows weigh between 94 - 137 g; Puerto Rican Nightjars weigh 35 - 37 g), Chuck-will's-widows may have home ranges larger than 5.2 ha. Once an area of potential habitat was determined, I visited it the next day to delineate and survey transects 2 m apart. Again, the number and lengths of transects varied with the size of potential habitat.

Finally, some species of nightjars are known to exhibit site fidelity, with females sometimes nesting near sites where they successfully nested in previous years (Ganier 1964, Wilkinson 2009, C. Bedel, pers. observ.). Therefore, I searched areas where Chuck-will's-widows were known to have nested in 2009 and 2010 (N = 6; C. Bedel, unpubl. data).

When a nest was located, I noted the number of eggs and recorded its location using a GPS unit. Thereafter, I visited nest sites at intervals of 1 day (N = 1), 2 days (N = 22), 3 days (N = 7), and 4 days (N = 2) to monitor nest status (e.g., still active or predated) and determine nesting stage (e.g., incubating or brooding). If an adult was flushed and eggs were not immediately noticeable, I searched the area for young and, if found, determined the adult was brooding. When flushed, I recorded the sex of adult either incubating or brooding. Sex of adults was determined by observing the outer rectrices of adults; male Chuck-will's-widows have white outer rectrices and females do not (Pyle 1997). I estimated dates of clutch initiation by backdating from the estimated

day of hatching and assuming that the incubation period of Chuck-will's-widows is 20 days (Hoyt 1953).

After eggs hatched, I continued to check young at intervals of 1 day (N = 9), 2 days (N = 6), 3 days (N = 5), 4 days (N = 1), and 5 days (N = 1) to examine their development and set up cameras. However, because young were able to move from nest sites as soon as two days after hatching, I was unable to locate the young during some visits. During each visit in 2011 when I located brooding adults and young, I recorded the GPS coordinate of where I flushed the adult so I could determine the distance the young had moved from nest sites. Each successive location was measured as the distance from the nest site.

Nest-site characteristics. I quantified nest-site characteristics 14- 29 days after young fledged or after nests were abandoned or predated. To determine if females might lay replacement clutches after nest failure, I re-walked transects in the failed nesting areas (i.e., area previously determined to be suitable nesting habitat in which failed nest was found). I began transects the day a failed nest was discovered and then continued to re-visit the area at least once a week for 7 – 10 days. Again, transects were walked in a random cardinal direction and the number of transects varied depending on size of suitable habitat. After a failed nest-site was thoroughly searched for a replacement clutch, I set up a plot around the failed nest-site to quantify nest-site characteristics. I also delayed nest site measurements at successful nests to allow adults and young to move a sufficient distance from nest sites to avoid disturbing them.

Measurements were collected following a modified version of methods described by James and Shugart (1970). Within an 11.3-m radius of nests, I counted all trees (dbh \geq

2.5 cm) and shrubs (dbh < 2.5 cm) and determined tree basal area with dbh tape. I also measured the height of all trees using a clinometer. Four transects radiating from nest sites in each of the four cardinal directions were established and, at 2.2-m intervals (from nest to 11.3 m away) along each transect, I recorded the presence or absence of canopy cover (and, if present, whether canopy cover was coniferous or deciduous), the type of ground cover (i.e., shrub, tree, grass, forbs, or bare ground), and foliage cover. Foliage cover was measured at intervals of < 0.25 m, 0.25-0.5 m, 0.5-1.0 m, and > 1 m above ground with a 2-m tall ruler with graduations of 0.25 m. Within each interval, I recorded the number of hits from stems or leaves that came in contact with the ruler. Canopy cover and ground cover type were determined using a densitometer. Because Chuck-will's-widows are known to associate with forest edges (Oberholser 1974, Imhof 1976, Peterjohn and Rice 1991), I measured the distance from the nest site to the nearest edge. Edges were defined as the boundaries of any opening (≥ 10 m wide; Rodewald 2002) within the forest.

To determine habitat features important in nest-site selection by Chuck-will's-widows, I compared the characteristics of nest sites to those of randomly selected, unused sites. For each nest site, I identified an unused site by selecting a randomly determined direction (from 1 - 360°) and a randomly determined distance from the nest in that direction. Distances were limited to a range between 20 and 125 m. The minimum distance of 20 m insured that the area measured around random sites did not overlap that of nest sites. To determine the maximum distance of 125 m, I assumed that Chuck-will's-widows defended territories comparable in size to those of other caprimulgids in North America (~ 5 ha for Whip-poor-wills, Straight and Cooper 2012; ~100-150 m long in

canyons for Buff-collared Nightjars, Bowers and Dunning 1997; territory size has not been documented for Chuck-will's-widows, Straight and Cooper 2012), and a circle with a radius of 125 m encompasses an area of about 5 ha. Characteristics of random sites were measured in the same manner as nest sites.

Because my sample size was too small for multivariate analysis, characteristics of nest sites and randomly selected unused sites were compared using analysis of variance. Analyses were conducted using the Statistical Analysis System (SAS Institute 2004).

Breeding behavior and nest fate. To examine the incubation behavior of Chuck-will's-widows, I simultaneously measured nest temperatures and ambient temperatures near nests. Temperatures in and near nests were recorded using iButtons (Model DS1921G-F5#; Maxim, Sunnyvale, CA). iButtons are small, self-contained thermal data loggers that measure temperature with an accuracy of $\pm 2^{\circ}\text{C}$. Depending on the position of eggs, iButtons were either placed at the base of eggs so that each side of an iButton was touching, almost touching, or in-between eggs (Figure 1)¹. Eggs were not handled or touched while placing iButtons in nests. Because iButtons need to be manually programmed to start, and I wanted to minimize the disturbance to incubating adults, I waited two days after nests were located to insert iButtons. Using cyanoacrylate glue (instant crazy glue; Krazy Glue, Columbus, OH), I glued iButtons to the top of 7.5-cm-long metal screws and glued brown polyester fabric on top of the iButtons for camouflage. Screws were then pushed by hand into the soil until the iButton was flush with the ground (Hartman and Oring 2006). iButtons used to measure ambient

¹ All figures and tables located in appendix.

temperature were randomly placed in the ground at least 5 m from nests along the edge of an opening or trail within the forest.

I programmed iButtons to record temperatures every 10 min and, at that frequency, they collected temperature data for about 14 days. Because the incubation period of Chuck-will's-widows is approximately 20 days (Hoyt 1953), iButtons had to be replaced no more than once at each nest. I placed most iButtons in nests (N = 6) at dusk (i.e., between 19:28 and 20:42) when Chuck-will's-widows become active and were either absent from nests or were likely to return to nests quickly after being disturbed. I replaced iButtons at one nest at 17:10 and at another nest at 03:43.

After young left nest sites or a nest failed, I retrieved iButtons and uploaded the temperature data as text files and converted them into Excel format (2007, Microsoft, Redmond, WA) where data could then be plotted as a line graph and visually analyzed (Hartman and Oring 2006). Patterns of incubation behavior (e.g., duration of incubation on- and off-bouts) and nest status were determined by comparing ambient temperatures to nest temperatures. During the incubation period, nest temperatures remained constant, except when incubating adults left nests, whereas ambient temperatures fluctuated throughout the day. Times when adults left or returned to nests were apparent when nest temperatures began to either become more similar to ambient temperature (nest departure) or to deviate from ambient temperature and become more similar to typical incubation temperatures (return to nest). Nest failure was evident if nest temperatures became synchronous with ambient temperatures.

Because iButtons only recorded temperatures every 10 min, off-bout lengths could have been over- or underestimated by a maximum of 10 min. For example, if a

reading was taken at 05:30 hrs with an adult on the eggs, then the bird left at 05:35 hrs, and then another nest reading was taken at 05:40 hrs with the adult still off the eggs, I would assume an off-bout of 10 min based on the iButton data although the duration of the off-bout was actually 5 min. Additionally, off bouts shorter than 10 min may have been missed. To compensate for such possible errors and to gather more detailed information about incubation behavior, including the possibility of short breaks from incubation and interactions between adults (e.g., males feeding incubating females or nest-relief displays; Vilella 1995), nests were sometimes monitored with video cameras (Model CCD-TRV138; Sony Corporation, Tokyo, Japan). During incubation, nests were videotaped every 2 – 4 days (except for one instance of a one day interval) to limit the disturbance on nesting adults. After eggs hatched, I typically videotaped nests or young every 1 – 3 days; at two nests in 2012, the intervals between successive videotaping sessions were 4 and 5 days, respectively. Camcorders mounted on tripods were set up either at dawn (between 04:00 and 06:59), dusk (between 19:00 and 22:00), or during the night (between 22:01 and 03:59). I also recorded four nests, including two in 2011 and two in 2012, during the day (between 07:00 and 18:59) on six different occasions. Cameras were mounted on tripods at least 5 m from nests and recorded for 4 hrs. I left cameras and tripods at nest sites and changed tapes and batteries when I returned to nests for additional videotaping. Cameras were placed inside plastic Rubbermaid containers with holes cut in the bottom (for tripod attachment) and in the front. In 2012, to improve recording quality under low-light conditions, I attached portable infrared illuminators (25 LED, Phantom Lite, East Greenville, PA) that were aimed at nests or young to the central rod of tripods. Camcorders had a night vision mode that picked up infrared light and

using the illuminators improved the quality of the videotapes in the low-light conditions. I noticed no noticeable change in adult behavior when infrared illuminators were used versus not used.

Using video recordings, I quantified the amount of time spent brooding by adults. Brooding was separated into two categories: 1) true brooding and 2) partial brooding. I defined true brooding as when both nestlings were under an adult's breast or abdomen. Partial brooding was when one nestling came completely out from under the adult's breast while the other nestling remained under. When an adult was present, but not brooding, neither nestling was under the adult's breast.

Provisioning behavior was quantified as the number of visits per 30-min interval. To determine if Chuck-will's-widows provisioned at higher rates during certain time periods, I created 30-min blocks of time beginning at sunset. In total, 17 half-hour blocks spanned the period from 17:00 to 1:30 h. Each visit was assigned to one of those blocks.

I also compared the duration of incubation on- and off-bouts relative to incubation stage. For on-bouts and off-bouts, the incubation period was divided into three stages: early (days 4 – 9), middle (days 10 – 15), and late (days 16 – 21) incubation. Additionally, I examined the timing of off-bouts of Chuck-will's-widows (i.e., when, based on video and iButton data, they left nests) relative to the time of sunset (at dusk) and the time of sunrise (at dawn) to determine if timing changed during the incubation period. For analysis, the incubation period was divided into three periods: early (days 4 – 9), middle (days 10 – 15), and late (days 16 – 21) incubation.

Possible variation in the duration of on- and off-bouts and in time adults left nests relative to sunset and sunrise relative to incubation stage was examined using repeated

measures analysis of variance. Variation in feeding rates relative to time of sunset was also examined using repeated measures analysis of variance. All analyses were conducted using the Statistical Analysis System (SAS Institute 2004).

Chapter III

Results

Breeding behavior. I located six nests, including four in 2011 and two in 2012. Distances between nest sites (mean = 2.4 ± 0.4 km) ranged from 1.5 to 3.5 km (Figure 2). The two nests found in 2012 were 36.1 m and 60.3 m away from nest-sites in 2011 (Figure 3; 1A & 1B and 6A & 6B, respectively). Furthermore, in 2012, I flushed a roosting male approximately 29 m from the location of a 2011 nest-site (5A in Figure 3). However, because I did not capture and band adults, I could not determine if pairs nested in the same area in subsequent years.

Females (N = 2 each year) initiated clutches on approximately 1 May and 7 May, respectively, in 2011, and on approximately 9 and 10 May, respectively, in 2012. All nests had clutches of two eggs that were laid on either leaf litter (N = 4) or bare ground (N = 2). Substrates at randomly selected sites consisted of leaf litter (N = 4), bare ground (N = 1), or grass (N = 1). The duration of the incubation period could not be determined because all nests were discovered after clutches were complete. However, the average time from when nests were located to when eggs hatched (N = 4 nests) was 12.5 ± 3.8 (SE) days. Both males and females incubated eggs. However, when I was able to determine the sex of incubating adults, females were observed incubating more often (N = 12 observations at four nests) than males (N = 3 observations at two nests). In addition, during 16 visits to five nests to either change tapes or iButtons, females were flushed from nests more often (N = 14, or 87.5% of visits) than males (N = 2). Nest visits occurred during the day (07:00 – 18:59 hrs; N = 5), dusk (19:00 – 22:00 hrs; N = 9), or

dawn (04:00 – 06:59 hrs; N = 1) and ranged from 12 - 29 May. The time for one visit was unknown due to camera malfunctions. Females were flushed during dawn, daytime, and dusk, while males were flushed during the day (i.e., 15:28 hrs) and at dusk (i.e., 21:00 hrs).

Overall, incubation on-bouts averaged 442.1 ± 33.9 min (N = 94; females N = 12, males N = 3, and unknown N = 79; range = 2.0 – 970.0 min), and the duration of on-bouts differed significantly among nests ($F_{5, 88} = 4.1$, $P = 0.002$; Table 1). When I was able to determine the sex of the incubating adult, the incubation bouts of females were longer (mean = 274.5 ± 82.9 min, N = 12 at four nests, range = 11.0 – 897.0 min) than those of males (7.7 ± 5.2 min, N = 3 at two nests, range = 2 – 18). On occasions when I could not determine the sex of the incubating adult, the mean duration of incubation bouts was 484.0 ± 36.2 min (N = 79 at six nests, range = 7.0 – 970.0 min). Female on-bouts occurred during dusk (19:00 – 22:00 hrs), night (22:01 – 03:59 hrs), dawn (04:00 – 06:59 hrs), and day (07:00 – 18:59 hrs). The three known male incubation bouts all occurred at dusk (e.g., 20:33 – 20:51, 21:01 – 21:04, and 20:44 – 20:46 hrs), one of which was the male relieving the female.

I observed exchanges (one adult replacing the other) at two nests during incubation, including one at dusk (20:42 hrs) and one at dawn (05:14 hrs). In each case, the non-incubating adult flew in and landed next to the incubating adult and uttered a low frequency ‘growl’ vocalization. During one nest-relief, the male landed approximately 10 cm from the female and uttered one ‘growl’ call. After 33.4 sec, the female left the nest; the male moved to the nest 1.4 min later. In the second exchange, because of low-light conditions, neither the sex of the relieving adult nor the distance between adults when the

arriving adult landed could be determined. However, during this exchange, the relieving adult gave five 'growl' notes. After 9.96 sec, the incubating adult left the nest and, 42.9 sec later, the other adult moved to the nest.

Most incubation off-bouts occurred at dawn (04:00 – 06:59 hrs; N = 45 at six nests) and dusk (19:00 – 22:00 hrs; N = 48 at six nests) and averaged 35.0 ± 3.9 min (N = 104; female N = 12, male N = 3, unknown N = 89, range = 1.0 – 280.0 min; Figure 4). Ten off-bouts at five nests occurred during the night (22:01 – 03:59 hrs) and one off-bout occurred during the day (07:41 hrs). The mean duration of off-bouts did not differ among nests ($F_{5, 98} = 0.8$, $P = 0.53$; Table 1).

The mean departure time of Chuck-will's-widows from nests at dusk was 16.9 ± 2.1 min (N = 49) after sunset, but departure times ranged from 3 min before sunset to 66 min after sunset. At dawn, the mean time when adults left nests was 47.8 ± 4.2 min (N = 46) before sunrise, and departure times ranged from 100 min before sunrise to 89 min after sunrise. The mean duration of on-bouts ($F_{2, 72} = 2.3$, $P = 0.30$) did not differ during early (days 4 – 9), middle (days 10 – 15), and late (days 16-21) incubation stages (Table 2). However, the mean duration of off-bouts ($F_{2, 74} = 5.7$, $P = 0.05$) did differ during early (days 4 – 9), middle (days 10 – 15), and late (days 16-21) incubation stages (Table 2). I found no difference in departure time from nests relative to sunrise ($F_{2, 3} = 0.6$, $P = 0.60$) or sunset ($F_{2, 3} = 1.3$, $P = 0.38$) among incubation stages (early = days 4 – 9, middle = days 10 – 15, and late = days 16 – 21).

The mean hatch date for successful nests (N = 4) was 26 May ± 2 days. Two nests were unsuccessful; one was predated (i.e., eggs absent when nest was checked) and the other abandoned (i.e., multiple nest checks with eggs present, but no incubating adult;

Figure 5). No replacement clutches or second broods were found after failed nesting attempts.

The brooding behavior of adult Chuck-will's-widows was monitored by videotaping at 3 nests during the day and at dusk when young ranged in age from 1 – 7 days. In addition, during the day (07:00 – 18:59; N = 10) and at dusk (19:00 – 22:00; N = 8), I approached adults with young (N = 4; range in age of young = 1 – 16 days) 18 times after hatching to check their status and flushed adult females 16 times (88.9% of visits) and males twice (11.1% of visits).

Overall (males and females combined), the mean duration of brooding bouts (i.e., both young completely under an adult) was 20.0 ± 3.5 min (N = 54 at three nests, range = 6 sec – 118.7 min). When the sex of brooding adults was known, the mean duration of brooding bouts was 23.9 ± 4.7 min (N = 37 at two nests, range = 6 sec – 118.7 min) for females and 4.9 ± 2.0 min (N = 8 at two nests, range = 11 sec – 15.9 min) for males. Overall, the mean duration of partial-brooding bouts (i.e., one nestling under breast and the other completely out) was 52 ± 6 sec (N = 62 at three nests, range = 8 sec – 4.0 min). Mean duration of partial-brood bouts was 1.1 ± 0.3 min (N = 8 at two nests, range = 8 sec – 2.9 min) for males and 50 ± 7 sec (N = 43 at two nests, range = 9 sec – 4.0 min) for females.

The provisioning behavior of adult Chuck-will's-widows was videotaped at three of the four successful nests on six occasions (when young were 1, 2, 2, 3, 4, and 8 days old, respectively). I was unable to observe feeding at one nest because the young always moved out of view after I set up the camcorder. In addition, the young tended to move more with increasing age, increasing the probability that they would be out of view of the

camcorders. Videotaping during the nestling stage occurred during the day (07:00 – 18:59 hrs), dusk (19:00 – 22:00 hrs), and at night (22:01 – 03:59 hrs). During the period prior to and after sunset, I found that feeding rates differed significantly among 30-min time blocks ($F_{6, 10} = 7.8$, $P = 0.0026$) with rates highest during the two 30-min period just after sunset (Table 3).

During 20.58 hrs of video, I observed 23 feeding visits, including 8 by males, 3 by females, and 12 by adults of undetermined sex. Additionally, I observed seven non-feeding visits by adults, with three by males, two by females, and two unknown. Therefore, adults only fed young during 76.7% of all visits (23 of 30). All observed feedings occurred at dusk. At dusk, the earliest feeding observed on video was at 20:44 hrs (10 min before sunset). Feeding began at dusk with the non-brooding adult arriving at the nest to join the brooding adult and young. The brooding adult then left and the newly arrived adult fed and brooded the young. During feeding visits by adults, young Chuck-will's-widows begged for food by pecking at the breast and bill of adults and then grabbing the adult's bill with its own. Adults responded by vigorously shaking their head up-and-down, apparently regurgitating insects into the nestling's mouth.

During 17.87 hrs of video recorded at three nests during the day (07:00 – 18:59 hrs), there were no feeding visits by adults (the age of young during daytime recordings ranged from 2 – 16 days). During the day, an adult was always present with the young. Young remained active during the day, frequently moving in and out from under the breast of adults. When not being brooded, young Chuck-will's-widows were observed stretching their wings, hopping, and occasionally pecking at the ground.

Development of young. After hatching, all successful nests (N = 4) were monitored for an average of 11.8 ± 2.0 days (range = 7 - 16 days) to follow development of young (Table 4). At these nests, young Chuck-will's-widows moved from nest sites on days 2, 2, 3, and 5 days post-hatching (mean = 3.0 ± 0.7 days), respectively. Based on observations of young at two nests, young moved further from nest sites with increasing age (Figure 6). On eight occasions while I was videotaping (N = 3 broods, age of young ranging from 5 – 16 days), adults returning to nests or young landed variable distances away and uttered a low-frequency, guttural vocalization. On one occasion at 09:45, a female walked away from young and out of view of the camcorder. Young Chuck-will's-widows then ran or hopped towards the vocalizing adult to be fed or brooded. On eight of the nine occasions when adults moved away from the young, nestlings moved out of view of the camcorder. On one occasion when the camera was zoomed out, an adult landed ~5 m from the young, but still in view of the camcorder, and the young immediately went to the adult to be fed.

One day after hatching, nestling's eyes were open and covered in natal down. Natal down was similar to that described by Rohwer (1971), i.e., golden brown in color, being darker above than below with the darkest area on the lower back. Pin feathers on the alar tract were apparent by seven days post-hatching (N = 4) and were beginning to break through the outer sheaths by day 10 (N = 2) (Figure 7). By day 16 nestlings were incapable of sustained flight and could only fly short distances (about 15 – 30 m).

Nest-site characteristics. Comparison of nest-sites to randomly selected unused sites revealed a significant difference only for percent canopy cover ($P = 0.0044$; Table 5), with nest sites having less canopy cover (mean = $70.8 \pm 4.0\%$) than unused sites

(mean = $92.4 \pm 3.6\%$). Although not significantly different, nest sites tended to be closer to edges than random sites, and also tended to have more herbaceous ground cover compared to random sites.

Chapter IV

Discussion

Breeding phenology. Female Chuck-will's-widows in my study began egg-laying during the period from 1 to 10 May. Chuck-will's-widows form pairs and initiate nests within 7 – 10 days of arriving in their northern breeding grounds (Straight and Cooper 2012). Therefore, Chuck-will's-widows arrived at my study site in Adams County, Ohio, during late April or early May. These dates for time of arrival and clutch initiation are similar to those recorded previously for Chuck-will's-widows in southern Ohio, including the edge of Appalachia (C. Bedel, pers. observ.). Peterjohn and Rice (1997) also suggested that Chuck-will's-widows initiate breeding in Ohio during May. However, Peterjohn and Rice (1997) only reported nests ($N = 2$) with eggs during the first half of June, much later than in my study. Replacement clutches have been reported for Chuck-will's-widows (Sprunt and Chamberlain 1970, Straight and Cooper 2012), possibly explaining the late egg dates reported by Peterjohn and Rice (1997). Chuck-will's-widows leave their wintering grounds between late February to May (Straight and Cooper 2012) and arrive on breeding grounds earlier in southern states than northern states. For example, Chuck-will's-widows arrive on breeding grounds in mid- to late March in Florida (Stevenson and Anderson 1994) and March to early April in Georgia (Burleigh 1958). Sprunt and Chamberlain (1979) reported that Chuck-will's-widows arrived in South Carolina by early May and began incubation by mid- to late April. Straight and Cooper (2012) cite food availability as a possible factor affecting time of

arrival in breeding areas, with earlier arrival times further south due to the warmer weather and greater insect availability.

Nest sites and clutch sizes. Two nests located in 2012 were within 61 m of the location of nest sites in 2011. Given the proximity of these nest sites between years, these may have been nests of the same pairs of Chuck-will's-widows or the same females. Similarly, Sprunt and Chamberlain (1970) reported nests of Chuck-will's-widows located within 2 – 3 m of nest sites used the previous year, suggesting that pairs may use the same territories from year to year. Other species of nightjars are also known to exhibit site fidelity (Cleere 1999). For example, Silky-tailed Nightjars were observed using three nesting sites for five years and another for 10 years, and nests were within 5 – 170 m of one another in different years (Wilkinson 2009).

All clutches of Chuck-will's-widows in my study consisted of two eggs laid on either leaf litter or bare ground. Other investigators have also reported that Chuck-will's-widows typically lay eggs on a substrate of pine needles, dead leaves, or bare ground (Cleere 1999, Straight and Cooper 2012). Hoyt (1953) and Ganier (1964) also reported eggs laid on pine needles and dead leaves. Although some investigators reported Chuck-will's-widows creating a small nest depression on the ground for eggs (Baird et al. 1874, Burleigh 1958, James and Neal 1986, Brush 1990), I found no evidence to suggest they create a depression. Cleere (1999) suggested that it was more likely that depressions develop when incubating birds and adults dislodge debris during changeovers. I also observed incubating adults shifting and changing positions while incubating, which could create the false appearance of a purposefully created depression.

Although most nightjars nest on the ground, some have been reported to nest in trees (Cleere 1999). For example, a Short-tailed Nighthawk (also known as Semi-collared Nighthawk; *Lurocalis semitorquatus noctivagus*) was found nesting on a tree branch 6 m above the ground where it laid a single egg into a natural depression on a branch (Seutin and Lezer 1995). Also, Common Nighthawks (*Chordeiles minor*) sometimes nest on flat, gravel roofs in urban areas (Brigham et al. 2011). Like other ground-nesting nightjars, the cryptic coloration of Chuck-will's-widows conceals them from predators while incubating or brooding (Straight and Cooper 2012).

Although clutch sizes of Chuck-will's-widows can range from one to four eggs (Cleere 1999), Straight and Cooper (2012) reported that 95% of Chuck-will's-widow egg sets and nest records (N = 353) were two-egg clutches. Among caprimulgids, clutch sizes are generally either one or two (Cleere 1999). The relationship between metabolism and the evolution of life history traits (Sibly et al. 2012, Brown and Sibly 2006, Brown et al. 2004) may explain the relatively small clutch sizes of caprimulgids. Because egg production is driven by metabolism (Brown et al. 2004), Sibly et al. (2012) posited that avian productivity ($[\text{egg mass} \times \text{number of eggs per clutch} \times \text{clutch frequency}] \div \text{body mass}$) decreases with increasing body size, due to the mass-specific decrease in metabolic rates. Sibly et al. (2012) compared the relationship between productivity and body mass for 966 species of bird and found a continuous decrease in productivity with increasing body mass. Furthermore, some members of the order Caprimulgiformes exhibit a lower metabolic rate for their body size than would be expected by allometry (Lane et al. 2004). For example, Lane et al. (2004) found that the basal metabolic rate of Whip-poor-will's was 59% of that predicted by allometry for body mass (Reynolds and Lee 1996).

Furthermore, the low basal metabolic rates of caprimulgiformes cannot be explained by their phylogenetic affiliations (Lane et al. 2004). Therefore, the small clutch sizes (i.e., low productivity) of caprimulgids may be reflective of their low metabolic rates.

Alternatively, small clutch sizes may be a result of low mortality rates (Sibly et al. 2012). The life span of caprimulgids is relatively long (e.g., Atanasov 2007), with one account of a Chuck-will's-widow living almost 15 years (Klimkiewicz 1997). Sibly et al. (2012) suggested that species that forage on abundant insects during twilight periods can satisfy their food requirements while spending little time foraging. Reduced time spent foraging may limit exposure to predators, contributing to lower mortality rates and, in turn, low productivity (Sibly et al. 2012). The relationship between low mortality rate and low productivity can be interpreted as a trade-off between present and residual (future) reproductive value to adults (Williams 1966). Birds with longer life spans may invest less (e.g., smaller clutches or less nest defense) in current breeding attempts because the reproductive value of future mating opportunities is greater than the present reproductive value. In contrast, high adult mortality may lead to increased reproductive effort (e.g., large clutch size or multiple broods), thereby increasing the fitness of adults by increasing the chances of producing young before mortality occurs (Martin 2004).

Incubation. Although I found that both male and female Chuck-will's-widows spent time incubating eggs, females appeared to spend much more time incubating eggs than males. Indeed, based on observations when the sex of adults could be determined, I could only confirm that males incubated eggs on three occasions and for an average of only 7.7 minutes. A possible explanation for such results is that male Chuck-will's-widows are not incubating, but, rather, are simply guarding eggs while females are taking

breaks from incubating. In support of this hypothesis, male Chuck-will's-widows do not have brood patches (Pyle 1997). Similarly, male Common Nighthawks do not have brood patches and incubation is usually only by females (Brigham et al. 2011).

Males in other species of nightjars have incubation or brood patches, e.g., male Common Poorwills (Csada and Brigham 1994) and male Eastern Whip-poor-will's (Cink 2002). In these species (as well as other species of nightjars where it has yet to be determined or reported that males have incubation or brood patches), both sexes incubate eggs (e.g., Csada and Brigham 1994, Vilella 1995, Wilkinson 2009), but the roles of males and females appear to vary. Both male and female Eastern Whip-poor-will's incubate eggs, but the time spent incubating by each varies among different pairs (Cink 2002). Csada and Brigham (1994) found that male Common Poorwills incubated more than females regardless of time of day, whereas females invested more time in brooding. Wilkinson (2009) found that female Silky-tailed Nightjars incubated eggs during the day and males incubated at night. In contrast, with the exception of one nest, Vilella (1995) only observed male Puerto Rican Nightjars incubating eggs during the day.

Female Chuck-will's-widows in my study incubated eggs throughout the day (i.e., dawn, dusk, and during the day and night). However, based on observations when the sex of adults could be determined, males only incubated (or guarded eggs) at dusk and during the day, suggesting that males spend little time at nests during the night. One possible explanation for such behavior is that, at night, males are engaged in other activities such as territory defense and foraging. Most nightjars are territorial (Cleere 1999) and, by spending little or no time at nests during the night, males may have more time to defend their territories. For example, Vilella (1995) found that male Puerto Rican Nightjars left

nests after incubating eggs during the day and flew around their territories singing on favored perches.

During the incubation period, my results indicate that Chuck-will's-widows remain on the eggs throughout most of the day. Straight and Cooper (2012) suggested that adult Chuck-will's-widows are reluctant to flush because their white eggs are obvious against the brown leaf litter. A second explanation for long incubation bouts is their nocturnal lifestyle. Being active at night likely constrains them from being off the eggs for too long because of lower ambient temperatures at night. Conway and Martin (2000) showed that ambient temperature had a significant effect on the incubation behavior of passerines, with off-bouts shorter in duration for species in colder environments. By incubating eggs throughout most of the night when temperatures are cooler, Chuck-will's-widows may be ensuring proper embryonic development.

Most incubation off-bouts in my study occurred at dusk and dawn, and eggs were typically left unattended for about 35 min per off-bout. Eastern Whip-poor-wills and Common Poorwills have also been reported to leave eggs unattended at dawn and dusk when adults exchange incubation duties (Cink 2002, Woods et al. 2005). Weller (1958) studied the incubation behavior of Common Nighthawks and observed two off-bout events on separate nights where the female left the eggs or young shortly after sunset to forage for 20 and 17 minutes, respectively. Vilella (1995) reported that Puerto Rican Nightjars left eggs unattended at dawn and dusk, often for more than an hour. However, on average, Puerto Rican Nightjars only left eggs unattended for about 30 min each day (Vilella 1995). Ganier (1964) observed a female Chuck-will's-widow leaving eggs at 04:20 and 04:10 for 15 min and 24 min, respectively. Ganier (1964) also reported six off-

bouts at night, all 2 min in duration, and suggested that the female left the eggs to be fed by the male. I found no evidence suggesting males feed females during incubation.

Nightjars are visually oriented crepuscular or nocturnal insectivores (Woods and Brigham 2008), so eggs are likely left unattended at dusk and dawn so adults can forage. As with on-bouts, incubation off-bouts are also going to be constrained by ambient temperatures. For optimum development, egg temperature must be kept at around 37 – 38° C (Gill 2007). Being active after sunset means ambient temperatures will be cooler than daytime temperatures, therefore limiting the amount of time adults can leave eggs unattended before egg temperature drops and affects embryonic development.

I found that incubation off-bouts were shorter in duration as incubation progressed, with off-bouts shorter during the middle and late incubation stages than the early incubation stage. To my knowledge, other investigators have not provided data concerning nest attentiveness by other caprimulgids. However, investigators have reported that Chuck-will's-widows (Straight and Cooper 2012), Eastern Whip-poor-wills (Cink 2002), and Puerto Rican Nightjars (Villela 1995) exhibit increased aggression and more nest defense displays as the incubation period increases. Cink (2002) also observed an increased reluctance in Eastern Whip-poor-will's to flush from eggs later in the incubation period. Temporal changes in nest attentiveness and nest defense displays may be related to the increased reproductive value of eggs as the incubation period progresses. Andersson et al. (1980) suggested that the intensity of nest defense increases during the breeding season as the difference between the reproductive value of offspring and parent decreases. The reproductive value of older embryos is greater because they are more likely to hatch and ultimately survive than younger embryos.

Brooding and feeding young. Both male and female Chuck-will's-widows brooded young after hatching, although males spent less time brooding than females. Stevenson and Anderson (1997) reported that brooding was by female Chuck-will's-widows only, but provided no supporting data. As with incubation, female Chuck-will's-widows likely brooded more because they have brood patches and males do not (Pyle 1997). Male Chuck-will's-widows were only observed brooding for short bouts at dusk after feeding young.

Little is known about the brooding behavior of other caprimulgids. Brigham et al. (2011) indicated that only female Common Nighthawks brooded young during the day, but provide no information about brooding behavior at night. Woods et al. (2005) reported that both male and female Common Poorwills brood young, but provided no details concerning the contributions of each sex. Similarly, Cink (2002) indicated that both male and female Eastern Whip-poor-wills brood young, but provided no information concerning the relative contributions of each sex. Both sexes brood young in Common Paurques (*Nyctidromus albicollis*), with males and females alternating in brooding young at 2-3 hr intervals (Latta and Howell 1999). The brooding behavior of Lesser Nighthawks appears comparable to that of Chuck-will's-widows in my study, with females doing most of the brooding of young and males only brooding young for brief periods during feeding visits (Latta and Baltz 2012). In the order Caprimulgiformes, additional study is needed to further clarify the respective roles of males and females in brooding young and to examine factors that might contribute to differences among species in the relative contributions of males and females.

Both male and female Chuck-will's-widows fed young and all observed feedings occurred at dusk and during the night. Prior to and after sunset, I found that feeding rates were highest during the 60-min period immediately after sunset and that adults did not provision young either during the period 31 – 240 min before sunset or the period 121 – 270 min after sunset. Nightjars are visual predators and their foraging behavior may be constrained by light levels (Bayne and Brigham 1995). Furthermore, the greatest amount of insect biomass may be available at dusk and dawn (Jetz et al. 2003). For example, Jetz et al. (2003) found that prey availability for two species of nightjars, Standard-winged Nightjars (*Macrodipteryx longipennis*) and Long-tailed Nightjars (*Caprimulgis climacurus*), was greatest at dusk and significantly lower at dawn and during the night. Jetz et al. (2003) also found that both nightjar species foraged most intensely at dusk. Chuck-will's-widows may feed young at the highest rates immediately after sunset because prey availability is higher and light levels are sufficient for effective foraging.

My results indicate that male Chuck-will's-widows help care for young, through direct incubation or guarding eggs during incubation and, after hatching, feeding and brooding young. Males were especially involved with feeding young where males fed more than females. Biparental care of young has also been reported in Whip-poor-wills (Cink 2002) and Common Poorwills (Woods et al. 2005), although information on relative roles of males and females was not provided. Cleere (1999) noted that, among caprimulgids, both sexes typically provide parental care, but females generally spend more time at nests during the day. Biparental care is common in birds, and has been reported in about 75% of all species (Cockburn 2006). Parental care will vary depending on the condition of young at hatching, with altricial young needing more parental care

(Dial 2003). Among birds, 59.3% of species (5,753 of 9702; Gill 2007) in the world belong to the order Passeriformes where young are born altricial. The helpless condition of altricial young constrains either sex from desertion because their reproductive success will be greater by staying together. Biparental care in Chuck-will's-widows, particularly in feeding young, may be a consequence of being visually oriented crepuscular insectivores. Insects represent a variable prey source with densities dependent on ambient temperatures (Ashdown and McKechnie 2008). Ashdown and McKechnie (2008) saw aerial insect densities change by over three orders of magnitude depending on ambient temperature. Thus, the dependence on warmer air temperatures for insect availability and on sufficient light levels for successful foraging may put a reproductive constraint on adult Chuck-will's-widows. On cold and cloudy nights, both parents may be needed to successfully feed both young.

Development of young. In my study, pin feathers on the alar tract of young Chuck-will's-widows were present and sheathed by day 7. At day 16, the young were still incapable of sustained flight, with flights limited to distances of approximately 15 to 30 m. Straight and Cooper (2012) indicated that young Chuck-will's-widows could fly by day 16 post-hatching, but not how well or how far. Rohwer (1971) examined one young Chuck-will's-widow that was 6 – 10 days old and noted that the natal down was beginning to be replaced by the juvenile plumage, with juvenile primaries and secondaries emerging from the sheath and the rectrices completely ensheathed. Ganier (1964) followed nestlings and reported that the young were capable of short flights of about 15 m by day 17 post-hatching when they were completely feathered.

Within two days after hatching, I found that young Chuck-will's-widows began moving away from nest sites. Similar observations have been reported for other caprimulgid species (Villela 1995, Cleere 1999, Aragonés 2003), including Chuck-will's-widows (Hoyt 1953, Ganier 1964). Hoyt (1953) found young 3 m from a nest site one day after hatching and 7.6 m away three days after hatch. Ganier (1964) found young Chuck-will's-widows 9.1 m from a nest site five days after hatch. Cleere (1999) reported that young White-throated Nightjars (*Eurostopodus mystacalis*) were capable of moving 10 m each night until about 10 days old, and greater distances thereafter. Some movements by young Chuck-will's-widows in my study occurred when adults vocalized at varying distances away and the young then moved toward the adults. Similar behavior has been noted in other species of caprimulgids (Villela 1995, Cleere 1999, Wilkinson 2009). Cleere (1999) describes nestling movements being triggered by adults landing nearby and calling to the young. Villela (1995) observed Puerto Rican Nightjars capable of short (< 50 cm) movements within 24 hours of hatching and occurred when adults landed nearby and vocalized to young. Swenson and Hendricks (1983) suggested that movements by young Common Poorwills were of two types: 1) thermoregulatory responses (e.g., moving away from sunlight), and 2) anti-predator responses triggered by disturbance from the investigators (e.g., handling). For example, short movements of 1 m or less (Csada and Brigham 1994) may be a thermoregulatory response by young to avoid wet areas (Swisher 1978) or too much sunlight (Dexter 1956). Short movements into dense canopy may also be an anti-predator response from aerial predators (Swenson and Hendricks (1983). Swenson and Hendricks (1983) observed two long movements (> 3 m;

Csada and Brigham 1994) by young Common Poorwills following handling, presumably an anti-predator response.

Nest-site characteristics. The only significant difference between nest sites and unused sites in my study was canopy cover, with nest sites having less canopy cover than unused sites. Nest sites in areas with less canopy cover may have increased light levels and thus may provide better foraging habitat for visual predators like Chuck-will's-widows. Cooper (1981) conducted call counts for Chuck-will's-widows and Eastern Whip-poor-wills in Georgia and found significant differences in abundance of the two species in different habitats (pasture, forest, and suburban). Chuck-will's-widows appeared to prefer more open habitat (pasture) whereas Whip-poor-wills were more abundant in forest habitat (Cooper 1981).

Although the size of the territories or home ranges of Chuck-will's-widows is unknown (Straight and Cooper 2012), Baumgartner and Baumgartner (1992) reported that 3 – 9 pairs of Chuck-will's-widows were present in a 40-ha area in Oklahoma. Assuming that pairs occupy similar-sized territories or ranges, territories or ranges in that 40-ha area would average about 4.5 – 13 ha per pair. If so, then Chuck-will's-widows would likely spend most of their time foraging away from nest sites and a relatively open canopy above nest sites may be important for reasons other than providing better foraging habitat. One possibility is that a more open canopy may make it easier for adults flying to and from nest sites. Poulin et al. (1998) suggested that Common Nighthawks should prefer unobstructed space at locations where they must take-off and land because they have high aspect ratio wings. Chuck-will's-widows also have high aspect ratio wings and so may prefer more open canopies above nest sites to make it easier to visit and leave

nests under low light conditions. Improving lighting conditions under areas with less canopy cover may also make it easier for adults to see eggs and young as they fly back to nest sites.

The overall similarity of nest sites and randomly selected sites in my study suggests that many sites in my study area may be suitable as nest sites for Chuck-will's-widows. If so, then perhaps selection for characteristics at the level of nest sites may be less important for Chuck-will's-widows than selection for characteristics of habitat at the territory level. For example, Straight and Cooper (2012) suggested that openings, including forest gaps and scrub, appear to be important foraging areas for Chuck-will's-widows. A broader, landscape-level comparison of the characteristics of randomly selected unused areas and those of areas used by Chuck-will's-widows may be needed to improve our understanding of factors potentially important in the selection of breeding sites.

Literature Cited

- Andersson, M., C. G. Wiklund, and H. Rundgren. 1980. Parental defence of offspring: a model and an example. *Animal Behaviour* 28: 536-542.
- Aragonés, J. 2003. Breeding biology of the Red-necked Nightjar *Caprimulgus ruficollis* in southern Spain. *Ardeola* 50: 215-221.
- Ashdown, R. A. M., and A. E. McKechnie. 2008. Environmental correlates of Freckled Nightjar (*Caprimulgus tristigma*) activity in a seasonal, subtropical habitat. *Journal of Ornithology* 149:615-619.
- Atanasov, A. T. 2007. The near to linear allometric relationship between total metabolic energy per life span and body mass of nonpasserine birds. *Bulgarian Journal of Veterinary Medicine* 10: 235-245.
- Baird, S. F., T. M. Brewer, and R. Ridgway. 1874. A history of North American birds. Little, Brown and Co., Boston, MA.
- Baumgartner, F. M., and A. M. Baumgartner. 1992. Oklahoma bird life. University of Oklahoma Press, Norman, OK.
- Bayne, E. M., and R. M. Brigham. 1995. Prey selection and foraging constraints in Common Poorwills (*Phalaenoptilus nuttallii*: Aves: Caprimulgidae). *Journal of Zoology* 235: 1-8.
- Berry, R. 1979. Nightjar habitats and breeding in East Anglia. *British Birds* 72:207-218.
- Bowers, R. K., Jr., and J. B. Dunning. 1997. Buff-collared Nightjar (*Caprimulgus ridgwayi*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online:

<http://bna.birds.cornell.edu/bna/species267>.

- Brigham, R. M., J. Ng, R. G. Poulin and S. D. Grindal. 2011. Common Nighthawk (*Chordeiles minor*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/213>.
- Brown, J. H., and R. M. Sibly. 2006. Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences USA* 103: 17595-17599.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771-1789.
- Brush, T. 1990. Chuck-will's-widow nesting in eastern Iowa. *Iowa Bird Life* 60:107-108.
- Burleigh, T. D. 1958. Georgia birds. University of Oklahoma Press, Norman, OK.
- Cink, C. L. 2002. Eastern Whip-poor-will (*Antrostomus vociferus*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/620>.
- Cleere, N. 1999. Family Caprimulgidae (Nightjars). In: Handbook of the birds of the world, vol. 5. Barn-owls to hummingbirds (J. del Hoyo, A. Elliott, and J. Sargatal, eds.), pp. 302-386. Lynx Edicions, Barcelona, Spain.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B* 273: 1375-1383.
- Conway, C. J., and T. E. Martin. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 54: 670-685.
- Cooper, R. J. 1981. Relative abundance of Georgia caprimulgids based on call-counts.

- Wilson Bulletin 93: 363-371.
- Csada, R. D., and R. M. Brigham. 1994. Breeding biology of the Common Poorwill at the northern edge of its distribution. *Journal of Field Ornithology* 65: 186-193.
- Dexter, R. W. 1956. Further banding and nesting studies of the Eastern Nighthawk. *Bird-Banding* 27: 9-16.
- Dial, K. P. 2003. Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. *Auk* 120: 941-952.
- Ganier, A. F. 1964. The alleged transportation of its eggs or young by the Chuck-will's-widow. *Wilson Bulletin* 76: 19-27.
- Gill, F. B. 2007. *Ornithology*, third ed. W. H. Freeman and Co., New York, NY.
- Hartman, C. A., and L. W. Oring. 2006. An inexpensive method for remotely monitoring nest activity. *Journal of Field Ornithology* 77: 418-424.
- Hoyt, S. F. 1953. Incubation and nesting behavior of the Chuck-will's-widow. *Wilson Bulletin* 65:204-205.
- Imhof, T. A. 1976. *Alabama birds*, 2nd edition. University of Alabama Press, Tuscaloosa, AL.
- James, D. A., and J. C. Neal. 1986. *Alabama birds: their distribution and abundance*. University of Arkansas Press, Fayetteville, AR.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727-736.
- Jetz, W., J. Steffen, and K. E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* 103: 627-639.

- Klimkiewicz, M. K. 1997. Longevity records of North American birds. Version 97.1, Patuxent Wildlife Research Center, Bird Banding Lab. Laurel, MD. Online: <http://www.pwrc.usgs.gov/BBL/homepage/longvre.htm>.
- Lane, J. E., D. L. Swanson, R. M. Brigham, and A. E. McKechnie. 2004. Physiological responses to temperature by Whip-poor-wills: more evidence for the evolution of low metabolic rates in Caprimulgiformes. *Condor* 106: 921-925.
- Latta, S. C., and C. A. Howell. 1999. Common Pauraque (*Nyctidromus albicollis*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/429>.
- Latta, S. C., and M. E. Baltz. 2012. Lesser Nighthawk (*Chordeiles acutipennis*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/314>.
- Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future?. *Auk* 121: 289-301.
- Mills, A. M. 1985. The influence of moonlight on the behavior of goatsuckers (Caprimulgidae). *Auk* 103: 370-378.
- Nicholson, C. P., and W. B. Fowler. 1997. Chuck-will's-widow. In: Atlas of the breeding birds of Tennessee (C. P. Nicholson, ed.), pp. 155-156. University of Tennessee Press, Knoxville, TN.
- Oberholser, H. C. 1974. The bird life of Texas, vol. 1. University of Texas Press, Austin TX.

- Palmer-Ball, B. L., Jr. 1996. The Kentucky breeding bird atlas. University Press of Kentucky, Lexington, KY.
- Peterjohn, B. G., and D. L. Rice. 1991. The Ohio breeding bird atlas. Ohio Department of Natural Resources, Columbus, OH.
- Poulin, R. G., L. D. Todd, and R. M. Brigham. 1998. Male Common Nighthawk use of gravel roads at night. *Prairie Naturalist* 30:85–90.
- Pyle, P. 1997. Identification guide to North American birds, Part I: columbidae to ploceidae.
- Reynolds, P. S., and R. M. Lee III. 1996. Phylogenetic analysis of avian energetics: passerines and nonpasserines do not differ. *American Naturalist* 147: 735-759.
- Rodewald, A. D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* 66:634-640.
- Rohwer, S. A. 1971. Molt and the annual cycle of the Chuck-will's-widow, *Caprimulgus carolinensis*. *Auk* 88: 485-519.
- SAS Institute. 2004. SAS 9.1.2 user's guide. SAS Institute Inc., Cary, NC.
- Seutin, G., and M. Letzer. 1995. The Short-tailed Nighthawk is a tree nester. *Journal of Field Ornithology* 66: 30-36.
- Sibly, R. M., C. C. Witt, N. A. Wright, C. Venditti, W. Jetz, and J. H. Brown. 2012. Energetics, lifestyle, and reproduction in birds. *Proceedings of the National Academy of Sciences USA* 109: 10937-10941.
- Sprunt, A., and E. B. Chamberlain. 1970. South Carolina bird life. University of South Carolina Press, Columbia, SC.
- Stevenson, H. M., and B. H. Anderson. 1994. The birdlife of Florida. University Press of

Florida, Gainesville, FL.

Straight, C. A., and R. J. Cooper. 2012. Chuck-will's-widow (*Antrostomus carolinensis*).

In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/499>.

Swenson, J. E., and P. Hendricks. 1983. Chick movements in Common Poorwills. *Wilson Bulletin* 95: 309-310.

Swisher, O. D. 1978. Poor-wills nesting in southwestern Oregon. *North American Bird Bander* 3: 152-155.

Vilella, F. J. 1995. Reproductive ecology and behaviour of the Puerto Rican Nightjar *Caprimulgus noctitherus*. *Bird Conservation International* 3:349-366.

Weller, M. W. 1958. Observations on the incubation behavior of a Common Nighthawk. *Auk* 75: 48-59.

Wilkinson, F. A. 2009. Observations on the breeding biology of the Silky-tailed Nightjar (*Caprimulgus sericocaudatus mengeli*). *Wilson Journal of Ornithology* 121: 498-505.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Woods, C. P., and R. M. Brigham. 2008. Common Poorwill activity and calling behavior in relation to moonlight and predation. *Wilson Journal of Ornithology* 120: 505-512.

Woods, C. P., R. D. Csada, and R. M. Brigham. 2005. Common Poorwill (*Phalaenoptilus nuttallii*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of

Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online:
<http://bna.birds.cornell.edu/bna/species/032>.

APPENDIX:
TABLES AND FIGURES

Table 1. Mean duration (\pm SE) of on-bouts and off-bouts of adult Chuck-will's-widows during the incubation period in 2011 and 2012 at the Edge of Appalachia Preserve in Adams County, Ohio.

Nest ^a	On-bouts			Off-bouts		
	Mean (min)	SE ^b	N	Mean (min)	SE ^b	N
1A	693.3	98.6	6	33.3	5.0	9
5A	273.0	145.7	6	63.5	40.3	6
6A	87.0	37.6	5	22.0	5.9	6
8A	357.1	120.4	11	36.0	9.0	13
1B	577.7	49.8	30	36.7	8.2	32
6B	390.6	51.9	36	31.0	4.2	38

^a Nest sites between years. Numbers represent the territory nest was found in and the letter represents the year ([A] for 2011 nests and [B] for 2012 nests).

^b Standard error

Table 2. Mean duration (in minutes) of on- and off-bouts of adult Chuck-will's-widows at four nests during the early (days 4 – 9), middle (days 10 – 15), and late (days 16 – 21) stages of incubation.

Variable	Early			Middle			Late			P
	Mean	SE	N	Mean	SE	N	Mean	SE	N	
On-bout	430.0	81.5	22	521.3	67.6	23	330.6	51.9	37	0.30
Off-bout	57.36	18.9	22	29.6	4.0	41	25.5	1.9	25	0.05

Table 3. Mean provisioning rates (visits to feed young/30 min) of three pairs of Chuck-will's-widows (males and females combined) during 2011 and 2012 at the Edge of Appalachia Nature Preserve, Adams County, Ohio. Provisioning rates were significantly higher from 0 – 30 min and 31 – 60 min after sunset than during the other periods of time (Tukey's test; $P < 0.05$).

Time period ^a	Mean feeding rate	SE	N
31 – 240 min before sunset	0	-	11
0 – 30 min before sunset	0.6	0.4	5
0 – 30 min after sunset	2.0	0.7	6
31 – 60 min after sunset	1.8	0.3	4
61 – 90 min after sunset	0	-	4
91 – 120 min after sunset	0.5	0.3	4
121 – 270 min after sunset	0	-	13

^aTime 0 = time of sunset

Table 4. Characteristics of young Chuck-will's-widows from the Edge of Appalachia Nature Preserve in Adams County, Ohio.

Days post-hatching	Characteristic
1	Eyes open
2-3	Nestlings able to move from nest site.
7	Pin feathers established
10	Primary feathers beginning to break through sheath; coverts almost completely unsheathed.
16	Incapable of sustained flight; can jump and flutter short distances.

Table 5. Comparison of the characteristics of nest sites of Chuck-will's-widows and randomly selected, unused sites in southeastern Ohio.

Variable	Used (N = 6)		Random (N = 6)		F _{1,10}	P
	Mean	SE	Mean	SE		
Distance to road (m)	255.8	28.1	229.5	39.0	0.3	0.60
Nearest edge (m)	14.3	7.2	27.4	8.0	1.5	0.25
Nearest shrub (cm)	69.0	36.2	45.8	9.0	0.4	0.55
Nearest tree (cm)	125.3	21.1	128.3	30.3	0.1	0.94
Number of shrubs	455.8	61.1	415.0	44.8	0.3	0.60
No. trees 2.5-8 cm dbh	63.3	16.6	76.2	15.5	0.3	0.58
No. trees > 8 cm dbh	33.7	3.3	29.5	3.5	0.8	0.40
Above branch height (cm) ^a	204.2	50.2	174.0	18.8	0.3	0.62
% canopy cover	70.9	4.0	92.4	3.6	15.8	0.0044
% canopy coniferous	27.7	8.2	23.6	9.2	0.1	0.74
% canopy deciduous	43.1	11.4	68.8	11.7	2.5	0.15
Foliage cover, <0.25 m ^b	32.2	7.4	34.0	11.3	0.1	0.89
Foliage cover, 0.25-0.50 m	5.7	1.9	4.2	1.0	0.5	0.50
Foliage cover, 0.5-1 m	5.5	2.0	5.2	3.0	0.1	0.93
Foliage cover, >1 m	19.7	2.7	29.5	8.0	1.4	0.27
% bare ground	11.8	2.9	11.1	1.4	0.1	0.83
% herbaceous cover	22.9	7.3	13.9	3.2	1.3	0.28
% shrub cover	11.8	4.5	14.6	4.7	0.2	0.68
% grass cover	13.9	7.7	10.4	6.3	0.1	0.73
% leaf litter cover	31.8	9.3	41.7	8.6	0.6	0.45
Tree height (m)	6.8	1.1	7.2	0.5	0.1	0.78
Diameter breast height (cm)	9.3	1.2	8.4	0.6	0.5	0.51
Basal area	0.97	0.13	0.86	0.08	0.5	0.49
% coniferous	47.2	9.7	32.7	10.8	1.0	0.34
% deciduous	52.8	9.7	67.3	10.8	1.0	0.34

^aDistance to nearest branch above nest-site

^bUsing a 2-m ruler with 25-cm graduations, counted number of hits from stems and leaves in each interval.



Figure 1. iButton placement in the ground at a Chuck-will's-widow nest.

Arrow is pointing to the iButton located between the eggs.



Figure 2. Aerial photograph of nest sites of Chuck-will's-widows in 2011 (green circles) and 2012 (red circles) at the Edge of Appalachia Preserve System, Adams County, Ohio.

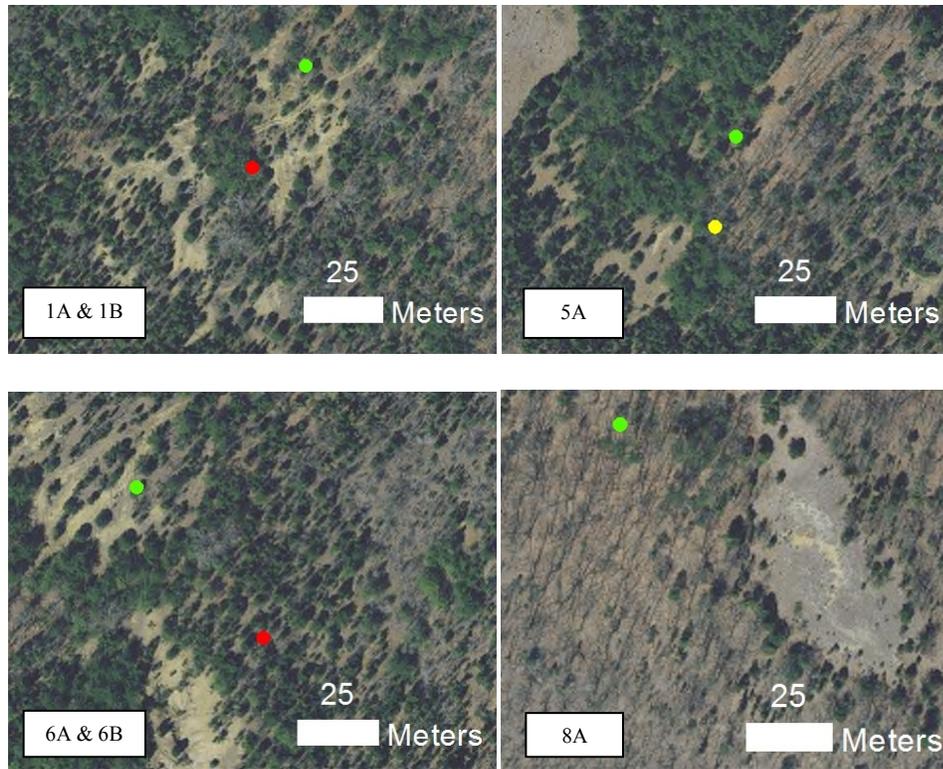


Figure 3. Aerial photographs of nest sites of Chuck-will's-widows in 2011 and 2012 at the Edge of Appalachia Preserve in Adams County, Ohio. Green circles are nests from 2011 and red circles nests from 2012. Yellow circle is where an adult was heard calling.

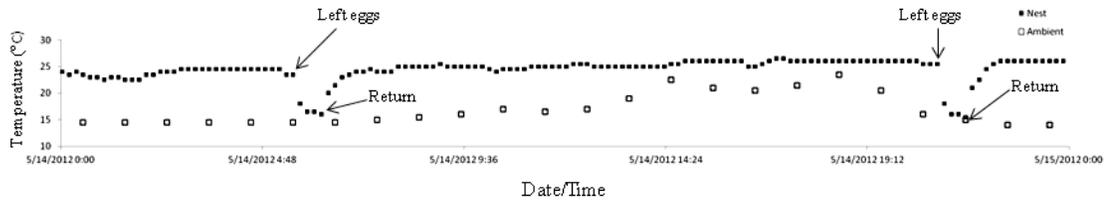


Figure 4. Incubation behavior of a Chuck-will's-widow on 14 May 2012. Two off-bouts, one at 05:32 hrs and the other at 20:52 hrs, are shown. Off-bouts are represented by the dip in nest temperature (black squares) towards ambient temperature (white squares). Each nest square represents 10 min and each ambient square 60 min.

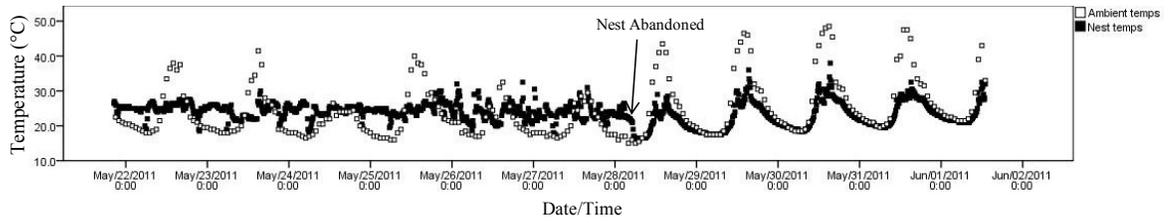


Figure 5. Nest temperatures and ambient temperatures of an unsuccessful Chuck-will's-widows nest in 2011. Nest abandonment occurred on 28 May at approximately 03:50 h and is signified by the synchronous patterning of ambient and nest temperatures.

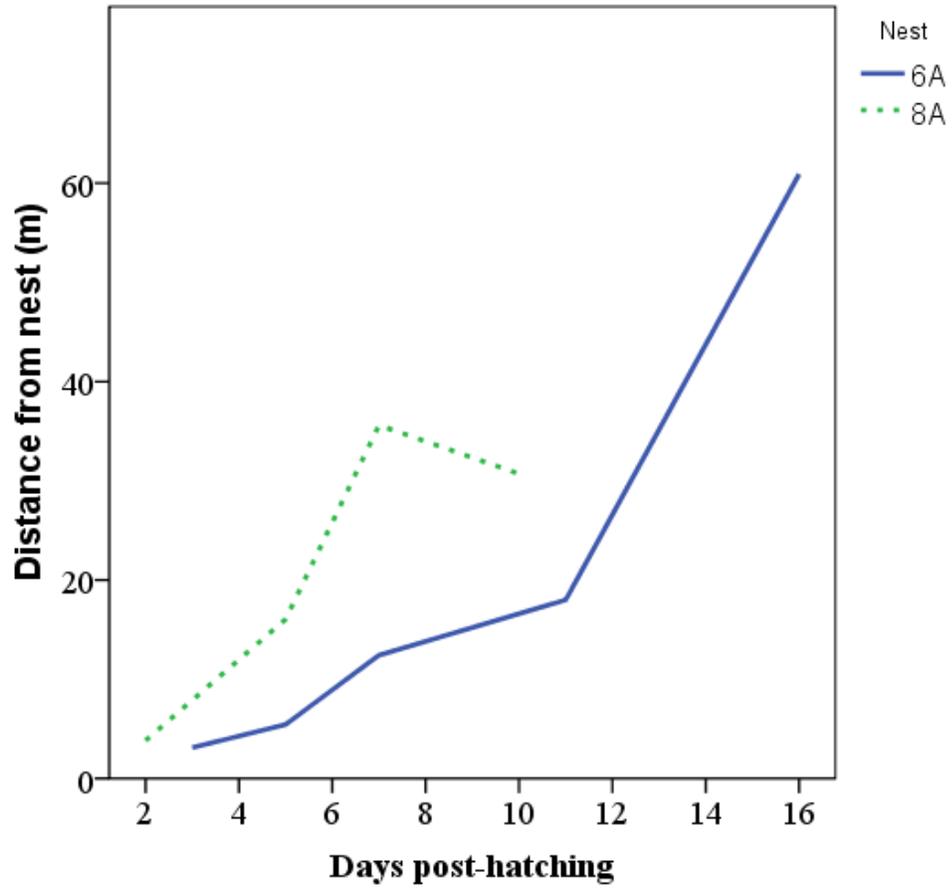


Figure 6. Movements of Chuck-will's-widow chicks from nest site for two nests from 2011.

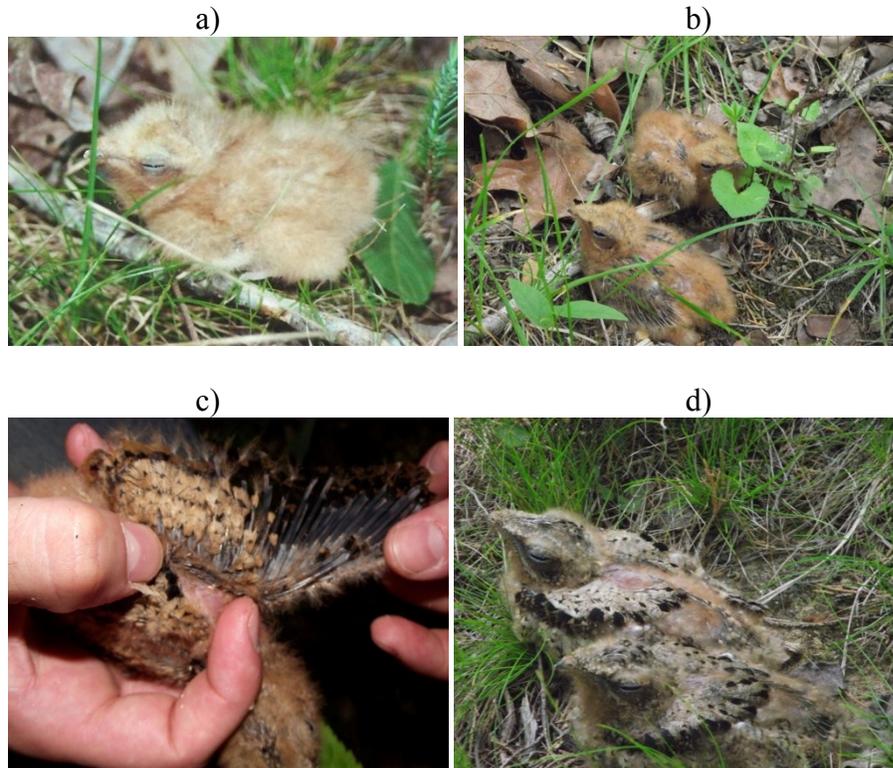


Figure 7. Plumage development of young Chuck-will's-widows. (a) three-day-old nestling. Still covered in down and no sign of pin feathers, (b) seven-day-old nestling. Pin feathers apparent but still sheathed, (c) 10 days post-hatching. Secondary coverts almost completely developed. Primary flight feathers still sheathed although beginning to break through at the tips, and (d) 14 days post-hatching, coverts appear to be completely unsheathed. Primaries still not completely developed.