Filling gaps in the full annual cycle of the Black-crowned Night-Heron (*Nycticorax nycticorax*)

Thesis

Presented in Partial Fulfillment of the Requirements for the Degree Master of Science in

the Graduate School of The Ohio State University

By

Kristie A. Stein, B.S.

Graduate Program in Environment and Natural Resources

The Ohio State University

2018

Thesis Committee:

Christopher Tonra, Advisor

Jacqueline Augustine

Suzanne Gray

Laura Kearns

Abstract

Migratory birds carry out different stages of their life cycle in geographically disparate locations complicating our ability to track individuals over time. However, the importance of connecting these stages is underscored by evidence that processes occurring in one stage can influence performance in subsequent stages. Over half of migratory species in North America are declining, and it follows that understanding the factors limiting population growth is a major focus of current avian conservation.

Globally, Black-crowned Night-Herons (*Nycticorax nycticorax*) are common and widespread, but populations across the Great Lakes region in long-term decline. Within Ohio, Black-crowned Night-Herons historically nested at 19 colonies but currently occupy only five of those sites. The largest colony, West Sister Island, represents an important breeding area for many species of wading birds and currently hosts the majority of the night-heron breeding population in Ohio. The number of nesting pairs at West Sister Island has been monitored since the 1970s, but little is known about the population outside of the breeding season. My research is the first to examine multiple stages of the full annual cycle of Black-crowned Night-Herons. My overall objectives were twofold: (1) to examine how conditions experienced in the nest carry over to influence survival during the post-fledging period and (2) to describe the migratory behavior and nonbreeding ecology of Black-crowned Night-Herons.

To examine rates of reproductive success, I monitored Black-crowned Night-Heron nests at two mixed-species breeding colonies in Lake Erie. I found that nest

success rates were high in relation to breeding colonies in other parts of the range and predation events were uncommon. Additionally, I identified potential limiting factors to individual nestlings by confirming that youngest nestlings within a brood are at a disadvantage in terms of growth rates, as those with slow growth were also less likely to survive to fledging. Black-crowned Night-Herons that occupied nests higher in the canopy produced more offspring to fledging. I utilized an automated telemetry array in Ohio and Michigan to track post-fledging movements and survival. I did not find evidence that carry over effects were present from pre- to post-fledging, but female birds experienced higher mortality rates compared to males during the six months following fledging.

Aside from a small number of recoveries of banded birds, little information exists on the migratory or stationary nonbreeding portions of the annual cycle of Black-crowned Night-Herons. To measure movements throughout the annual cycle, I deployed satellite transmitters on adult night-herons during the post-breeding season. All Black-crowned Night-Herons exhibited migratory movements and two strategies were evident, where the total duration of migration was greatly influenced by the time spent at stopover locations. These different strategies indicated that stopover habitat requirements vary between individuals during both autumn and spring migration. Migratory routes followed the same general patterns in autumn and spring. The majority of Black-crowned Night-Herons spent the nonbreeding season in the southeastern United States, but the spread of locations spanned five countries. Unlike many migratory species, where the nonbreeding period is characterized by stationary behavior, Black-crowned Night-Herons made large

scale movements during the nonbreeding period, relocating up to 902 km from one home

range to the next. The information that our research has provided fills large gaps in our

knowledge of the full annual cycle and can be used to inform conservation planning both

within Ohio and in other declining populations.

Acknowledgments

v

Vita

<u>Education</u>

May 2009…………………………………....Diploma, Archbishop Chapelle High School

Metairie, LA

May 2013…………………………………B.S. Natural Resource Ecology and

Management, Louisiana State University,

Baton Rouge, LA

<u>Professional Experience</u>

Jan 2016 - present………………………...Graduate Research Assistant, The Ohio

State University, Columbus, OH

Aug 2015 to Nov 2015……..…………..Field Biologist, University of British

Columbia, Peru

Jul 2015 – Aug 2015………………….…..Research Assistant, The Ohio State

University, OH

Apr 2015 – Jun 2015………………….…..Field Biologist, University of Minnesota,

Northeastern US

Jan 2015 – Feb 2015………………………...Field Biologist, Auburn University, AL

Sept 2014 – Dec 2014……………………….Field Biologist, McMaster University,

Puerto Rico, US

May 2014 – Aug 2014……………………Field Biologist, Smithsonian Migratory Bird

Center, IN

Sept 2013 – Nov 2013………………………...Americorps Intern, US Fish and Wildlife

Service, MS

May 2013 – Aug 2013…..………………..MAPS Bird Bander, Louisiana Department

of Wildlife and Fisheries, LA

May 2012 – May 2013………………….....Undergraduate Researcher, Entomology

Department, Louisiana State University, LA

Jan 2012 – May 2013…………………......Soybean Entomology Lab Assistant,

Louisiana State University, LA

May 2011 – Dec 2011………………….....Forest Entomology Lab Assistant,

Louisiana State University, LA

Fields of Study

Major Field: Environment and Natural Resources

Specialization: Fisheries and Wildlife Science

Table of Contents

List of Tables

List of Figures

Chapter 1: Ecological correlates of growth and survival in juvenile Black-crowned Night-Herons (*Nycticorax nycticorax*)

INTRODUCTION

In animals, survival rates during early life stages can both influence the fitness of parents (Klug and Bonsall 2014) and have important impacts on the population dynamics of a species (Dahlgren et al. 2016). Compared to other stages, the juvenile period is often characterized by high mortality. The juvenile period of birds can be separated into two distinct stages: hatching to departure from the nest (pre-fledging) and from fledging to first breeding (post-fledging; Etterson et al. 2011). For migratory birds, the post-fledging period is often constrained to only include the period from fledging to migration/dispersal (Cox et al. 2014). Traditionally, measures of reproductive success included information on the number of nestlings that successfully fledge from a nest or whether any nestlings survive to fledge (Ricklefs 1969). Later, the measure of reproductive success shifted to estimating a daily survival rate by incorporating the time period over which nests were monitored (Mayfield 1961, 1975). However, both measures neglect survival during the post-fledging period. Post-fledging survival can be especially low in altricial species (i.e. species where offspring require considerable parental care) during the first few weeks when individuals are most susceptible to predation (e.g. Ausprey and Rodewald 2011) and adverse environmental conditions (e.g. Dybala et al. 2013). Therefore, without consideration of post-fledging survival, estimates of reproductive success may be biased

(Naef-Daenzer et al. 2001, Keedwell 2003, Grüebler and Naef-Daenzer 2008, Balogh et al. 2011).

Conditions experienced in one stage of a species' annual cycle can carry over to influence performance of individuals in a subsequent stage (reviewed in Harrison et al. 2011). Within birds, many studies have established this link between nonbreeding and breeding season processes using stable isotopes. Stable isotope ratios of tissues grown during the nonbreeding period can identify individuals to a range of different quality habitats (i.e. xeric or mesic), and individuals occupying higher quality habitats arrive earlier to the breeding grounds in better condition and produce more offspring (Marra et al. 1998, Norris et al. 2004, Paxton and Moore 2015, Goodenough et al. 2017). Less attention has been placed on the individual or population level effects due to transitions between other stages (Marra et al. 2015). For example, few studies have explicitly examined effects of pre- to post-fledging (but see Blomberg et al. 2014, Bosman et al. 2016, Jones et al. 2017) (Blomberg et al. 2014, Bosman et al. 2016, Jones and Post 2016)(Blomberg et al. 2014, Bosman et al. 2016, Jones and Post 2016)(Blomberg et al. 2014, Bosman et al. 2016, Jones and Post 2016)(Blomberg et al. 2014, Bosman et al. 2016, Jones and Post 2016)and even fewer between pre-fledging and recruitment (Cleasby et al. 2010, Saunders et al. 2014).

Many factors including parent-mediated traits (e.g. foraging efficiency, nesting phenology, nest-site characteristics), species traits (e.g. hatching asynchrony, brood size), and juvenile traits (e.g. sex, body condition) have immediate effects on individual fitness

through impacts on growth and survival and these effects may carry over to the post-fledging period (reviewed in Maness and Anderson 2013). Foraging performance of the parents is strongly related to patterns of nestling growth (Gebhardt-Henrich and Richner 1998), and higher rates of growth influence survival (Ricklefs 1984). The timing of nesting is matched with the highest resource abundance in the most successful nests (Thomas and Shutler 2001, Durant et al. 2007). Brood size can influence survival, but relationships vary by species and populations. For example, increased competition can reduce growth and subsequent survival when brood sizes are large (Gilliland et al. 2016), or survival can be higher in large broods due to the efforts of high-quality parents (Lescroël et al. 2010). Similarly, hatching order in the brood, mediated through unequal resource acquisition or increased sibling aggression, can influence survival whereby later hatched nestlings within a brood grow slower and are less likely to survive (Fujioka 1985, Mock and Parker 1997). In addition, survival can be biased towards one sex; although not exclusive, the pattern is most common in sexually size dimorphic species (Clutton-Brock 1991). Most studies have included only one or a few of these possible predictors because simultaneous collection can be logistically challenging, and thus their relative influence on juvenile survival is unknown for most species and systems (reviewed in Maness and Anderson 2013).

Knowledge of post-fledging ecology and the factors influencing survival during this period, while gaining traction in avian research, is still mostly limited to studies of passerines and some precocial species (Maness and Anderson 2013, Cox et al. 2014). Studying wading birds, or other large species, during this period is challenging because

movements can be unpredictable in direction and scale. However, advances in tracking technology via automatization have improved our ability to track individuals over larger scales and longer time periods (Taylor et al. 2017). The Black-crowned Nigh-Heron (*Nycticorax nycticorax*) serves as a good candidate for a study on the post-fledging period for multiple reasons. Black-crowned Night-Herons are of conservation concern throughout the Great Lakes region (Hothem et al. 2010). Within Ohio, the number breeding pairs and active breeding colonies has declined beginning in the 1970s (Shieldcastle and Martin 1997, Rodewald et al. 2016), resulting in the species being listed as state-threatened. The breeding ecology of Black-crowned Night-Herons is well documented throughout the breeding range (Jungsoo and Tae-Hoe 2007, Brussee et al. 2016, Hunt 2016), but outside of the nestling period, the juvenile stage is relatively unknown (but see Erwin et al. 1996a).

The principle goal of this study was to understand the extent to which individual phenotypic variation in nestling growth and survival carries over to influence survival rates during the post-fledging stage. First, I investigated probabilities of nest success (probability that at least one nestling survived to fledge) at two island breeding colonies of Black-crowned Night-Herons in Ohio. Second, I examined growth rates of nestling night-herons in relation to intrinsic and climatic variables. I predicted that growth rate would be (1) higher for earlier hatched nestlings within a brood and (2) higher for nestlings with fewer nestmates. Third, I evaluated the effect of intrinsic and nest site characteristics on nestling survival rates using trail cameras in conjunction with nest monitoring visits. I predicted that survival would be (1) higher for earlier hatched

nestlings within a brood, (2) higher for nestlings with fewer nestmates, and (3) higher for nestlings with a faster growth rate. Lastly, I used an automated telemetry array to track individuals during the post-fledging period and analyzed how conditions experienced in the nest carry over to influence post-fledging survival rates. I expected that the predictions for nestlings would hold true as sub-lethal effects on fledglings during the post-fledging period. In the modeling framework, I also considered other relevant and/or potentially confounding variables (e.g. site, year, sex, and hatch date).

METHODS

Study area - I conducted nest monitoring during May – August of 2016 and 2017 at two mixed-species breeding colonies in the Western basin of Lake Erie, West Sister Island (41.73°N 83.10°W) and Turning Point Island (41.61°N, 83.13°W; Figure. 1.1). West Sister Island is a 31 ha Wilderness Area managed as a satellite of the Ottawa National Wildlife Refuge located 13.42 km from the southern shore of Lake Erie. Turning Point Island (2 ha, 0.22 km to shore) is a manmade island located in Sandusky Bay, near the city of Sandusky. I chose these two islands because they host the highest numbers of breeding Black-crowned Night-Herons in Ohio. Following fledging, I focused tracking efforts within the western Lake Erie basin in Ohio and Michigan (Figure. 1.1).

Nest monitoring - I visited nesting colonies towards the end of the incubation period and selected up to 24 nests per year from each colony. On the first visit, I recorded nest contents, assigned an identifier to each nest, and attached a motion sensitive camera

(Browning Strike Force HD 2015, Reconyx PC 900, Moultrie Panoramic 150) to a tree 1-2 m away. I programmed trail cameras to take two pictures (separated by 10 seconds) after being triggered by motion in the nest. If nestlings were present, I hand-captured and held them in a cloth bag for processing. I collected physical measurements from each nestling (culmen length, tarsus length, wing chord, and mass) and clipped one nail for subsequent identification. On return visits, I checked the contents of each nest and re-measured all nestlings. When nestlings weighed at least 200 g, I banded each nestling on the left tibiotarsus with a stainless steel US Geological Survey Bird Banding Lab leg band. I checked nests every 2-14 days until nestlings reached 25 days old after which they were mobile and difficult to relocate. When nestlings were > 500 g, I chose 1-2 nestlings from each nest to mark with a digitally coded nanotag (Tag mass: 4.8g, model NTQB-6-2, Lotek Wireless Inc.) attached to a figure-8 harness (Rappole and Tipton 1991). Each nanotag is programmed on the same frequency (166.380), but tags are coded with a unique series of radio transmissions that repeat at a fixed interval. Nanotags weighed < 1% of each fledgling's body mass at tagging. Those marked with nanotags were also banded with a plastic band (West Sister Island – white with black lettering, Turning Point Island– blue with white lettering) engraved with a unique alphanumeric code (1 letter, 2 numbers) to aid in re-sighting.

After all nestlings had fledged or nests failed, I measured the diameter (m) and height (m) of each nest as well as recorded a GPS location. Additionally, I measured the distance from each nest to the shoreline using the tracks function (Garmin GPSMAP

64st) and the 'near' feature in the ArcMAP 10.3 proximity toolset (ESRI, Redlands, CA, USA).

Sexing - At capture, I collected 1-4 scapular or breast feathers from each nestling of 10 days or older. Feathers were placed in envelopes and stored at -20° C until processing. DNA was extracted from 151 nestling samples by making a lengthwise cut 5-10 mm from the calamus, then cutting 1 mm pieces into 150 µL of Chelex solution. Samples were vortexed, incubated at 60° C overnight, vortexed again, incubated at 95° C for 20 minutes, and centrifuged for 2 minutes at 10,000 g in a microcentrifuge. I removed a 100 µL aliquot of the DNA solution and stored at -20° C until amplification. Polymerase chain reactions (PCR) were conducted using the WZ-common, W-specific, and P8 primers for amplification following the PCR protocol of Wang et al. (2011). The PCR products were electrophoresed on 2% agarose gels and visualized using dye.

Correlates of growth and survival - I recorded hatching order and age of nestlings by observed hatch date or when unknown, by relative size (length of the bird's culmen) following Custer and Peterson Jr. (1991). Growth rates of nestlings were calculated using the changes in mass, culmen, tarsus, and wing chord recorded between the first and second measurement dates, divided by the number of days between measurements. The four measures of growth were combined as one composite measure via a principal component analysis (see *statistical analysis* below). I recorded two measures of brood size. The first measure represents the maximum number of nestlings present in the nest at any point. Because most mortality occurred early in the nesting period, our second

measure of brood size was determined by the number of chicks present in the nest by day seven of the last hatched chick. I used the first measure in reporting the range of brood sizes and the second in our analyses of growth and survival. Because brood reduction (where mortality is higher for younger nestmates; Lack 1968) occurs early in the nestling period of Black-crowned Night-Herons, the reduced measure of brood size represents the number of nestlings present for the majority of the nestling period (29 – 34 days; Thompson et al. 1979) and thus, provides a more biologically relevant predictor of nestling growth and survival. To examine the effect of environmental conditions on rates of growth, I obtained meteorological data from a NOAA weather station in Sandusky, Ohio (https://www.ncdc.noaa.gov/, 41.45° N, -82.71° W) located 46.3 km and 1.2 km from West Sister Island and Turning Point Island, respectively.

Pre- and post-fledging survival - I monitored survival of Black-crowned Night-Herons in two stages (nestling and post-fledging). All nestling Black-crowned Night-Herons from selected nests were monitored via trail cameras and nest checks from day 0 to day 25. Following tagging, I tracked fledgling night-herons during the post-fledging period defined as mid June – November. Within this period, I defined thirteen 13-day periods over which to track survival and attempted to locate each radio-marked bird at least once within each 13-day period. I used an array of 13 radio telemetry towers on the western and southern shores of Lake Erie, with sites in both Ohio and Michigan to track night-herons within the study area (Figure 1.1). Each tower is fixed with two 9-element Yagi antennas connected to an automated receiver (models SRXDL, SRX600, SRX800; Lotek Wireless, Inc.) powered by a solar panel and marine battery. Antennas were

8

located approximately 10 m above the ground on all towers resulting in a maximum detection radius of approximately 15 km while birds are in flight. Tag identification number, antenna number, date, time, and signal strength were recorded for each received detection. In addition to the telemetry tower array, I also covered the study area using hand held receivers (model SRX800-M1; Lotek, Inc.) and roof-mounted 5-element antennas on trucks, strut-mounted 3-element antennas on fixed-wing aircraft, and hand-held antennas on foot or by boat. As part of this coverage, I drove a standardized route and visited wildlife areas twice within each survival interval (Appendix A, Figure A.1). Additionally, I flew over the study area 5 times in 2016 and 4 times in 2017 (Appendix A, Figure A.2). Upon signal detection, I visually located tagged night-herons through radio telemetry homing techniques to determine mortality status and record a GPS location. Because Black-crowned Night-Herons are mostly nocturnal, I often located birds while roosting (e.g. in cattail stands). To minimize disturbance caused by flushing the individual, I would use triangulation to estimate the bird's location and return at a later date. If individuals were located in the same area on three consecutive tracking events, I would navigate to the exact location to determine if the individual was alive or dead. Where mortalities were confirmed, I recovered bands and nanotags and recorded observations of bird remains. With this protocol, I was able to accurately determine the timing of mortality to one of the 13 survival intervals.

Statistical analysis – To examine differences in environmental conditions over the two years of the study, I compared total precipitation with Welch's Two Sample t-test and used linear regressions to analyze minimum and maximum temperatures. Tests were

9

conducted for the nestling period, which I defined as a 35-day window of ordinal dates 144 – 178 (May 23 – June 26) for 2016 and 139 - 173 (May 19 – June 22) for 2017. I chose these windows as they represented the maximum periods each year when nestlings were present in nests based off known or estimated hatch dates for all nestlings. I also summarized precipitation and temperature data into four measures (mean daily precipitation, total precipitation, minimum mean daily temperature, and maximum mean daily temperature) calculated over the period of growth measurements for each nestling. Variation in maximum brood size was examined using a linear regression across years and sites.

I performed a principal component analysis (PCA) to generate a composite measure of growth among the four traits (mass, wing, culmen, and tarsus). These growth rates loaded on four axes with PC1 explaining 63%, PC2 20%, PC3 10%, and PC4 7% of the variation in the data. I used the estimates of PC1 for each individual as the response variable in all models of variation in growth rate. Our dataset contained missing values for sex (32%) and rank (4%). Because these values were missing at random, I used multivariate imputation by chained equations using package 'mice' (Buuren and Groothuis-Oudshoorn 2011) in Program R (v 3.4.4; R Core Development Team 2018) to generate values. Imputation is appropriate when missingness is random, and simulation studies show that multiple imputation performs well where 50% of data is missing (Nakagawa and Freckleton 2011, Nakagawa 2015).

To analyze variation in nestling growth rates, I constructed 24 *a priori* linear mixed effects models fit with restricted maximum likelihood using package 'lme4" (Bates et al. 2015) in R. The fixed-effects of interest were: sex, year, rank in brood, brood size, site, mean maximum daily temperature, mean minimum daily temperature, mean daily precipitation, total precipitation, and hatch date. I examined Pearson's correlation coefficients for combinations of all fixed-effects and avoided models containing strongly correlated relationships ($-0.6 < r > 0.6$). Our model set included a full and null model, all univariate relationships (11), relevant multivariate models with additive combinations of fixed-effects (10) and a model with the interaction between brood size and rank in brood. In all models, I included nest ID as a random effect to account for the inclusion of multiple nestlings per nest.

I analyzed survival separately for nestlings (0-25 days) and fledglings (26-194 days). For the analysis of nestlings, I used the non-parametric Kaplan-Meier estimator (package 'survival' in R; Therneau 2015) to derive daily survival estimates and the log-rank test to compare differences in survival among groups (site, rank, year). Due to small sample size ($n = 2$), I removed fifth-ranked chicks from the comparisons of rank. Additionally, because sex was unknown for 60% of our sample (due to mortality occurring before feather collection, i.e. missing not at random), I did not include it in our analysis of nestling survival. To compare the relative value of continuous and discrete predictors, I then constructed generalized linear mixed effects models with a binomial response variable (0 = survived, 1 = died) to test 30 *a priori* models. Fixed-effects tested included rank, year, site, brood size, growth rate, hatch date, nest diameter, nest distance

to shore, nest height. Our dataset contained missing at random values for rank (11%),

nest diameter (13%), nest height (6%), growth rate (43%), and brood size (10%),

therefore I imputed values for each missing value by multiple imputation. Continuous

fixed-effects were scaled and centered. I examined Pearson's correlation coefficients and

did not include models with both site and nest distance to shore as this relationship was

highly correlated ($r = 0.97$). The final model set included all univariate relationships (9),

additive combinations (19), as well as a full and null model. All models contained nest ID

as the random effect.

For the analysis of post-fledging survival, I used package 'RMark' (Laake 2013)

in R to build known-fate models. I constructed 29 *a priori* models including univariate

and additive combinations of time, sex, site, brood size, hatch date, rank, and growth rate

in addition to a full and null model to examine the influence of carryover effects on post-

fledging survival. I evaluated multicollinearity among all covariate relationships, but did

not find strong correlations. I used multiple imputation to generate missing values for sex

(1%), rank (35%), brood size (31%), and growth rate (35%) where values were missing at

random.

For each of the three model sets tested (growth, nestling survival, post-fledging

survival), I utilized an information theoretic framework accounting for small sample sizes

(AIC_c) to rank competing models considering relative weights (w_i) and differences in

AIC_c (ΔAIC_c). I considered those models where $\Delta AIC_c \leq 2$, were without uninformative

parameters, and where 95% beta confidence intervals did not overlap zero to be plausible (Burnham and Anderson 2002, Arnold 2010).

RESULTS

Environmental conditions - Minimum daily air temperature was significantly lower in 2017 ($F_{1,68} = 4.39$, $p = 0.03$) than 2016, but there was no difference in maximum daily air temperatures ($F_{1,68} = 3.06$, $p = 0.08$) between the years. Average daily precipitation was higher in 2016, but this difference was not significant ($t_{38} = -1.19$, $p = 0.06$); total precipitation during the nestling period was also greater in 2016 (6.19 cm) than in 2017 (1.5 cm).

Nest success - From 2016-2017, I monitored 41 nests at West Sister Island ($n = 21$ in 2016; $n = 20$ in 2017) and 35 at Turning Point Island ($n = 24$ in 2016; $n = 11$ in 2017). I define nest success as ≥ 1 nestling surviving to 25 days and failure as mortality of all eggs or nestlings by 25 days. I found 23 nests with eggs, 9 with chicks and eggs, and 44 with chicks. Nesting substrates included box elder (*Acer negundo*), hackberry (*Celtis occidentalis*), mulberry (*Morus rubra*), and black cherry (*Prunus serotina*). Nest heights ranged from 0.54 – 5.96 m (3.6 ± 1.1 m), and nest diameters from 0.20 – 0.50 m (0.34 ± 0.07 m). The distances of nests from the shoreline were 154.72 ± 24.43 m for West Sister Island and 6.97 ± 5.25 m for Turning Point Island. Maximum brood size ranged from 1 to 5 (mode = 3). Maximum brood size was smaller in 2017 than in 2016 ($F_{1,70} = 5.39$, $p = 0.02$), and there was no difference in maximum brood size between the two islands ($F_{1,70} = 0.75$, $p = 0.38$). Of 76 nests, 78% were successful, 22% failed, and 5% were unknown.

Of nests that failed at the egg stage, one failed due to structural collapse, one to Great Egret (*Ardea alba*) kleptoparasitism of nest material, and one to removal of eggs by a night-heron. Causes of failure in nests at the nestling stage were due to unknown in-nest mortality (64%, $n = 9$), raccoon predation (14%, $n = 2$), a fall from nest (14%, $n = 2$), and conspecific predation (7%, $n = 1$).

Nestling growth - Growth rates were recorded for 80 nestlings at West Sister Island ($n = 49$ in 2016; $n = 31$ in 2017) and 46 at Turning Point Island ($n = 33$ in 2016; $n = 13$ in 2017). On average daily growth rates for nestling Black-crowned Night-Herons were 29.56 ± 1.08 g (mass), 2.02 ± 0.05 mm (culmen), 3.06 ± 0.08 mm (tarsus), and 7.66 ± 0.22 mm (wing; see Appendix A for average rates by rank and year). The top ranked and only model with ΔAIC_c value < 2 showed effects of rank, brood size, and year on the growth rates (PCA: PC1 estimate) of nestling night-herons (Table 1.1). Based on the dataset and models compared, there was an 86% chance that this is the best model. Parameter estimates of the top model indicate that B- (-1.91 ± 1.19, $t = -1.60$, $p = 0.11$), C- (-6.30 ± 1.32, $t = -4.77$, $p < 0.001$), and D-ranked (-9.42 ± 2.62, $t = -3.60$, $p = 0.004$) nestlings grew on average slower than A-ranked nestlings (Figure 1.2). Growth rates were higher for night-herons in 2016 compared to 2017 (-3.67 ± 1.40, $t = -2.60$, $p = 0.01$; Figure 1.2). Night-herons with more nestmates had higher growth rates (3.08 ± 0.90, $t = 3.39$, $p = 0.001$; Figure 1.3).

Nestling survival - I tracked survival of 129 nestlings at West Sister Island ($n = 72$ in 2016; $n = 57$ in 2017) and 94 at Turning Point Island ($n = 64$ in 2016; $n = 30$ in 2017).

Considering the full cohort, survival by day 25 was 0.61 (95% CI: 0.55-0.68). The median age of mortality of all nestlings that died was 6 days. Further, the median age of mortality by rank was 8, 9, 8, and 3 days respectively for A-, B-, C-, and D-ranked chicks. Comparisons between groups revealed significant differences in survival rates among ranks (log-rank test: $p < 0.001$), but no difference in survival among years (log-rank test: $p = 0.87$) or sites (log-rank test: $p = 0.07$). Survival rates were similar among A- (0.71, 95% CI: 0.61-0.83) and B-ranked chicks (0.72, 95% CI: 0.61-0.84), but declined in C- (0.59, 95% CI: 0.46-0.76) and D-ranked chicks (0.39, 95% CI: 0.22-0.69; Figure 1.5). Considering the full suite of variables, daily nestling probability of mortality was best explained by rank, brood size, growth rate, and nest height (Figure 1.6); this model contributed 91% of the total weight. Out of all models tested, this was the sole model supported by ΔAIC_c values. Consistent with the Kaplan-Meier comparison, D-ranked chicks had significantly lower survival rates than first-ranked chicks (-3.31 ± 1.09, $z = -3.10$, $p = 0.002$). Individuals with higher growth rates were more likely to survive the nestling period (1.56 ± 0.048, $z = 3.22$, $p = 0.001$). Daily nestling survival was positively correlated with nest height (0.89 ± 0.34, $z = 2.6$, $p = 0.009$). Lastly, night-herons with more nestmates had a higher probability of surviving the nestling period (1.68 ± 0.42, $z = 4.00$, $p < 0.001$).

Post-fledging survival – In 2016 and 2017, I nanotagged 79 nestlings at West Sister Island ($n = 40$ in 2016; $n = 39$ in 2017) and 30 at Turning Point Island ($n = 20$ in 2016; $n = 10$ in 2017) and monitored survival during the post-fledging period (day 26-194). Sexing revealed our sample included 58 males and 46 females; 5 were unknown

sex. Among the 26 individuals with known mortalities, 20 occurred while on the breeding colonies, 5 were recovered within the study area, and 1 was found outside the study area. The probability of survival the entire post-fledging period was 0.70 (95% CI: 0.61 - 0.81; Figure 1.7). The top ranked post-fledging survival model included sex as the sole parameter. Five models were within 2 ΔAIC_c units of the top ranked model; however, the 95% beta confidence intervals for all parameters in the top model set contained zero (Table 1.4). Additionally, the third ranked model was the null indicating low overall support for the parameters evaluated. Of the parameters, sex was included in four of the six top models suggesting some support. Post-fledging survival of males (0.75, 95% CI: 0.60 – 0.86) was greater than that of females (0.59, 95% CI: 0.43 – 0.73; Figure 1.8).

DISCUSSION

I predicted that parameters affecting survival during the nestling period would carry over to influence survival rates during the post-fledging period. First, we quantified measures of growth and nestling survival. Consistent with our predictions, we found that nestling rank influenced both growth and survival rates of nestlings in that earlier hatched nestlings both grew faster and had higher survival. Additionally, contrary to our expectations, nestlings with more nestmates had higher growth rates and were more likely to survive the nestling period. I did not find strong support that rank, brood size, or growth rate carried over to influence post-fledging survival probability. However, I provide some evidence that female night-herons were less likely to survive the post-fledging period than male night-herons (Figure 1.8). Our study shows that factors

affecting juvenile survival may vary during the pre-fledging and post-fledging periods; therefore, these life stages should be considered separately in studies of juvenile survival.

Nest success – Nest success rates in our colonies were comparable to other Black-crowned Night-Herons colonies in North America. Success rates of 78% slightly exceed those reported from Alcatraz Island, CA (36-77%; Hothem and Hatch 2004) and Chincoteage Bay, VA (71%; Erwin et al. 1996b). Predation is the main cause of nest failure in most populations of Black-crowned Night-Herons (Blus et al. 1997, Hothem and Hatch 2004). In our study however, predation pressure was low, with only 2 of 76 failing due to raccoon predation. Black-crowned Night-Herons may benefit by nesting on islands as opposed to inland colonies due to reduced predation pressure from non-avian predators. Although, this may only be true regionally as American Crows (*Corvus brachyrhynchos*), Common Ravens (*Corvus corax*), Ring-billed Gulls (*Larus delawarens*) are important predators during the egg stage in some populations (Wolford and Boag 1971, Tremblay and Ellison 1979, Brussee et al. 2016). The most common cause of failure in this population was unknown in-nest mortality, likely due to starvation of nestlings. I also noted two previously undescribed causes of nest failure in Black-crowned Night-Herons: heterospecific kleptoparasitism of nesting material and conspecific predation. In the first case, I documented a Great Egret (*Ardea alba*) removing nesting material from a Black-crowned Night-Heron nest at Turning Point Island during the egg phase. The Great Egret returned to the nest until all nest material was removed, destroying the eggs in the process. All species of colonial wading birds that nest at the breeding colonies utilize similarly sized sticks to form their nests, and thus,

17

competition for nesting material is potentially high. The Black-crowned Night-Heron parents did not attempt to re-nest in the same location. In the second case, an adult Black-crowned Night-Heron (likely not the original nest owner) forced four nestlings to fall from the nest. Two night-herons (one juvenile, one adult) then began nest maintenance (i.e. adding new sticks to nest) before eventually abandoning the site.

Nestling growth - Black-crowned Night-Herons exhibit hatching asynchrony whereby eggs within a nest hatch on different days, resulting in age differences of chicks. Additionally, night-heron egg sizes of later laid eggs are smaller than those laid earlier in clutch sizes of two and three (Custer and Frederick 1990). In combination, egg size and hatching order can magnify the size discrepancy between nestmates, especially in cases where brood size is large and hatch dates of first to last nestmates are separated by multiple days (Bitton et al. 2006, Bosman 2014). I found that hatching order had a significant effect on our combined measure of growth rate in this study in that later hatched nestlings grew slower than their older nestmates. Black-crowned Night-Herons in other parts of the breeding range exhibit this same relationship (Custer and Peterson Jr. 1991, Erwin et al. 1996b, Jungsoo and Tae-Hoe 2007). In broods with multiple nestlings, parents are likely to feed the closest, largest, and/or most responsive nestlings (Kilner and Johnstone 1997, Kölliker et al. 1998), and where there are developmental differences in chicks within a nest, younger nestlings likely receive less food than their older nestmates (Saino et al. 2000, Smiseth et al. 2003). Additionally, aggressive interactions between nestlings are widespread in Ardeidae and can contribute to feeding success rates (Mock 1985).

I found that growth rates differed between the two years of the study in that 2017 rates were lower than 2016. Environmental causes of growth variation are often linked to local weather conditions (Ricklefs 1968, Pérez et al. 2016) or prey availability (Naef-Daenzer et al. 2000, Dodson et al. 2016). Here, I did not find that growth rates were related to temperature or precipitation during the nestling period. This is understandable given that I did not find much environmental variation between the two years; however, minimum temperature was significantly lower in 2017. In Black-crowned Night-Herons, nestlings require almost constant brooding until day 10 (Chapman et al. 1981). Low ambient temperatures during this early nestling period would require more time spent at the nest versus other behaviors such as foraging and self-maintenance. In addition to the year effect of growth rates, I found that brood sizes were significantly different between the two years of the study, with smaller broods in 2017. I did not quantify prey availability in this study, but given the little environmental variation present, perhaps differences in prey would better explain the yearly growth trend. Quantifying both prey availability and environmental conditions simultaneously as well as over a longer monitoring period would increase our understanding of the temporal drivers of growth rate in this system.

Larger brood sizes require greater energy expenditure from parents, and parents often adjust their provisioning rate according to the number of nestlings in a nest (Conrad and Robertson 1993, Čech and Čech 2017). Studies of natural variation in brood size often show a negative relationship with brood size and growth rate (Kalmbach and Becker 2005, Gilliland et al. 2016). However, Black-crowned Night-Herons with more

nestmates exhibited faster growth rates in our study. Other studies on Black-crowned Night-Herons failed to show a relationship between growth rate and brood size (Erwin et al. 1996b). One possibility suggests that brood size is reflective of the ability of the parents in that healthier, more experienced parents are able to provide more food and fledge more nestlings overall than younger, less experienced conspecifics. Age-assortative mating is common in some breeding colonies of Black-crowned Night-Herons and pairs of older, more experienced birds have higher reproductive success (Fasola et al. 2001). Most night-herons were from even aged pairs in our population, but of the two nests with one juvenile and one adult, neither were successful. Alternatively, parents may adjust food delivery rates according to brood size where larger broods are provisioned more frequently. In brood size manipulation experiments of long-lived species, parental feeding rates increased in response to brood enlargement (Schreiber 1996, González-Medina et al. 2010). In both natural and manipulated brood sizes of Northern Flickers (*Colaptes auratus*), parents increased feeding rates in larger broods, but this did not result in increases in body mass of nestlings (Gow et al. 2013, Musgrove and Wiebe 2014). Although larger broods were fed more frequently overall, the per-nestling feeding rates declined (Gow et al. 2013, Musgrove and Wiebe 2014). This suggests that night-heron parents possibly increased feeding rates such that the per-nestling delivery rates were higher than that of smaller broods, facilitating the increase in growth.

Nestling survival – Our estimate of nestling survival to day 25 (0.61) is lower than that reported from a colony in Chincoteage Bay, VA (0.70-0.94; Erwin et al. 1996b). However, the negative relationship between hatching order and survival was consistent

between studies. Reduction of brood size in herons and egrets typically occurs early in the nesting period, usually within the first two weeks (Mock and Parker 1986). I found that most mortality occurred before day 10, and that the median age of mortality was earlier for D-ranked nestlings (day 3) than A-, B-, or C-ranked nestlings (days 8-9). Under Lack's original brood reduction hypothesis, the degree of brood reduction is related to temporal patterns in resource abundance. In years of high resources, reproductive output is unaffected by hatching asynchrony, but in poor years, parents reduce brood size in relation to local food supply (Lack 1947, 1954). However, one assumption of Lack's hypothesis is that mortality rates are higher in larger broods. I found that as brood size increased, so did survival probability. Brood sizes of one had the slowest growth rates and lowest survival. Similarly, in Great Blue Herons, survivorship declined with smaller broods and was lowest in brood sizes of one (Mock and Parker 1986). Herons may abandon broods of one if sufficient time remains to produce a larger brood (Mock and Parker 1986). Because growth rates were higher in larger nests, and growth rate was positively related to survival, it follows that larger broods had higher survival. In our system, it seems that, following the brood reduction period, it is beneficial to maintain a larger brood size.

Our study provides evidence that parental nest-site selection promoted survival. In mixed-species wading bird colonies, vertical nest site selection is related to body size os adults where nest heights increase with larger body sizes (Burger 1979, Park et al. 2011). Colonial wading bird colonies often host many species breeding in close proximity. At our study sites, Black-crowned Night-Herons nest with up to 5 other species of waders in

the canopy (Great Blue Heron: *Ardea herodias*, Great Egret: *Ardea alba*, Cattle Egret: *Bubulcus ibis*, Little Blue Heron: *Egretta caerulea*, Snowy Egret: *Egretta thula*). Vertical stratification of nests may reduce aggressive interactions between heterospecifics (Burger 1978). Of the nest characteristics I examined, nest height was the only predictor of nestling survival. At our colonies, parents that nested higher had more nestlings surviving to fledging. Nesting higher may provide some advantages in relation to the parents' ability to see predators, reduced potential of flooding, or simply easier access to the nest (Burger 1979). Evidence is mixed regarding the influence of nest site characteristics on fledging success in different populations of night-herons. For example, in two colonies, night-heron fledging success was also positively related to nest height, and higher nests were less likely to be predated by black rats (Ashoori and Barati 2013, Etezadifar and Barati 2015). In another study, nest height was unrelated to fledging success, but was negatively related to the distance from the tree trunk where mortality was associated with adverse weather (Kim and Koo 2009). These mixed effects suggest that nest site selection of night-herons is site specific and likely related to local predation pressure as well as competition with other wading birds.

Because our nestling dataset contained a high level of missingness for the variable 'sex', I was unable to include it in our nestling analysis and I cannot rule out the potential contribution of sex as a predictor of nestling survival rate. Most commonly, sex-biased survival occurs where sexual size dimorphism is present and survival is related to the body size and/or weight of an individual (e.g. Martin et al. 2007). However, sex-biased survival can also occur where there is no size difference (Clutton-Brock 1991). I used

feathers as genetic material in this study, but contour feathers do not become unsheathed until day 10 in Black-crowned Night-Herons resulting in no data for individuals that died during the brood reduction period. Future studies should prioritize collection of genetic material early in the nesting period and investigate the role of sex on nestling survival probability given that differences appear to exist post-fledging.

Post-fledging survival – Of the models I evaluated, I found some evidence that survival during the post-fledging period is influenced by the sex of the fledgling. During this period, survival was higher for males than females. Sex-biased mortality can be related to size differences between sexes where the larger sex faces greater consequences of reduced food availability given their higher nutritional requirements (Anderson et al. 1993). Alternatively, mortality can be higher for the smaller sex and related to sibling competition during the nestling stage (Arroyo 2002). Size differences of male and female Black-crowned Night-Herons are moderate with males being slightly larger (Pyle 1997), and I did not detect a difference in growth rates of nestling male and females. Regardless, sex-biased juvenile mortality is one mechanism that can contribute to variation in adult sex ratio, especially when natal philopatry is high (Kalmbach and Benito 2007). A reduction in the number of breeding females can greatly alter the trajectory of a population (Donald 2007). To further understand the relative impact of male-biased juvenile survival in this population, I would need to quantify rates of recruitment at our study colonies and examine the sex ratio of adult birds.

Although I believe that the assumptions of the known-fate model were met in this study and that the post-fledging survival estimates are valid, there may be some bias in the evaluation of hatching order as a survival predictor. The proportion of fledglings of different ranks was uneven in our dataset, with only 4% of values represented by third-ranks and no fourth-rank individuals. Since survival differences between first-ranked and second-rank night-herons were marginal during the nestling period, it is not surprising that I didn't detect a difference in survival between ranks during the post-fledging period. Consistent with our results however, in Little Egrets (*Egretta garzetta*), rank in brood had no effect on survival during the first year (Hafner et al. 1998).

Few studies have examined post-fledging survival rates in wading birds, but from what is known, survival estimates seem to vary considerably among species and cohorts. In Wood Storks and Little Egrets, studied over 4 and 7 years respectively, rates of survival varied widely among years (Hafner et al. 1998, Hylton et al. 2006, Borkhataria et al. 2012). In the Wood Stork study, yearly trends of hydrological conditions were closely linked to lower survival rates in that early onset of the rainy season created unfavorable foraging conditions which caused individuals to disperse far from their natal area in the Everglades (Borkhataria et al. 2012). I found little variation in environmental conditions between the two years of the study, and it follows that survival rates were consistent (0.68 ± 0.07 in 2016 and 0.66 ± 0.09 in 2017). In a study of Reddish Egrets where survival analysis continued past the dispersal/migratory period, survival rates declined during the second year indicating that overwinter survival could be an important bottleneck for hatch-year wading birds (Geary et al. 2015).

Conclusion – While predictors of juvenile survival have been widely examined in avian research, the logistical and technical difficulties associated with collection of simultaneous predictors and the geographic and temporal scale at which birds move during the juvenile period has limited our understanding of this stage. As technology used to track birds continues to expand, it will become increasingly feasible to follow survival of individuals over longer periods of time, which is necessary for species with delayed reproduction. Like previous studies, my research indicates that survival of nestling wading birds is strongly related to individual variation associated with hatching order, growth rate, and brood size. Although I failed to find a link between predictors of survival from pre- to post-fledging, I identified that survival may be male-biased during the post-fledging period. With knowledge of the spatial scale of movement during the post-fledging period, future studies could examine additional predictors such as local prey availability and hydrological conditions. Importantly, my research highlights the need to consider predictors separately during the pre- and post-fledging periods, as overall survival rates and drivers of survival may operate differently between these two periods. Black-crowned Night-Heron populations are declining throughout the Great Lakes region (Rush et al. 2015), and are protected as a threatened species in Ohio (Ohio Department of Natural Resources 2017). Thus, given their status and the apparent complexities affecting post-fledging survival, further investigations of this life stage, especially studies that follow cohorts through their second year (age at first breeding), would increase our understanding of the relative contribution of juvenile survival rates to the population dynamics of Black-crowned Night-Herons.
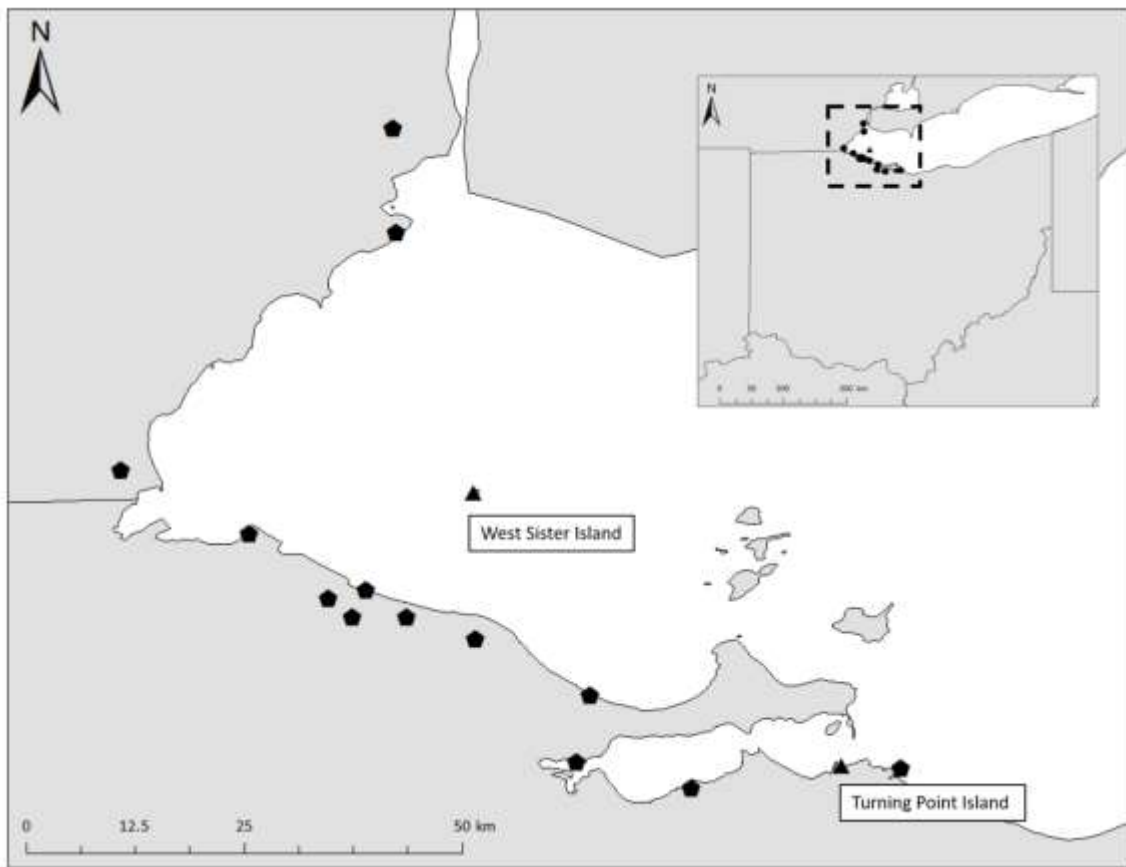
Figure 1.1. Location of the Black-crowned Night-Heron colonies (triangles) where sampling and tagging occurred and the telemetry towers (pentagons) used to detect night-herons during June through November in 2016 and 2017.
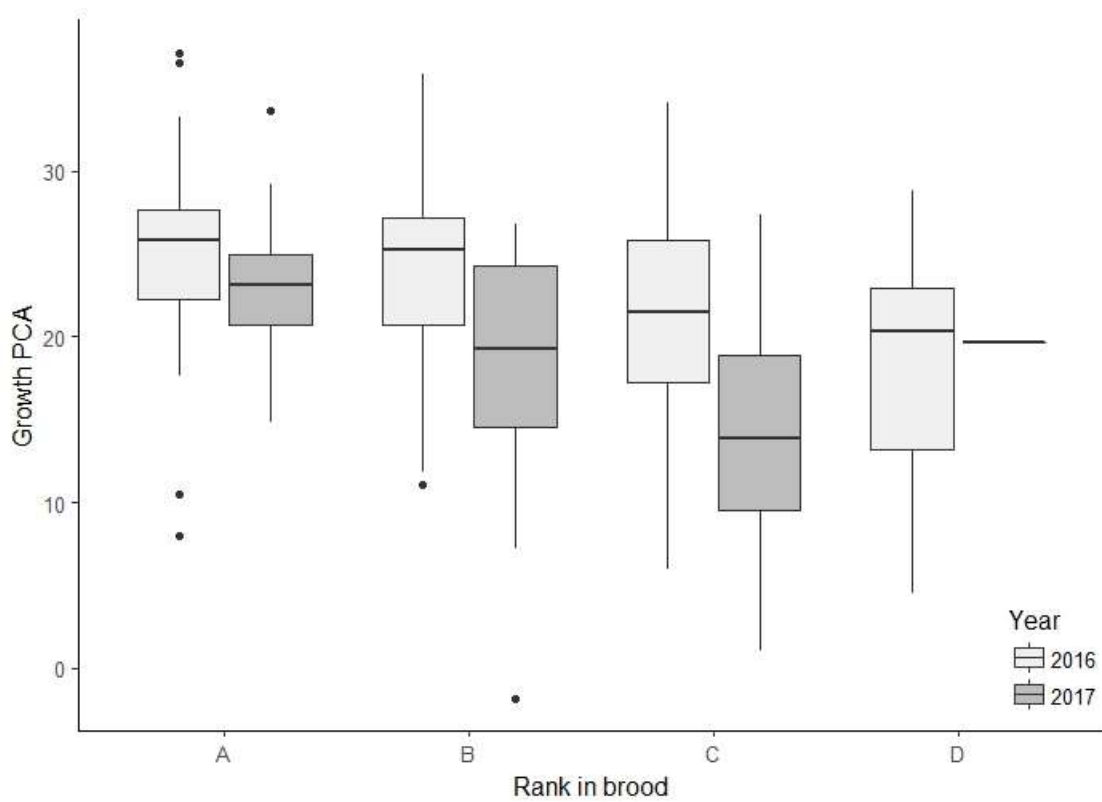
Figure 1.2. Relationship between nestling growth rates (PCA: PC1 estimate) with rank and year for 125 Black-crowned Night-Herons at West Sister Island and Turning Point Island in Lake Erie, OH in 2016 and 2017.
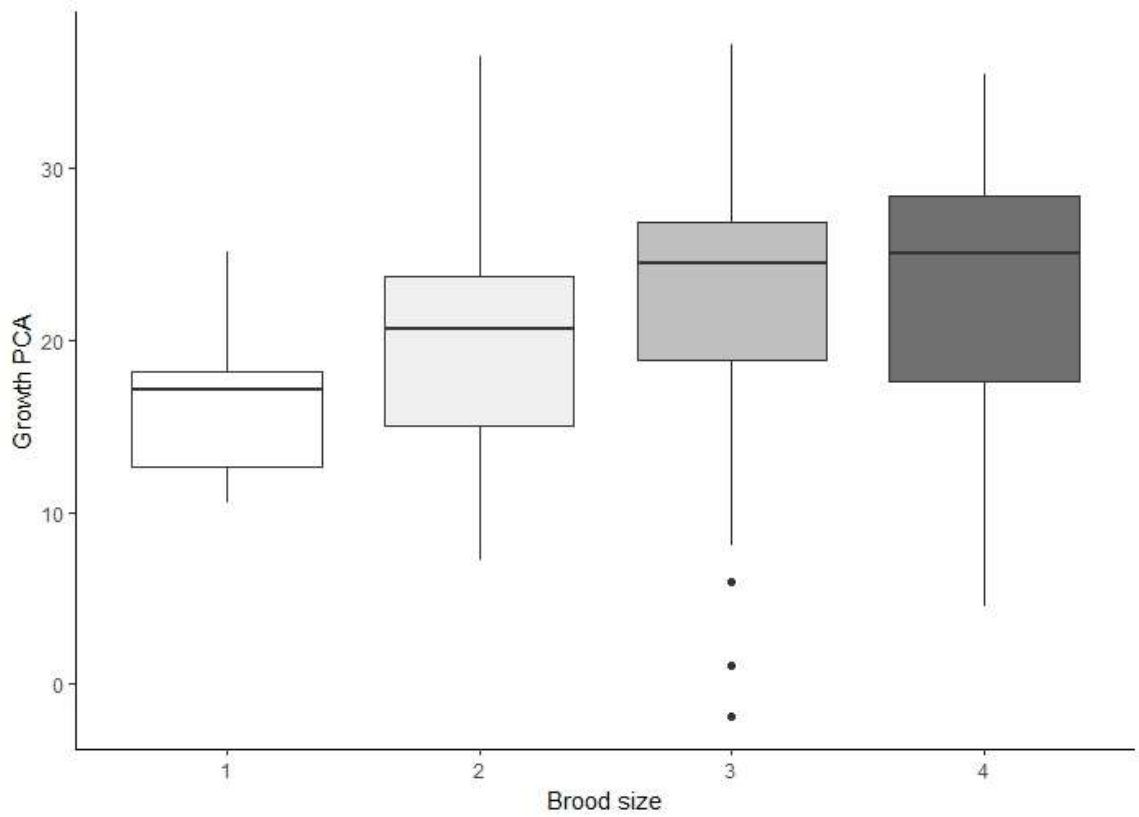
Figure 1.3. Relationship between growth rates (PCA: PC1 estimate) and brood size for

125 Black-crowned Night-Herons at West Sister Island and Turning Point Island in Lake

Erie, Ohio in 2016 and 2017.
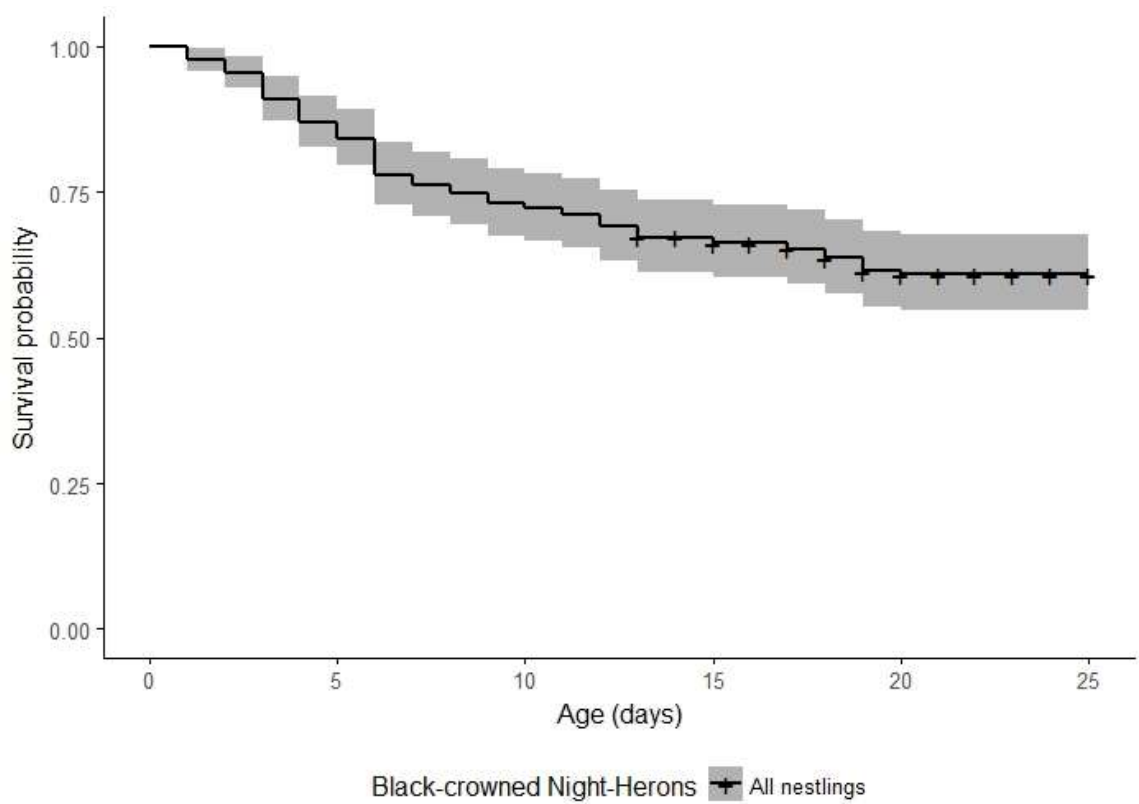
Figure 1.4. Daily survival rate for 223 Black-crowned Night-Heron nestlings from West Sister Island and Turning Point Island in Lake Erie, Ohio monitored in 2016 and 2017.
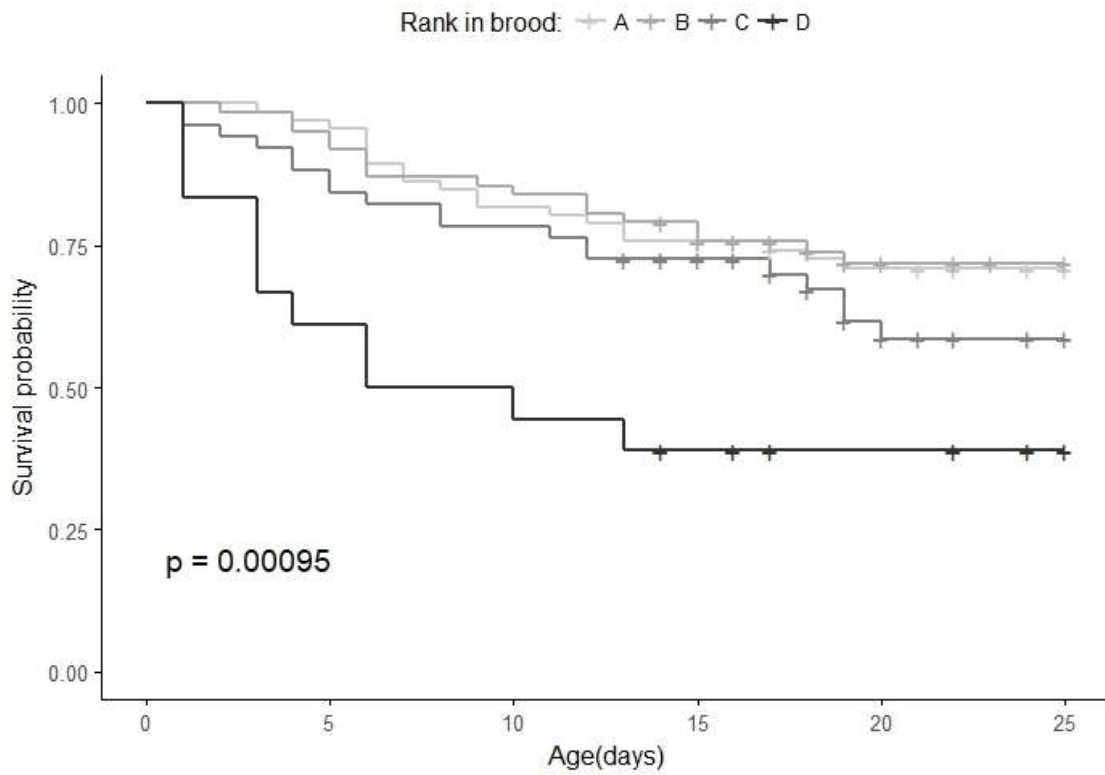
Figure 1.5. Daily survival rate for 199 Black-crowned Night-Heron nestlings of different ranks from West Sister Island and Turning Point Island in Lake Erie, Ohio monitored in 2016 and 2017.
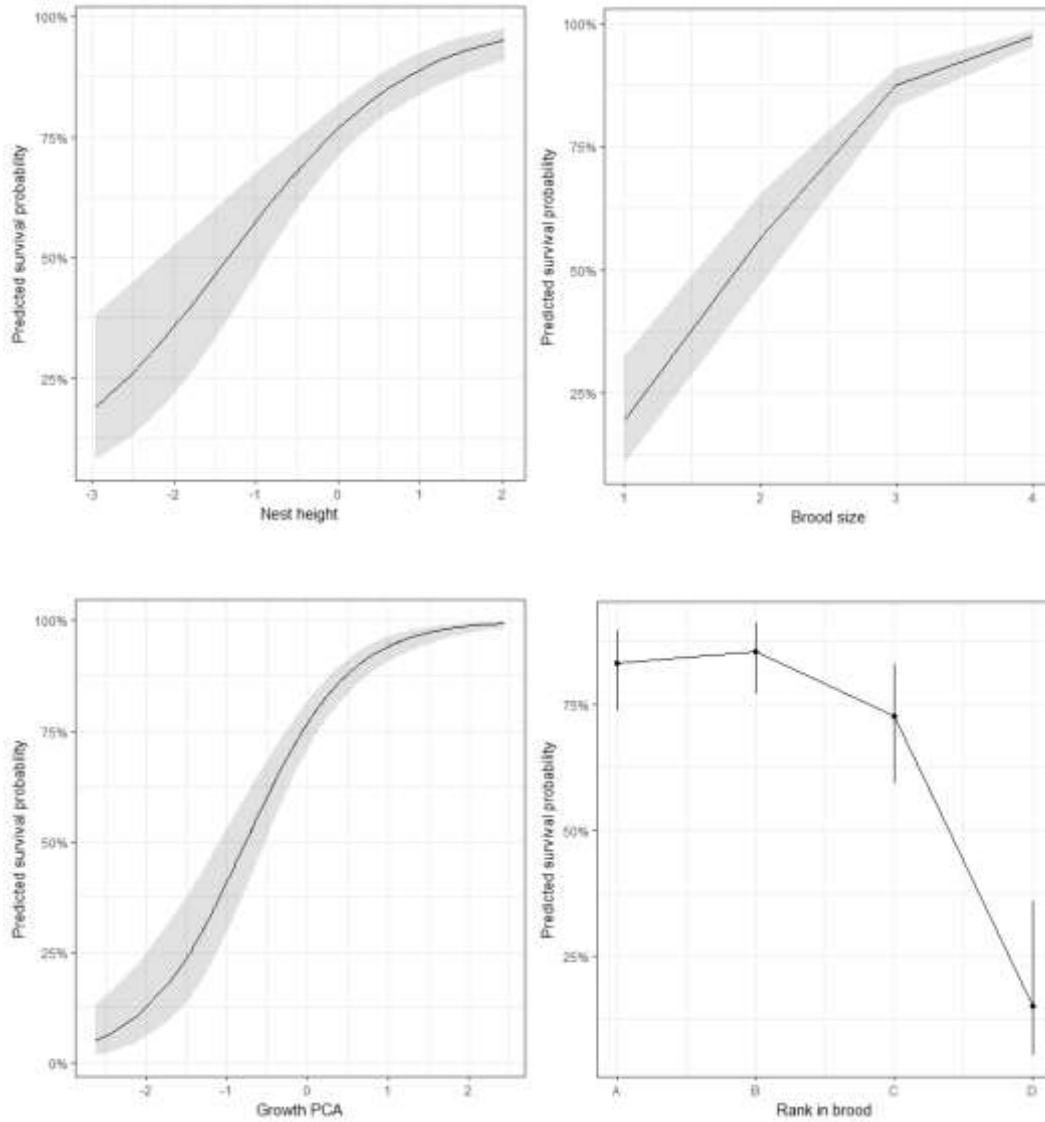
Figure 1.6. Marginal effects of the top model predicting nestling survival probability of

Black-crowned Night-Herons in Lake Erie, Ohio during 2016 and 2017. Shaded regions

and error bars represent 95% confidence intervals.
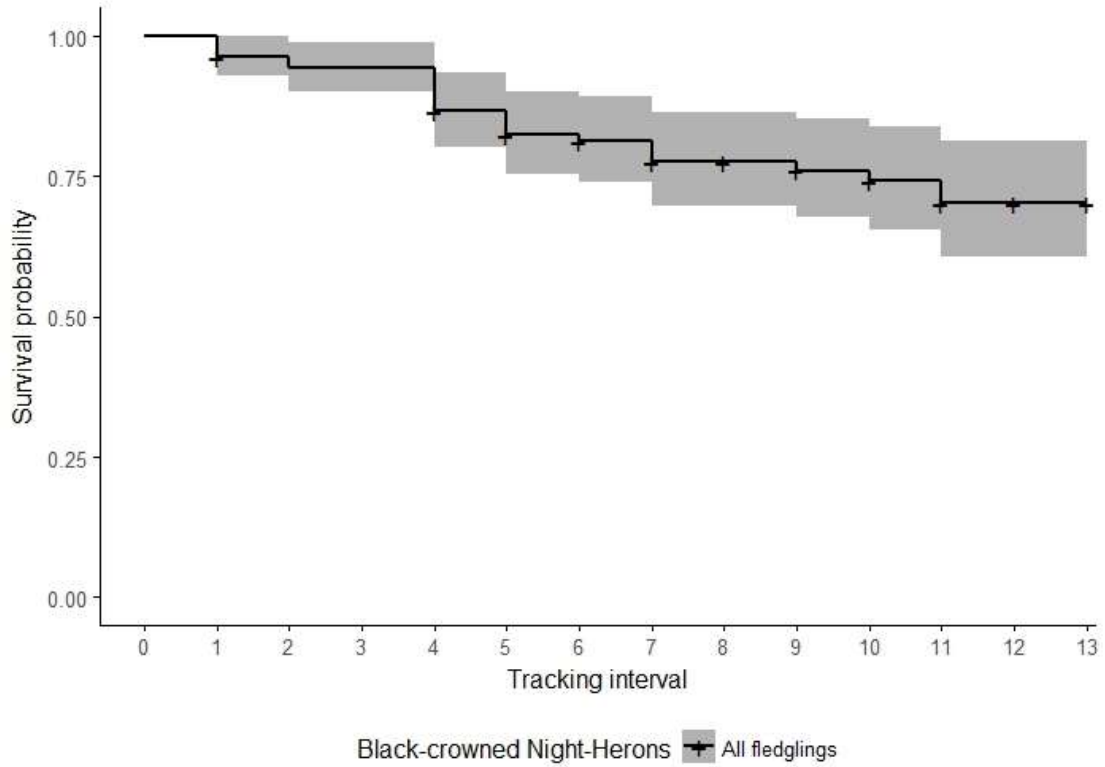
Figure 1.7. Interval (13-day) survival rate for 109 Black-crowned Night-Heron fledglings from West Sister Island and Turning Point Island in Lake Erie, Ohio monitored in 2016 and 2017. Tracking intervals begin on June 13 and ended on November 28.
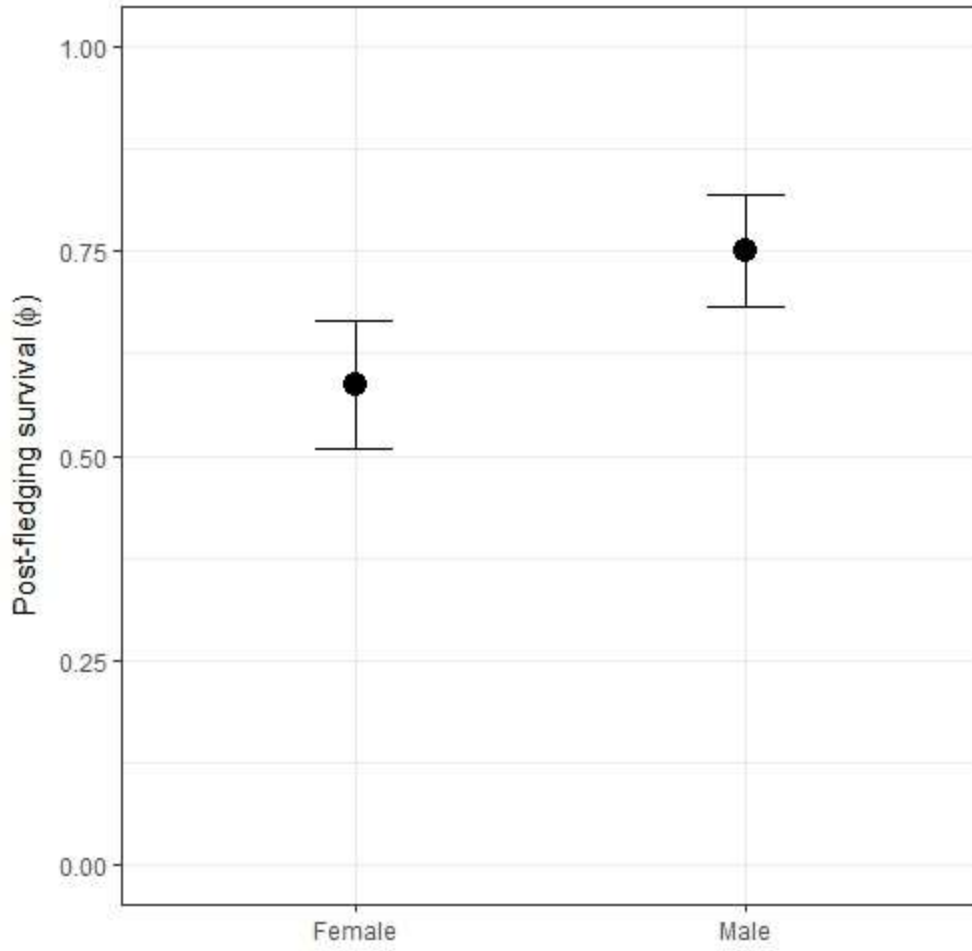
Figure 1.8. Estimates of post-fledging survival (± SE) for male and female juvenile

Black-crowned Night-Herons monitored in western Lake Erie from June to November

2016-2017.

Table 1.1. Akaike's Information Criterion (AIC$_c$) rankings of our full set of linear mixed effects models examining the effects of sex, year, rank in brood, brood size, site, mean maximum daily temperature, mean minimum daily temperature, mean daily precipitation, total precipitation, and hatch date on Black-crowned Night-Heron growth rate (PCA: PC1 estimate) at two island breeding colonies in Lake Erie, Ohio.

Growth models	AIC$_c$	ΔAIC$_c$	w_i	Log-likelihood	k
brood size + rank + year	826.03	0.00	0.86	-404.40	8
brood size + rank	829.94	3.90	0.12	-407.49	7
full model	836.00	9.96	0.01	-403.36	13
brood size*rank	836.38	10.34	0.00	-407.22	10
rank + sex + year	836.97	10.94	0.00	-409.87	8
rank	839.98	13.95	0.00	-413.63	6
rank + site	842.10	16.07	0.00	-413.57	7
mean precipitation + minimum temperature + rank	843.92	17.88	0.00	-413.34	8
maximum temperature + rank + site + total precipitation	846.40	20.37	0.00	-413.42	9
brood size + sex + year	846.70	20.66	0.00	-416.99	6
year	847.01	20.98	0.00	-419.34	4
brood size	849.93	23.90	0.00	-420.80	4
hatch date + sex + year	850.34	24.31	0.00	-418.81	6
brood size + site	851.87	25.83	0.00	-420.68	5
brood size + mean precipitation + minimum temperature	852.02	25.99	0.00	-419.66	6
null model	853.60	27.56	0.00	-423.70	3
minimum temperature	855.32	29.28	0.00	-423.49	4
mean precipitation	855.36	29.32	0.00	-423.51	4
sex	855.57	29.54	0.00	-423.62	4
maximum temperature	855.67	29.64	0.00	-423.67	4
total precipitation	855.68	29.65	0.00	-423.67	4
hatch date	855.71	29.67	0.00	-423.69	4
site	855.71	29.68	0.00	-423.69	4
brood size + maximum temperature + site+ total precipitation	856.13	30.10	0.00	-420.59	7

Table 1.2. Akaike's Information Criterion (AIC$_c$) rankings of our full set of generalized

linear mixed effects models examining the effects of sex, year, rank in brood, brood size,

site, hatch date, nest height, nest distance to shore, and nest diameter on nestling survival

probability of Black-crowned Night-Herons at two island breeding colonies in Lake Erie,

Ohio.

Nestling survival models	AIC$_c$	ΔAIC$_c$	w_i	Log-likelihood	k
brood size + rank + growth + nest height	184.93	0.00	0.91	-84.12	8
full model	190.15	5.22	0.07	-82.32	12
brood size + rank + growth	192.52	7.59	0.02	-89.00	7
brood size + rank + growth + site + year	195.24	10.31	0.01	-88.19	9
brood size + rank	208.39	23.46	0.00	-98.00	6
growth	208.83	23.91	0.00	-101.36	3
growth + rank	209.28	24.35	0.00	-98.44	6
growth + hatch date	210.52	25.59	0.00	-101.17	4
growth + site + year	211.30	26.38	0.00	-100.51	5
brood size	241.00	56.07	0.00	-117.45	3
brood size + site + year	244.74	59.82	0.00	-117.23	5
brood size + nest diameter + site	244.75	59.82	0.00	-117.24	5
brood size + nest distance to shore + year	245.08	60.15	0.00	-117.40	5
rank	256.46	71.53	0.00	-123.09	5
rank + site + year	259.35	74.43	0.00	-122.41	7
null model	272.31	87.38	0.00	-134.13	2
hatch date	272.34	87.41	0.00	-133.11	3
nest height	272.58	87.65	0.00	-133.23	3
nest distance to shore	272.81	87.88	0.00	-133.35	3
nest diameter	273.25	88.33	0.00	-133.57	3
site	273.62	88.69	0.00	-133.75	3
year	274.34	89.41	0.00	-134.11	3
site + nest distance to shore + year	274.62	89.69	0.00	-132.17	5
nest height + site + hatch date	274.67	89.74	0.00	-132.19	5
nest height + nest distance to shore + nest diameter	274.91	89.98	0.00	-132.31	5
site + hatch date + year	275.97	91.04	0.00	-132.85	5
site + nest height + year	276.19	91.27	0.00	-132.96	5
site + nest diameter + year	276.90	91.97	0.00	-133.31	5

Table 1.3. Akaike's Information Criterion (AIC_c) rankings of our full model set of known-fate models examining the effects of sex, year, rank in brood, brood size, site, hatch date, and time on post-fledging survival probability of Black-crowned Night-Herons at two island breeding colonies in Lake Erie, Ohio.

Post-fledging survival models	AIC_c	ΔAIC_c	w_i	Log-likelihood	k
sex	234.56	0.00	0.12	97.94	2
sex + rank	234.77	0.21	0.11	94.11	4
null model	235.03	0.47	0.10	100.42	1
rank	236.11	1.55	0.06	97.47	3
rank + sex + site	236.20	1.64	0.05	93.53	5
sex + growth	236.50	1.94	0.05	230.47	3
year + sex	236.57	2.01	0.04	97.93	3
sex + rank + growth	236.57	2.01	0.04	226.50	5
hatch date	236.62	2.06	0.04	232.60	2
growth	236.91	2.35	0.04	232.90	2
hatch date + sex + site	236.94	2.38	0.04	228.89	4
year	236.99	2.43	0.04	100.37	2
site	237.01	2.45	0.04	100.39	2
brood size	237.03	2.47	0.04	233.02	2
time	237.37	2.81	0.03	78.34	13
rank + growth	237.83	3.27	0.02	229.78	4
brood size + rank	238.12	3.56	0.02	230.07	4
brood size + sex + site	238.16	3.60	0.02	230.11	4
sex + year + growth	238.51	3.95	0.02	230.47	4
hatch date + growth	238.58	4.02	0.02	232.55	3
hatch date + brood size	238.62	4.06	0.02	232.60	3
brood size + growth	238.92	4.36	0.01	232.89	3
growth + time	239.24	4.68	0.01	210.74	14
year + time	239.44	4.88	0.01	78.33	14
brood size + rank + growth	239.77	5.21	0.01	229.70	5
site + brood size + hatch date	240.62	6.06	0.01	232.57	4
brood size + rank + time	240.70	6.14	0.01	208.06	16
site + year + time	241.50	6.94	0.00	78.33	15
full model	244.63	10.07	0.00	201.52	21

Table 1.4. Parameter estimates (β), standard error (SE), and 95% confidence intervals (CI) for parameters in the six most supported models examining the effect of covariates on the post-fledging survival of Black-crowned Night-Herons at two island breeding colonies in Lake Erie, Ohio. Parameter estimates were derived from the highest-ranking model for which each effect is included. Sex [M], rank [A], and site [West Sister Island] are not shown, since they are the baselines from which survival in other levels were compared.

Parameter	β	SE	95% CI
sex [F]	-0.6338	0.4091	[-1.4356, 0.1680]
rank [B]	0.2683	0.4185	[-0.5520, 1.0886]
rank [C]	17.8487	7595.5655	[-14869.4600, 14905.15700]
site [Turning Point Island]	0.3407	0.4512	[-0.5436, 1.2250]
growth	0.0072	0.0260	[-0.0437, 0.0580]

Chapter 2: Migration strategies and nonbreeding ecology of Black-crowned Night-Herons (*Nycticorax nycticorax*)

INTRODUCTION

Effective conservation of declining wildlife populations relies upon accurate knowledge of where and when individuals are throughout their annual cycle. In migratory birds, the annual cycle is made up of four stages: breeding (and post-fledging), feather molt, migration, and nonbreeding. As many as 60% of North American migratory birds are in decline (Rosenberg et al. 2016), and populations can be limited during one or more stages of the annual cycle. These stages are often linked through carry-over effects whereby individual fitness in a given stage is determined by events and experience in a preceding stage (Harrison et al. 2011, O'Connor et al. 2014). Within avian research however, there are a disproportionate number of studies conducted solely during the breeding stage (Marra et al. 2015). For example, the breeding ecology of wading birds has received much attention (e.g. Frederick et al. 1992, Kelly et al. 1993, Auclair et al. 2015, Brzorad et al. 2015, Brussee et al. 2016), while the remaining stages of their life cycle have received comparably little (but see Ledwón and Betleja 2015, Stier et al. 2017, Koczur et al. 2018). By ignoring certain stages or overlooking carry-over effects occurring across stages, we limit our understanding of processes that regulate the population dynamics of a species (Schaub and Abadi 2011, Marra et al. 2015).

Over half of the bird species that breed in North America are migratory and although migration frequently represents a small portion of the annual cycle, it is often the most energetically costly and hazardous stage (Newton 2008). As a result, mortality levels are often greatest during this stage (Sillett and Holmes 2002, Klaassen et al. 2014). Accordingly, individuals minimize either the amount of time spent and/or the amount of energy expended while migrating, and strategies operate differently in spring and autumn (Alerstam and Lindström 1990). In autumn, migrants generally conserve energy by travelling slower and stopping more, compared to spring when migrants adopt a time minimization strategy of travelling at higher speeds for shorter durations (Nilsson et al. 2013). Arriving early to the breeding grounds in spring can confer important fitness benefits such as acquisition of high quality nesting sites and greater reproductive output (Currie et al. 2000, Morbey and Ydenberg 2001, Smith and Moore 2005). Although less understood, early arrival to nonbreeding areas may influence body condition and survival during the nonbreeding period especially of territorial species (e.g. Stutchbury et al. 2010).

Migratory strategy with regard to routes and stopover behavior can differ markedly within and between populations (Yosef and Wineman 2010, Weimerskirch et al. 2015). For example, in the UK population of common cuckoos (*Cuculus canorus*), there are two distinct migratory routes in autumn and the choice of route can influence mortality risk (Hewson et al. 2016). Stopover behavior is influenced by an individual's energetic condition during migration (Smith and McWilliams 2014), and stopover decisions may be different between sexes and age classes due to differing selective

pressures and experience levels (Morbey and Ydenberg 2001, Yosef and Wineman 2010). Migration phenology and, in some cases, migration strategy appear to be changing in response to recent global climate change (Mills 2005, Gilbert et al. 2016). Therefore, our ability to predict and respond to individual or population changes in migration relies on solid baseline knowledge of migration behavior in autumn and spring.

The nonbreeding period often makes up the largest portion of the annual cycle of migratory species (Marra et al. 2015), although knowledge about general ecology during this period is lacking for many species. For many migratory species with large breeding ranges, their nonbreeding ranges often span similarly large areas, encompassing considerable environmental variation (Newton 2008). Choice of nonbreeding habitat can influence survival rates (Johnson et al. 2006) and overall energy expenditure which can, in turn, carry over to affect individual fitness in subsequent stages (Reudink et al. 2009, Harrison et al. 2011, Alves et al. 2013).

The oldest and most widely used form of tracking birds throughout the annual cycle is through bird banding (Newton 2008). Avian research programs result in a vast number of birds captured annually in the United States, but recapture rates at distant sites are often quite low (i.e., < 0.1% for passerines; Ryder et al. 2011, Brown and Miller 2016), complicating any robust analysis attempts. However, our ability to track individuals throughout the annual cycle has improved greatly in the last two decades due to the advancements in tracking technology especially through tag minimization and increases in location accuracy (López-López 2016). Satellite tracking via global

positioning systems currently offers the most accurate location data, but other methods such as geolocators and very high frequency telemetry are also widely used (López-López 2016). Because the cost of high resolution tracking devices is prohibitive, the number of individuals that can be tracked is often limited. Integrating multiple data sources can be an attractive way to overcome this issue and ultimately gain a more accurate picture of the full annual cycle of a species (Ryder et al. 2011, Van Wilgenburg and Hobson 2011, Rushing et al. 2013).

With recent advances in tracking technology came associated modifications and improvements in the statistical methodology of quantification of home range size (Walter et al. 2015). The home range is a fundamental spatial unit that defines an area in which animals carry out daily and/or seasonal tasks of foraging, reproduction, offspring care, and resting over a defined period of time (Burt 1943). Moreover, home range sizes may vary between individuals, and in many cases home range sizes are related to resource abundance and population size (Sprent and Nicol 2012, Efford et al. 2016). Accordingly, animals may shift the size of their home ranges or relocate to new areas in response to seasonal changes in availability of resources (e.g. Stirrat 2003). Examining space use during stopover and nonbreeding periods can also elucidate the degree to which species and individuals use the same habitat types in different periods. For example, species may track ecological niches through different seasons or switch to a different niche between seasons (Martinez-Meyer et al. 2004). Quantifying differences in home range size and spatial overlap within and across species can provide crucial information necessary for effective management at appropriate scales of species of conservation concern.

While most populations of North American herons are at least partially migratory, we have little information on migratory behavior or connectivity of populations to specific nonbreeding areas (but see Mikuska et al. 1998). This is likely due to the large overlap in stationary nonbreeding and year-round ranges of many species within Ardeidae along with the lack of data from tracking studies (but see Huschle et al. 2013). One such heron species, the Black-crowned Night-Heron (*Nycticorax nycticorax*), is listed as threatened, endangered, or a species of concern in ten states, seven of which can be found in the Great Lakes region (Hothem et al. 2010). I studied the species in Ohio where the number of active breeding colonies of Black-crowned Night-Herons has declined significantly since the 1970s, likely due to land use changes, in particular the large-scale conversion of wetlands to agriculture (Dahl and Johnson 1991, Rodewald et al. 2016). To date, fine-scale tracking of Black-crowned Night-Heron movements has been limited to one study documenting post-breeding migration of two night-herons from a population in the Upper Vistula Valley of Poland (Ledwón and Betleja 2015). This study documented a strategy of traveling slowly with several long stopovers resulting in a migration of at least two months ending in the Sahara Desert, some 4000 km from the breeding grounds. Other knowledge of migration routes and nonbreeding locations of Black-crowned Night-Herons has been derived from recoveries and resightings of birds banded within North America. From these data, three strategies were identified: short-distance (< 2,000 km), long-distance (>2,000 km), and sedentary (Danny Bystrack, USGS Bird Banding Lab, unpublished data). Recoveries indicate that birds breeding in

the Upper Midwest Great Lakes Region can be found during the nonbreeding period in the Caribbean, with Cuba serving as the core nonbreeding site (Marra et al. 2014).

In this study, I investigated the migratory and nonbreeding seasons of Black-crowned Night-Herons to fill gaps in our understanding of the full annual cycle of this species. I combined tracking and band recovery data to: 1) determine the migratory strategy of Ohio night-herons 2) identify autumn and spring migratory routes 3) examine correlations between migratory characteristics within and between seasons (timing, duration, distance, speed) 4) describe the nonbreeding distribution of Black-crowned Night-Herons captured in Ohio 5) estimate winter home range sizes, and 6) identify habitat types available during stopover and nonbreeding areas.

METHODS

Field Methods - I captured 17 adult Black-crowned Night-Herons at 3 sites in the western basin of Lake Erie, Ohio from June to September 2016-2017. I marked 9 individuals at Turtle Creek Marina (41.61°N, 83.13°W), 5 individuals at Wild Wings Marina (41.60°N, 83.11°W), and 3 individuals at Turning Point Island (41.46°N, 82.73°W). I attracted night-herons to trapping sites baited with cleaned Walleye (*Sander vitreus*) and Yellow Perch (*Perca flavescens*) carcasses, and captured birds using a bungee net (*n*=15), a net gun (*n*=1), or a net launcher (*n* = 1; Woodin et al. 2012, Clark et al. 2014). Upon capture, I collected morphometric data (culmen length, tarsus length, wing chord, and mass) and banded birds with U.S. Geological Survey aluminum bands and one alphanumeric color band for field identification. I then attached platform

transmitting terminals (TAV-2630, Telonics, Inc.) to Black-crowned Night-Herons with a

backpack harness made of 6-mm Teflon ribbon (Telonics, Inc.). The transmitters transmit

data to low-orbiting satellites that collect and relay information to Argos processing

centers where location data is calculated using the Doppler Effect (Argos User's Manual

http://www.argos-system.org/manual/). Transmitters ranged from 3.4-5% of the

individual's body mass. At the time of capture, I also collected DNA samples (3-6

feathers), which I later used to determine the sex of all captured adults via PCR following

Wang et al. (2011).

     Data collection and processing - I varied duty cycles of transmitters among

seasons to optimize data collection, maximize battery life, and to meet the project

objectives. Units were programmed to gather locations from 1:30 – 5:30 UTC every day

during spring (30 Mar – 30 Jun) and autumn migration (31 Aug – 30 Nov), every other

day during nonbreeding (1 Dec – 29 Mar), and every third day during breeding (30 Jun –

30 Aug). Data were collected using the Argos system and processed using the Kalman

Filter (Argos User's Manual http://www.argos-system.org/manual/). Locations received

from the Argos system are categorized into a location class (LC) based on the level of

precision associated with each point. Argos reports the following estimated error values:

LC 3 (< 250 m), LC 2 (250 – 500 m), LC 1 (500 – 1500 m), and LC 0 (> 1500 m). LC A

and LC B are also reported, but no accuracy estimation is provided. Prior to analysis, I

used the hybrid Douglas Argos Filter in Movebank to filter the original locations

(Douglas et al. 2012). The Douglas filter flags implausible locations based on user-

defined thresholds of movement rate, spatial redundancy, and angles between movements

(Douglas et al. 2012). For measurements of distance and for mapping of migratory routes, I used only these filtered locations. I included all locations in calculating timing of migration. For home range analysis, I included only locations in LC3 and LC2. I performed all subsequent analyses in ArcGIS 10.3 (ESRI, Redlands, CA, USA) and Program R (v 3.4.4; R Core Development Team 2018). All movement data are archived at www.movebank.org.

I defined four periods of movement during Black-crowned Night-Herons' annual cycle: breeding, autumn migration, stationary nonbreeding, and spring migration. Additionally, I summarized migration characteristics into seven categories: departure date, arrival date, distance to nonbreeding area, migration duration, stopover events, stopover duration, and flight speed. Because all individuals traveled southward in autumn and northward in spring, I defined departure as the first day a bird was located $\pm 0.5°$ latitude away from stationary areas. Arrival at breeding/nonbreeding sites was defined as the first 15 or more days with locations clustered around a defined area. For instances when transmitters did not capture exact departure or arrival due to varying duty cycles, I report the date corresponding to the median of the collected locations. The geodesic distances (km) from capture site to nonbreeding areas in autumn and from nonbreeding areas to breeding areas in spring were calculated with the 'near' feature within the ArcMap proximity toolset (ESRI, Redlands, CA, USA). The migration duration was defined as the arrival date less the departure date. Stopover events were identified by groups of locations ≤ 15 km apart during migration preceded and followed by movements of > 15 km. I then calculated the duration of stopover events in days. Due to the duty

cycle of the transmitters, I was unable to identify stopover events of < 48 hours. I calculated flight speed (km/day) by dividing the migration distance by the migration duration, subtracted by the number of days on stopover. Migration routes were mapped by connecting consecutive locations with straight lines.

In addition to data from satellite tracking, I used two ancillary datasets to determine nonbreeding locations of Black-crowned Night-Herons. First, I examined band recovery and re-sighting data of Black-crowned Night-Herons banded in Ohio provided by the Bird Banding Lab, USGS Patuxent Wildlife Research Center. Initial banding occurred from 1936 to 2016, and all individuals were banded as nestlings or fledglings at five locations in Ohio. Second, I used locations of nanotagged night-herons detected on Motus telemetry towers (see Chapter 1). All nanotagged (Tag mass: 4.8g, NTQB-6-2, Lotek Wireless Inc.) individuals were marked as nestlings or fledglings at West Sister Island (41.73°N 83.10°W) or Turning Point Island as part of a study examining post-fledging survival (see Chapter 1). I include only recoveries, re-sightings, or detections of birds made during the nonbreeding period defined as December – March to ensure that these locations were during a stationary period.

Home range and stopover estimation - I estimated home ranges of Black-crowned Night-Herons while on their stationary nonbreeding areas. If birds moved > 20 km during the nonbreeding period and remained at a site for > 15 days, I considered these relocations to be separate home ranges. For the home range analysis, datasets of individuals that did not have spring migration data (either due to tag failure/loss or

mortality) were restricted by excluding locations once consecutive distances were below

the location error of LC 3 (< 250 m apart). I used the package 'BBMM' (Nielson et al.

2013) in R to calculate a 95% home range and a 50% home range to represent the core

area of use. By foregoing the assumption of independence between locations, the

Brownian Bridge movement model (BBMM) has advantages over traditional kernel-

density home range estimators. Because Argos locations depend on the spatial orientation

of satellites, the timing of consecutive locations is unpredictable and often autocorrelated.

The BBMM is particularly suited to Argos data because of its ability to incorporate

location error and serially correlated locations into the estimated utilization distributions.

In order to match the resolution of the land cover dataset (see below) and allow

comparisons between individuals, I set the cell size to be 30 m and the extent of each

home range to be 500 x 500 km.

I used package 'adehabitatHR' (Calenge 2006) in Program R to calculate

Minimum Convex Polygons (MCP) for each stopover event. While less accurate than

BBMM home ranges (Walter et al. 2015), MCPs are appropriate where sample size is

small (< 50 locations) (Seaman et al. 1999). Sample size was dependent on the length of

stopover, but was often fewer than 50 locations.

Stopover and nonbreeding habitat - To identify land cover types available to

night-herons during stopover and nonbreeding periods, I superimposed the BBMM 50%

core home ranges and stopover MCPs of Black-crowned Night-Herons with the National

Land Cover Database (NLCD; Homer et al. 2015). For BBMM home ranges located

outside of North America, I digitized habitat types in ArcGIS using the classifications in the NLCD by examining aerial imagery (Base imagery source: DigitalGlobe). Cell counts of habitat types were standardized by stopover MCP or BBMM home range size and weighted accordingly for individuals with multiple stopovers or home ranges. I report the cumulative percentage of each landcover type available within stopover areas and stationary nonbreeding home ranges.

Statistical analysis – Using Pearson's correlation coefficients, I evaluated the relationships between autumn and spring arrival dates and migratory parameters (departure date, stopover duration, flight speed, and migration distance). Pearson's correlations were also used to examine the relationships between spring and autumn departure and arrival. Differences in the speed, stopover duration, and migration duration of spring and autumn within individuals were compared using paired t-tests. I also conducted an *a posteriori* evaluation of autumn migration strategy. I identified a bimodal distribution of migration duration which was determined by whether an individual stopped over during migration and classified migration strategy accordingly ($0 = $ no stops, $1 = $ at least one stop). I used a logistic regression to examine the univariate relationships of departure date, arrival date, flight speed, and migration distance with migration strategy. Results are presented as mean $\pm$ standard error, and I used an α level of 0.05 for all tests.

RESULTS

I received 12508 location records from 17 PTTs between July 2016 and May 2018. Filtering retained 9466 (94.4%) location estimates with 58.4% of these locations being in LC3, LC2, or LC1. The time each heron was tracked ranged from 112 to 487 days. Molecular sex determination revealed our sample included 2 female and 15 male night-herons.

Migration and stopover – I obtained data for one autumn migration from 14 individuals and two autumn migrations from one individual. In all years, Black-crowned Night-Herons left the study site between 11 September and 20 November (Table 2.1, Figure 2.1). Departure differed by 10 days in two consecutive years for the one repeated individual, with 2017 earlier than 2016. Black-crowned Night-Herons that departed early from the study area also arrived early to the nonbreeding grounds ($r = 0.76$, $n = 15$, $p < 0.001$; Figure 2.2). Black-crowned Night-Herons travelled on average 1517 ± 138.22 km during autumn migration and took on average 17 ± 4 days to arrive at a nonbreeding location. Black-crowned Night-Herons that traveled further distances did not depart the study area earlier ($r = -0.31$, $n = 15$, $p = 0.25$). I recorded at least one stopover by 6 of 15 (40%) Black-crowned Night-Herons during autumn migration. Birds stopped 1-7 times for a total of 7 ± 3 days. Migration strategy (i.e. stopping or not stopping) was not correlated with departure date (-0.02 ± 0.02, $z = -0.66$, $p = 0.51$), arrival date (0.04 ± 0.03, $z = 21.5$, $p = 0.14$), flight speed (-0.01 ± 0.01, $z = -1.65$, $p = 0.09$), or migration distance (0.0004 ± 0.001, $z = 0.50$, $p = 0.61$). Migratory speed was on average 225.80 ± 35.55 km/day. Autumn arrival did not correlate with stopover duration ($r = 0.39$, $n = 15$, $p = 0.14$) or migration speed ($r = -0.48$, $n = 15$, $p = 0.06$). One (6.7%) Black-crowned

Night-Heron traversed the Gulf of Mexico to reach Honduras during autumn migration, another (6.7%) crossed the Straits of Florida to Cuba, and thirteen (86.7%) night-herons settled in the continental US (Figure 2.3). All birds arrived at a nonbreeding location by early December (18 Sept-10 Dec).

Spring migration was recorded for 6 individuals. Black-crowned Night-Herons initiated northward migration from early April through June (Table 2.1, Figure 2.1). Spring migration duration averaged 16 ± 3 days and ranged between 4 and 26 days. Night-herons travelled on average 1544 ± 137.39 km to reach breeding sites. Stopovers were common during spring migration: four night-herons stopped 1-2 times spending $6 - 14$ days at stopover sites. Migratory speed was on average 182.75 ± 27.03 km/day. Birds arrived at their breeding sites between April 13 and June 30. As in fall, migration departure timing was the only parameter positively related to arrival timing ($r = 0.96$, $n = 6$, $p = 0.001$; Figure 2.2).

Neither departure ($r = 0.58$, $n = 6$, $p = 0.21$) nor arrival dates ($r = 0.56$, $n = 6$, $p = 0.24$) were correlated between spring and autumn migration. Overall, the duration of spring migration (16 ± 3 days) was similar to that of autumn (17 ± 4 days); however, within individuals spring migration duration was significantly longer than in autumn ($t = 3.08$, $df = 5$, $p = 0.02$; Figure 2.4). Average migration speeds of all tracked night-herons were slower in spring. Five of six night-herons migrated at faster speeds in autumn ($t = -2.49$, $df = 5$, $p = 0.05$; Figure 2.4). All night-herons made the same number or more stops during spring compared to autumn migration. On average, stopover duration was similar

between seasons and was not significantly different within individuals ($t = 1.99$, $df = 5$, $p = 0.10$) (Figure 2.4). Additionally, the distance travelled was shorter in spring for two individuals (Heron 65 and Heron 80), yet the travel speed was slower and with more stopover days (Table 2.1).

   Nonbreeding areas, movements, and home range - I collected nonbreeding locations for 35 night-herons (satellite tagged: $n = 15$, band recoveries or re-sightings: $n = 15$, nanotagged: $n = 5$). Night-Herons marked in Ohio wintered in North Carolina, South Carolina, Florida, Cuba, Jamaica, Dominican Republic, and Honduras (Figure 2.5). For this satellite tagged individuals, the nonbreeding period lasted 178 ± 10 days. During this time, 33% of tracked night-herons used more than one nonbreeding site whereas 66% remained at one nonbreeding location throughout the nonbreeding period. Night-Herons relocated to up to four different nonbreeding sites (Figure 2.6). For individuals that made intraseasonal movements ($n = 5$), the mean distance traveled within the nonbreeding period was 643.79 ± 186.23 km. The timing and direction of movements on the nonbreeding grounds varied between individuals (Figure 2.6). Black-crowned Night-Herons that wintered in Cuba ($n = 3$) spent on average 94 ± 25 days in the country. In 2016, two birds departed Cuba on 5 February and 24 February to relocate to a new home range in Florida, and in 2017, one bird exited Cuba on 16 December and moved to Everglades National Park in Florida. The Black-crowned Night-Heron that was tracked for two autumn migrations utilized the same nonbreeding site in both years (i.e. < 1 km apart).

I collected sufficient locations to calculate winter home range sizes for 13 herons. Winter home range sizes representing the 50% BBMM core area varied from 0.93 – 381.90 km^2 and from 4.42 – 1527.63 km^2 for the 95% BBMM (Table 2.2). I identified fifteen habitat types available to Black-crowned Night-Herons during stopover and nonbreeding periods (Table 2.3). The five most available habitat types on stopover were pasture/hay, deciduous forest, developed (open space), cultivated crops, and open water (Table 2.3, Figure 2.7). Among the stopover areas with potential foraging habitat, rivers, lakes and estuaries were present at 56% of stopover events. Small emergent wetlands and ponds (< 1 km) were available at 44% of stopover locations. One individual stopped for 11 days at a catfish farm in Dallas County, Alabama. There was no overlap in stopover locations between individuals. Habitat types most available at nonbreeding areas included woody wetlands, emergent herbaceous wetlands, open water, pasture/hay, and cultivated crops (Table 2.3, Figure 2.7).

DISCUSSION

Our study provides novel insight into the annual cycle of Black-crowned Night-Herons. I identified migration routes and described the nonbreeding distribution of Black-crowned Night-Herons banded in Ohio. Most routes followed south from the study area including an Appalachian Mountain crossing and were generally consistent between autumn and spring. The nonbreeding distribution of Ohio's Black-crowned Night-Heron population is large, with locations spanning North Carolina to Honduras. I documented differences in migration strategies within and between seasons and identified strong

correlations in migratory departure and arrival timing in both autumn and spring. Black-crowned Night-Herons exhibited two strategies of movement during migration, where the total duration of migration was greatly influenced by the time spent at stopover locations. These different strategies highlighted that stopover habitat requirements vary between individuals. Our findings include the first description of large scale movements and overall space use of night-herons while on the nonbreeding grounds. Finally, I provide evidence that habitat utilization differs between stopover and nonbreeding periods with disturbed habitats more commonly used on stopover.

Migration routes - Although band recoveries from the Great Lakes region indicate that some individuals are sedentary or short-distance dispersers (Marra et al. 2014), all individuals in our study exhibited migratory movements. For the majority, migration occurred along a defined corridor connecting the Mississippi and Atlantic Flyways (U.S. Fish and Wildlife Service and Canadian Wildlife Service 2012) during autumn and spring. Only one night-heron deviated from this pattern, remaining in the Mississippi Flyway and crossing the Gulf of Mexico with a jumping off point connecting Alabama to the Yucatan Peninsula. Our findings are contrary to two previously hypothesized routes to reach the Greater Antilles: following the Mississippi River drainage then heading east and south through Florida or migrating through Mexico and hopping eastward from the Yucatan (Hothem et al. 2010). Apart from one individual, routes were generally reversed in spring. This individual followed a pattern more typical of loop migration, travelling west in autumn within the Mississippi Flyway and returning in the spring from a route in the Atlantic Flyway. During migration, birds face considerable risks *en route*, one of

which is collision with wind turbines (Loss et al. 2013). Our tracks indicate most Black-crowned Night-Herons are passing over or near the Appalachian Mountains during migration, a high traffic area for many neotropical migrants. Because wind energy in the Appalachian region (Appalachian Regional Comission 2006) and across the US (American Wind Energy Association 2017) is expected to increase in coming years, future migration studies should accurately identify areas of airspace (geographically and elevationally) that are used by many species as well as those that are of conservation concern in order to mitigate future mortality risks.

Nonbreeding distribution - Assuming that our data are representative of the entire Ohio population, the majority of night-herons winter in the southeastern US (60%, $n = 21$) with the remaining birds wintering in the Caribbean (31%, $n = 11$) and Central America (9%, $n = 3$). Night-herons exhibited a high level of population spread, with the maximum distance between nonbreeding areas exceeding 2,500 km. Population spread is important in determining the relative vulnerability of a breeding population to environmental change or catastrophic events (Finch et al. 2017). For example, where spread is high, populations may experience a buffering effect of hazardous conditions since some individuals would likely not be affected (Webster and Marra 2005). Although little is known about nonbreeding site fidelity in wading birds, the Black-crowned Night-Heron in our study for which we have two years of data returned to the same nonbreeding location in successive years. Determining the degree of intermixing of night-herons from Ohio with other Great Lakes colonies is an important next step in beginning to understand the relative influence of this period on the annual cycle.

Migration timing and strategy - Departure and arrival dates were highly variable in both autumn and spring. Black-crowned Night-Herons left the study area in autumn from September – December, similar in timing to observed departures of night-herons breeding in Oregon (Littlefield and Cornely 1984). Arrival to the breeding area occurred between mid-April and late June in our study. In other populations, night-herons arrive to breeding areas from February to May (New York: Allen and Mangels 1940, Maine: Wilson, Jr. et al. 1996, California: Hothem et al. 2010). Consistent with other studies (McKinnon et al. 2016, Ouwehand and Both 2016, Cooper et al. 2017), arrival timing was highly correlated with departure timing in both autumn and spring. This supports the idea that later departing Black-crowned Night-Herons do not adjust their speed to compensate for delayed departure.

Wintering at more northern latitudes is associated with early arrival to breeding areas in some species (e.g. Hötker 2002, Bregnballe et al. 2006). In this study, I found no evidence that Black-crowned Night-Herons wintering at more northern latitudes arrived at the breeding grounds earlier. Likewise, there was no relationship between migration distance and arrival timing to nonbreeding sites. Perhaps individuals wintering at more southern latitudes depart earlier in spring and catch up to those at northern latitudes, mediating the effect of distance. Another possibility is differential migration, whereby individuals of different ages, sex, or body sizes migrate different distances to nonbreeding locations (reviewed in Cristol et al. 1999). Although not examined in Ardeidae, differential migration is common among many other bird families. In Savannah Sparrows (*Passerculus sandwichensis*), males overwintered further north than females,

arrived earlier to the breeding grounds, and had earlier hatch dates than those wintering further south (Woodworth et al. 2016). I did not have an equal sex ratio (n=2 females, n=15 males) in the dataset necessary to fully examine the common differential migration hypotheses (early arrival, body size, and social dominance). The two females both wintered in Florida indicating that there may not be separation by sex in the nonbreeding distribution.

Stopover events were common, but not ubiquitous, in Ohio night-herons, with 40% stopping at least once in autumn and 60% in spring. A Black-crowned Night-Heron tracked from Poland to Africa made four stopovers *en route* from $9 - 20$ days in length (Ledwón and Betleja 2015). Agami Herons also stopped for long lengths ($24 - 62$ days) during their post-breeding migrations from French Guiana (Stier et al. 2017). Long stopovers seem to be less common in other species of wading birds (*Ardea purpurea*: van der Winden et al. 2010, *Botaurus lentiginosus*: Huschle et al. 2013). In our study, there was no overlap between individuals or years in the locations of stopover events. This lack of fidelity to specific locations indicates that birds are not utilizing staging areas (areas with abundant and reliable resources, typically associated in preparation for long, migratory flights; Warnock 2010), but rather stop in suitable areas as available *en route*. Because I recorded only one migration per season for most individuals, I could not address whether or not migratory strategies were flexible or consistent over time. However, the one night-heron that was tracked for two autumn migrations did not stop in either instance providing some evidence that strategies may be consistent. Longer term

studies would reveal if individual strategies are fixed, or if stopover behavior is related to certain temporal patterns (e.g. climate, resource availability, or individual condition).

Migratory species generally spend more time on migration in autumn than in fall (Nilsson et al. 2013). However, in this study, I found that the duration of spring migration was longer on average than autumn for the six individuals tracked during both migrations. While this pattern is generally less common, other waterbird species have been found to follow a similar pattern, and associated studies have identified several possible explanations. First, there may be individual costs associated with early arrival to the breeding grounds (White Stork: *Ciconia ciconia*, Janiszewski et al. 2013). For birds travelling to northern breeding areas, arriving too early could expose them to inclement weather and/or freezing temperatures, increasing energetic output and risking mortality. Lake Erie and its associated marshes usually freeze over during the winter months, and arriving before ice melt could face night-herons with limited access to foraging areas and increase starvation risk. Second, seasonal differences in wind conditions could cause differences in migratory speed leading to discrepancies in migration duration (Lesser Black-backed Gull: *Larus fuscus fuscus,* Bustnes et al. 2013, Kranstauber et al. 2015*).* Because the difference in migration duration was largely whether or not an individual stopped over, it is unlikely that wind conditions played an important role here, but for those individuals that did not stop, there may be differences if wind conditions were more favorable in autumn. For the two individuals that did not stop during spring and autumn, migratory speed was higher in autumn. Lastly, capital breeders (i.e. species that store energy in advance of breeding, buffering the effect of local environmental conditions;

Jönsson 1997) require energy stores acquired before arrival to breeding areas, often resulting in longer stopovers in spring (White-fronted Geese: *Anser albifrons*, Kölzsch et al. 2016). Capital breeding has been identified in several northerly-breeding species of waterfowl and shorebirds, although the extent to which endogenous reserves are used seems to exist on a spectrum (e.g. Morrison and Hobson 2004, Sénéchal et al. 2011). To my knowledge, the use of endogenous reserves has not been examined in Ardeidae, but capital breeding does not seem to be a probable strategy since stopover duration was not significantly longer in spring. I did not find any relationship between autumn and spring departure or arrival dates suggesting that local conditions (e.g. wind, temperature, resource availability) are more likely to drive timing of migration between seasons in Black-crowned Night-Herons than intrinsic factors (e.g. sex, age).

Home range and nonbreeding movements - Home range sizes were variable within and between individual Black-crowned Night-Herons, and larger than that reported for other wading birds (Koczur et al. 2018; Table 2.2). Intraspecific variation in home range size can be linked to many factors both intrinsic (e.g. body size, sex, or age) and extrinsic (e.g. resource quantity/quality or climate related variables (van Beest et al. 2011). During the nonbreeding period, five of fifteen Black-crowned Night-Herons relocated to as many as four geographically distinct nonbreeding sites spending a few weeks to a few months in each location. Until recently, except for a few species, long distance Neotropical migrants were assumed to remain relatively stationary throughout the nonbreeding period (Newton 2008). However, tracking studies have revealed that large scale movements during the nonbreeding period are not uncommon for a growing

number or passerine species (Stutchbury et al. 2016). In night-herons, relocation movements ranged from 62 - 902 km and there was no consistency in the direction of movements. Outside of passerines, nonbreeding movements of similar scale and behavior have been reported in waterfowl and raptors (King Eiders: *Somateria spectabilis,* Oppel et al. 2008; Swainson's Hawk: *Buteo swainsoni,* Kochert et al. 2011). Water depth, vegetation composition, and prey availability are the most reliable predictors in determining where and when wading birds forage (Bancroft et al. 2002, Gawlik 2002). Therefore, the large-scale movements I observed suggest regional rather than local changes in water levels or prey availability may drive within-season relocation. Additionally, the movements coincided with the typical seasonal drying patterns in the Greater Antilles (Taylor et al. 2002) adding further evidence that the night-herons that moved Cuba to Florida responded to changes in available foraging habitat. Given recent climate change, projections indicate increases in temperature and variability in precipitation in the Caribbean (Biasutti et al. 2012) which could lead to changes in the seasonal availability of resources and ultimately alter the movement behavior of wading birds.

Stopover and nonbreeding habitat – Our classification of available habitat types indicates that Black-crowned Night-Herons occupy different habitats between stopover and nonbreeding periods. Disturbed landscapes were more commonly found in stopover areas (47.93%) than nonbreeding home ranges (18.43%). The second most available habitat type during stopover events was deciduous forest. These forest patches often included a small wetland, but the total percentage of habitat types associated with water

was only 10.16% during stopover. Comparatively, within nonbreeding home ranges, 68.01% of landcover was comprised of wetland habitat including woody wetlands, emergent herbaceous wetlands, and open water. If refueling was critical to complete migration, I would expect that night-herons would use habitat types and scales similar to what is available during the nonbreeding season and that individuals would likely concentrate in a few critical areas. Cultivated crops were present in similar proportions between stopover areas and nonbreeding home ranges. Very little is known about the habitats night-herons utilize outside of the breeding season, and further research with higher resolution locations would allow a more sophisticated analysis of habitat use during stopover and nonbreeding.

Conclusion – This study represents the first instance of tracking Black-crowned Night-Herons throughout the full annual cycle. Black-crowned Night-Herons used two distinct strategies during spring and autumn migration and the timing of migration exhibited considerable flexibility. Population spread on the nonbreeding grounds was high, therefore Ohio night-herons may be less vulnerable to negative effects associated with environmental change. Our results also underscore the benefit of integrating multiple datasets when sample size may limit inference. Without incorporation of multiple datasets, the range of movement behaviors and/or the distribution of nonbreeding locations would have been underrepresented in my analysis. With evidence from the satellite tracking data, I found that Black-crowned Night-Herons are not among those species that remain sedentary during the nonbreeding period, rather individuals move long distances to occupy new home ranges. Expanding tracking efforts to include

other declining populations is an ideal next step to inform conservation planning and

investigate connectivity throughout the species' entire vulnerable range.
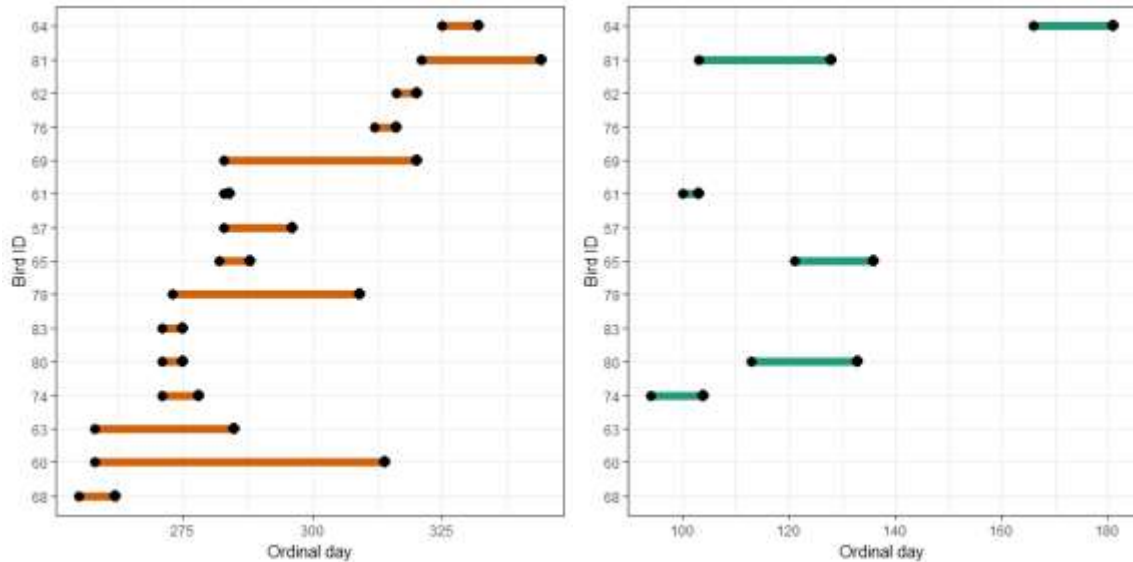
Figure 2.1. Autumn (left, $n = 15$) and spring (right, $n = 6$) migration phenology of

satellite-tagged Black-crowned Night-Herons captured in Ottawa and Erie counties, Ohio

in 2016 and 2017. Black circles represent departure and arrival dates derived from

location data, or when unknown, I used the median date between the collected locations.
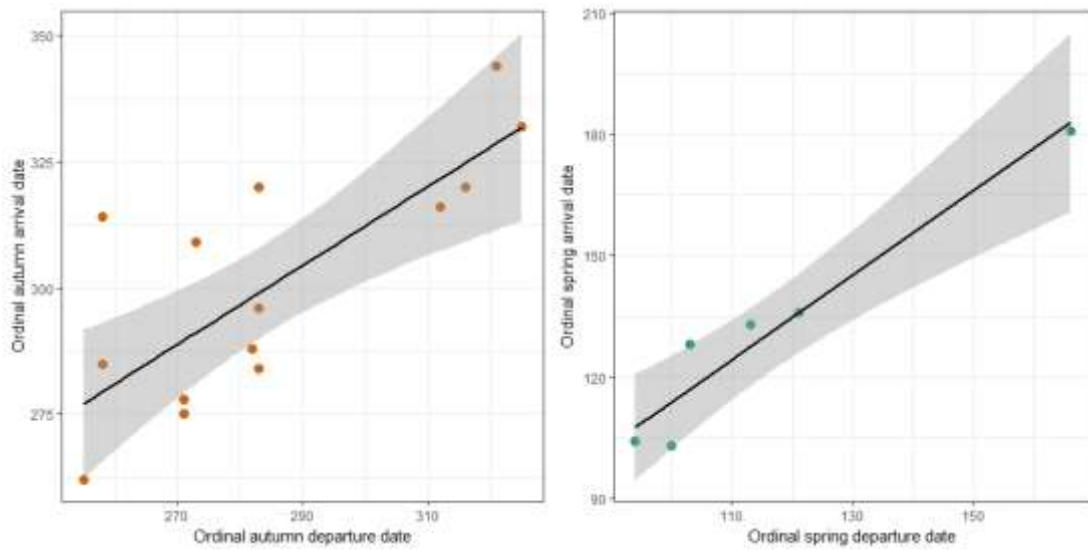
Figure 2.2. Relationships between departure and arrival dates for autumn and spring migration of satellite-tagged Black-crowned Night-Herons captured in Ottawa and Erie counties, Ohio in 2016 and 2017. Departure date was correlated with arrival date in both seasons (p = ≤ 0.001).
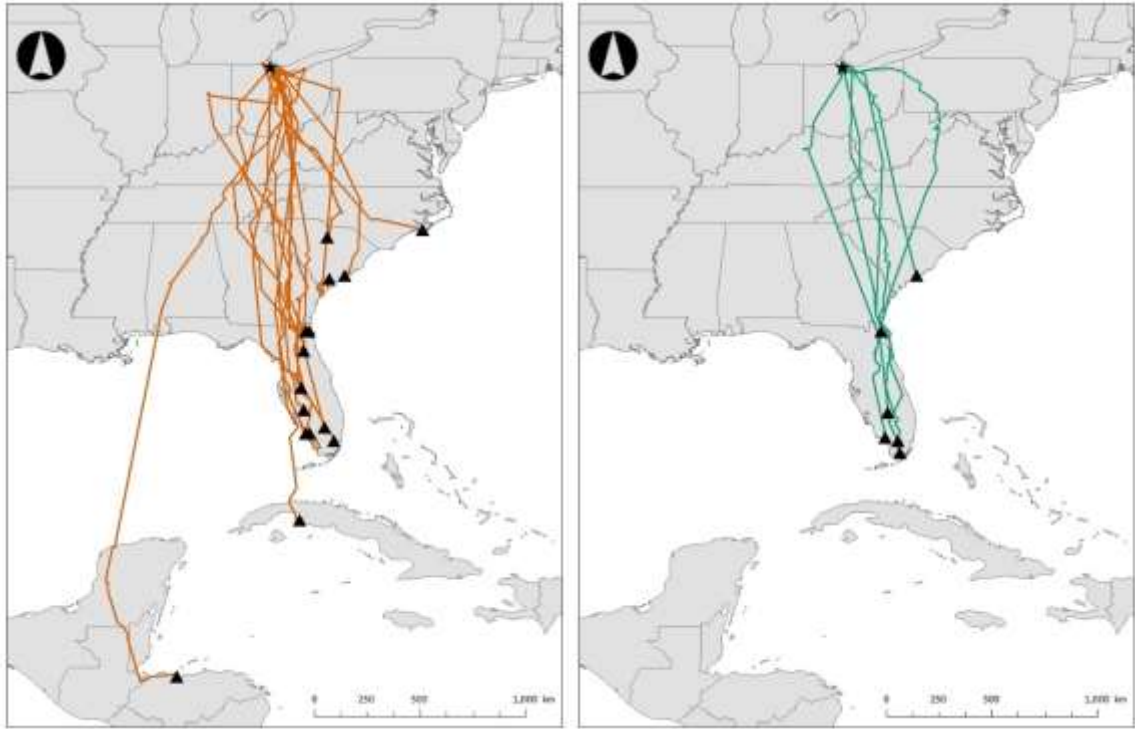
Figure 2.3. Autumn (left, *n* = 15) and spring (right, *n* = 6) migration routes of Black-crowned Night-Herons captured in Ottawa and Erie counties, Ohio in 2016 and 2017. Routes are estimated by connecting locations filtered using the Douglas Argos filter in Movebank. Positions of initial autumn and final spring stationary periods as represented by the center of the BBMM home range are shown by triangles. Differences in autumn endpoints and spring starting points are due to winter movements.
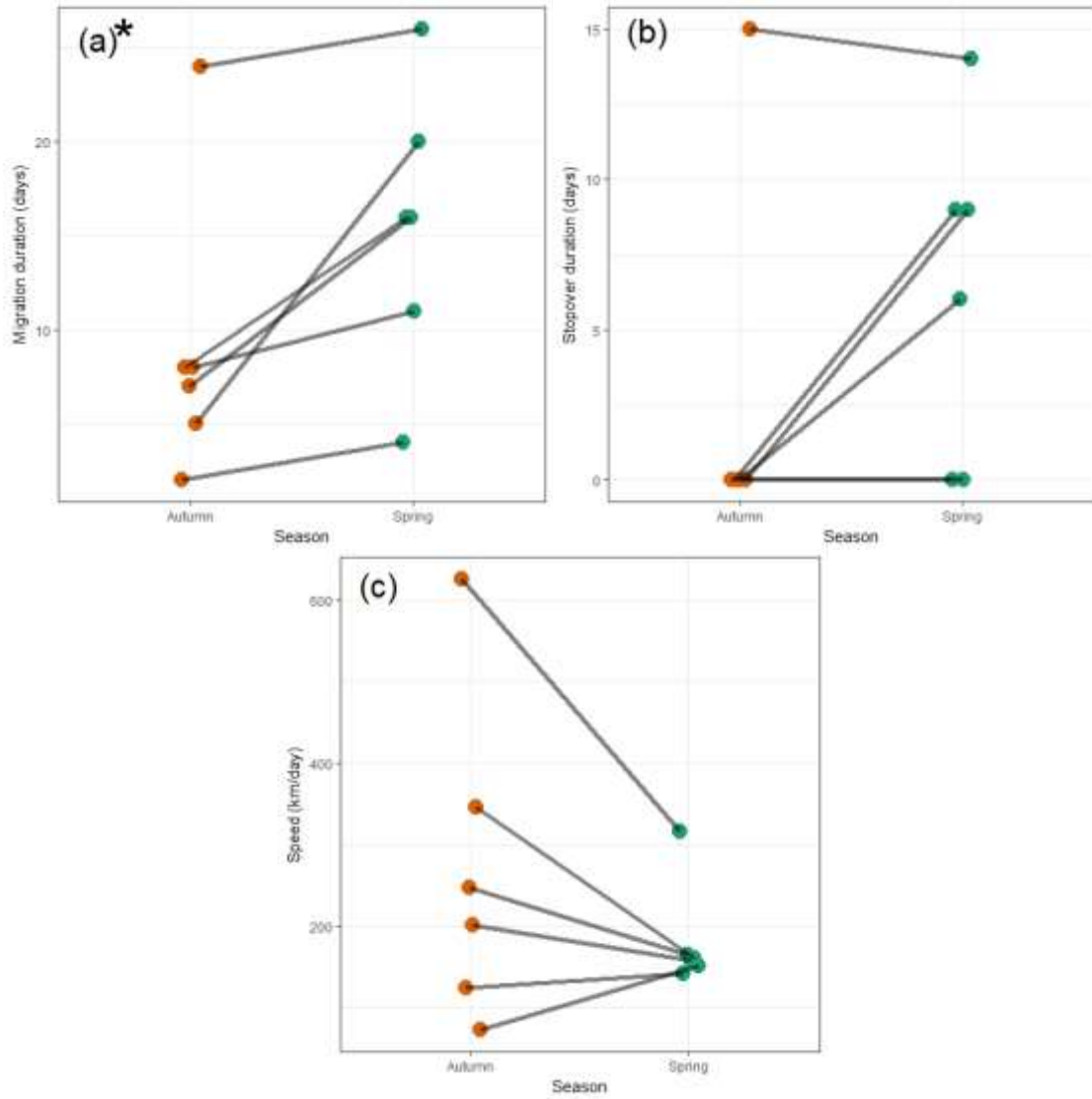
Figure 2.4. Seasonal difference in migration duration (a), stopover duration (b), and speed

(c) within individual Black-crowned Night-Herons ($n = 6$) tested by paired t-tests.

Migration duration was significantly longer in spring (p = 0.02; denoted with *).

Migration speed and stopover duration did not differ between seasons.
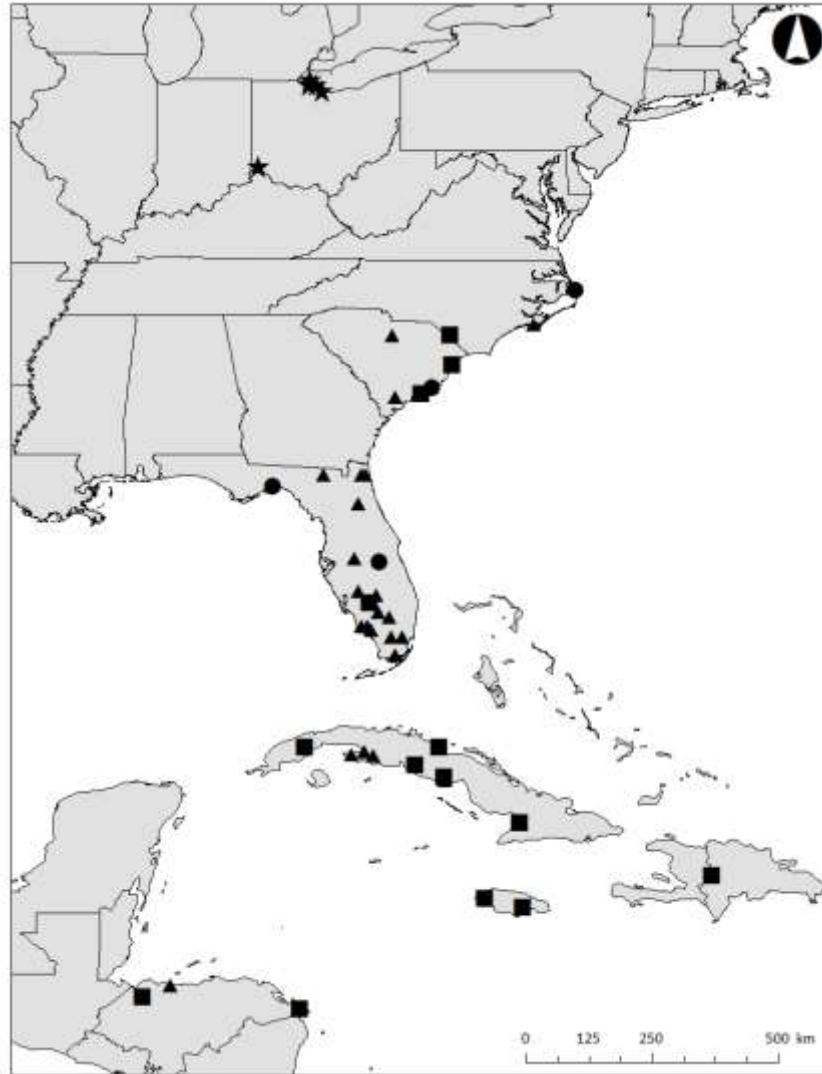
Figure 2.5. Nonbreeding locations of 35 Black-crowned Night-Herons captured in Ohio,

USA. Stars represent transmitter deployment and banding sites (n=5); triangles (n=24)

represent Black-crowned Night-Herons marked with satellite transmitters; squares (n=15)

represent recovery or resightings of banded Black-crowned Night-Herons; circles (n=5)

represent detections of nanotagged Black-crowned Night-Herons at Motus tower

locations.
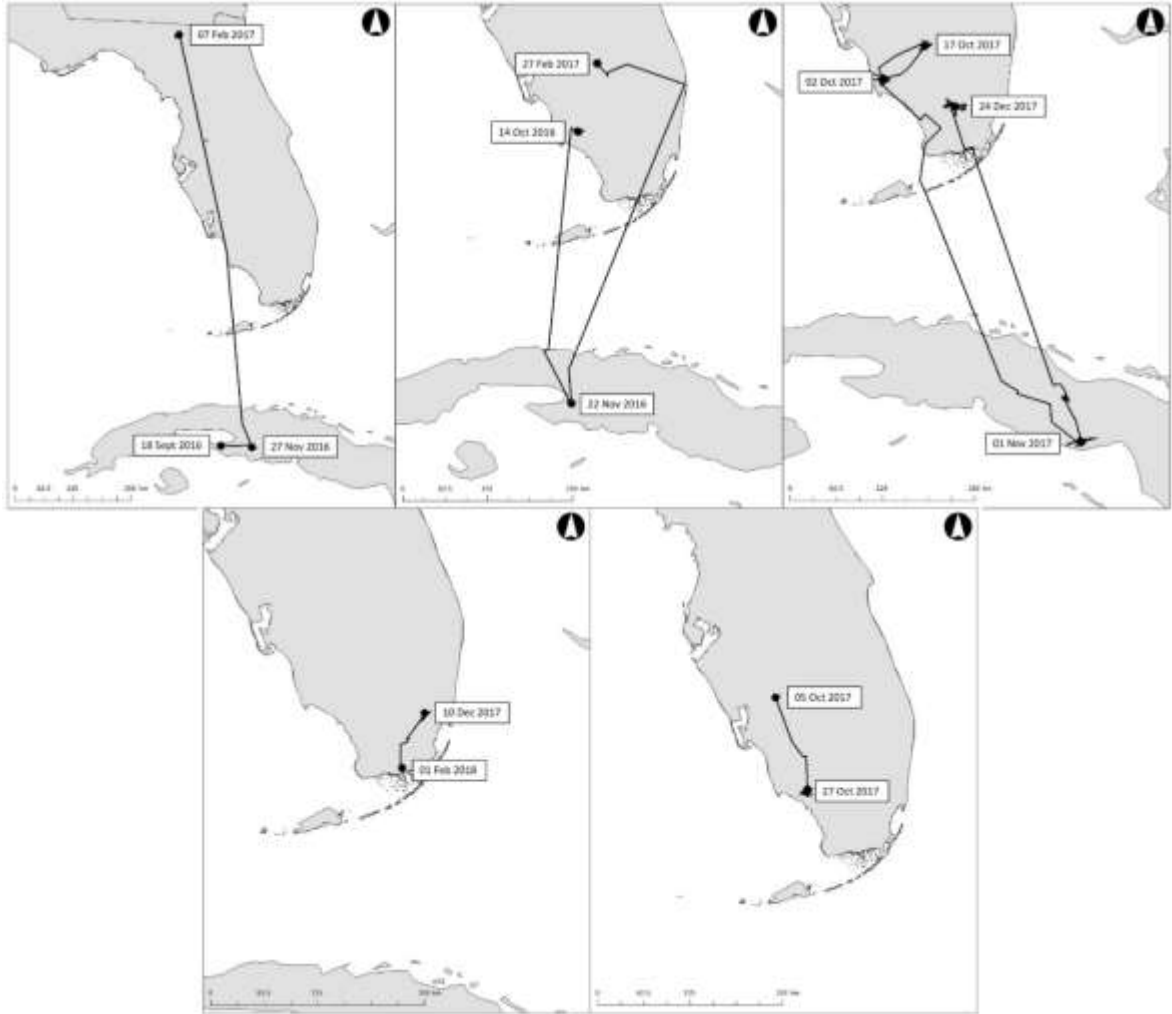
Figure 2.6. Intraseasonal nonbreeding movements of Black-crowned Night-Herons

captured in Ottawa and Erie counties, Ohio in 2016 and 2017. Circles represent the center

of BBMM home ranges. Dates represent initial arrival to a nonbreeding location.
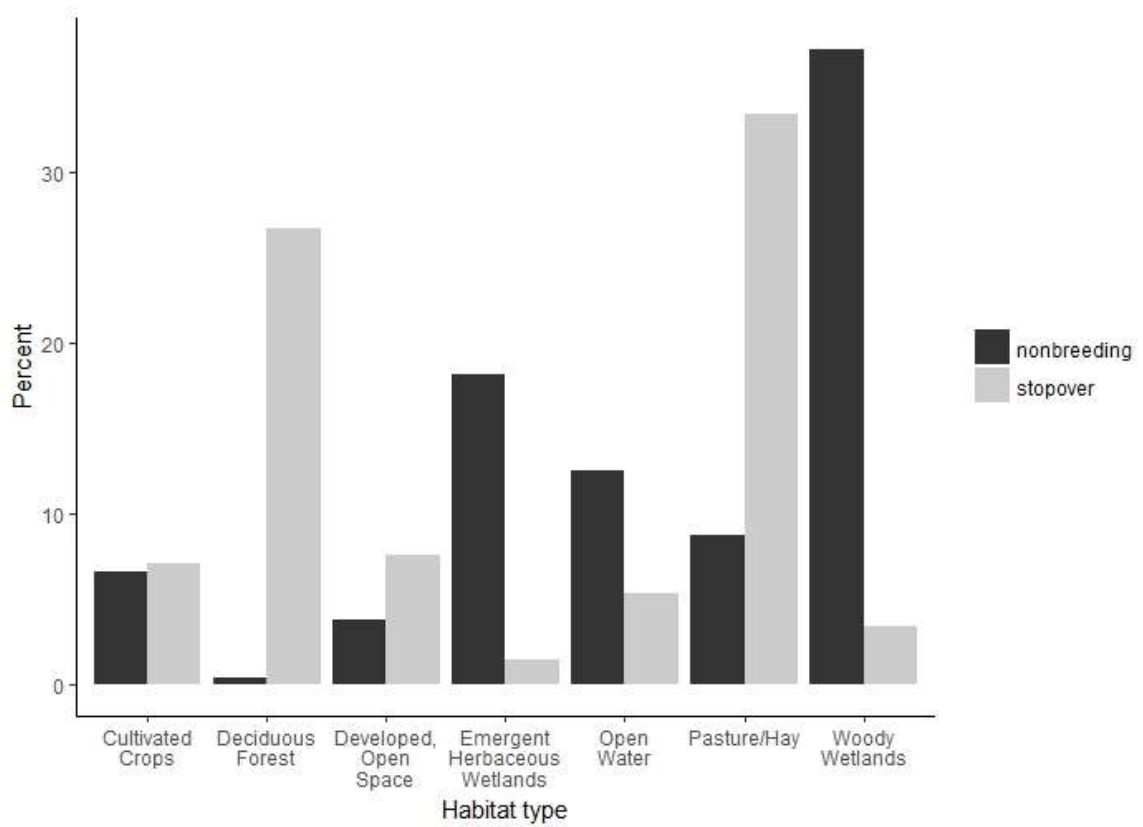
Figure 2.7. Frequencies of top land cover types available to Black-crowned Night-Herons during autumn and spring stopover and stationary nonbreeding seasons in 2016 - 2018. Habitat delineation was based on the National Land Cover Database (Homer et al. 2015).

Table 2.1 Migration characteristics of satellite-tagged Black-crowned Night-Herons captured in Ottawa and Erie counties, Ohio in 2016 and 2017. Data are missing for individuals where transmitters failed before spring migration or where location data was truncated before spring migration.

		Autumn migration							Spring migration						
ID	Sex	Departure	Arrival	Distance	Duration	Stopover events	Stops	Speed	Departure	Arrival	Distance	Duration	Stopover events	Stops	Speed
57	M	09 Oct 16	22 Oct 16	1710	14	1	8	285							
60	M	14 Sep 16	09 Nov 16	804	57	7	38	42							
61	M	09 Oct 16	10 Oct 16	1253	2	0	0	627	10 Apr 17	13 Apr 17	1267	4	0	0	317
62	M	11 Nov 16	15 Nov 16	950	5	0	0	190							
63	F	14 Sep 16	11 Oct 16	1342	28	2	11	79							
64	M	20 Nov 16	27 Nov 16	994	8	0	0	124	15 Jun 17	30 Jun 17	994	16	1	9	142
65	M	08 Oct 16	14 Oct 16	2130	7	0	0	304	01 May 17	16 May 17	1651	16	1	6	165
68	M	11 Sep 16	18 Sep 16	2142	8	0	0	268							
69	M	09 Oct 16	15 Nov 16	1537	38	4	23	102							
74	M	28 Sep 17	05 Oct 17	1746	8	0	0	218	04 Apr 18	14 Apr 18	1746	11	0	0	159
76	M	08 Nov 17	12 Nov 17	1021	5	0	0	204							
79	M	30 Sep 17	05 Nov 17	2894	37	2	24	223	22 Apr 18						
80	M	28 Sep 17	02 Oct 17	2245	5	0	0	449	23 Apr 18	12 May 18	1775	20	1	9	161
81	M	17 Nov 17	10 Dec 17	1775	24	2	15	197	13 Apr 18	08 May 18	1830	26	2	14	153
83	F	28 Sep 17	02 Oct 17	1252	5	0	0	250							
Means by year															
2016		09 Oct 16	26 Oct 16	1385	19	1	8	218							
2017		13 Oct 17	26 Oct 17	1714	14	1	7	237	09 May 17	20 May 17	1304	12	1	5	208
2018									15 Apr 18	01 May 18	1784	18	1	8	158
All				1517	17	1	7	226			1544	16	1	6	183

Distance (km), duration (days), stopover events (number of cumulative events), stops (total stopover days), speed (km/day)

Table 2.2. Brownian bridge home ranges (km^2) of Black-crowned Night-Herons during

the nonbreeding period 2016-2018.

ID	50%	95%
57	107.89	599.01
61	17.80	347.61
62	120.23	1342.62
64	37.69	798.75
65a	8.38	45.45
65b	381.90	1527.63
65c	3.53	16.23
68a	0.93	4.42
68b	149.29	1464.84
68c	132.58	969.53
69	33.41	148.29
74a	3.55	15.81
74b	27.56	106.21
76	37.34	154.82
79	30.68	113.00
80a	274.93	1315.15
80b	22.45	99.41
80c	113.86	483.67
80d	138.21	653.07
81a	70.89	387.30
81b	62.53	190.41
83	12.34	96.09

Table 2.3. Land cover types available to Black-crowned Night-Herons during autumn/spring stopover ($n = 10$) and nonbreeding periods ($n = 13$).

Habitat type	Stopover percent (%)	Wintering percent (%)
Barren Land (Rock/Sand/Clay)	0.48	1.36
Cultivated Crops	7.08	6.58
Deciduous Forest	26.76	0.38
Developed, High Intensity	0.63	0.58
Developed, Low Intensity	4.29	3.55
Developed, Medium Intensity	2.02	1.78
Developed, Open Space	7.53	3.79
Emergent Herbaceous Wetlands	1.40	18.18
Evergreen Forest	3.42	2.82
Grassland/Herbaceous	1.71	0.74
Mixed Forest	1.60	0.19
Open Water	5.36	12.58
Pasture/Hay	33.46	8.73
Shrub/Scrub	0.88	1.49
Woody Wetlands	3.40	37.25

Chapter 3: Conservation and Management Implications

Animals travel to different areas to complete various aspects of their life cycle, and for migratory birds these areas can be separated by thousands of kilometers (Newton 2008). Birds can face challenges during any portion of their life cycle, and without knowledge of each stage, it is difficult to pinpoint factors that may pose challenges to declining populations (Marra et al. 2015). One taxa, the colonial waterbirds, face unique threats with 64% of species considered to be of conservation concern globally (Kushlan et al. 2002). Threats are wide-ranging from anthropogenic disturbance through incidental bycatch of fisheries operations (Anderson et al. 2011) and debris ingestion (Wilcox et al. 2015) to habitat issues of invasive species (Wyman and Cuthbert 2017) and sea level rise (Erwin et al. 2011). Identifying limiting factors in the context of the annual cycle is central to modern avian conservation research. This study involved tracking both juvenile and adult Black-crowned Night-Herons during different portions of their life cycle and revealed several interesting findings.

Breeding and post-fledging - First, I measured rates of nest success at West Sister Island and Turning Point Island in Lake Erie, Ohio. I found that, of the 76 nests we monitored, 78% of them produced at least one nestling surviving to 25 days old. Rates of nest failure were higher at Turning Point Island (29%) than West Sister Island (17%). Predation events were not common in the nests I monitored, but two nests at Turning Point failed due to raccoon predation. Both events were at night (recorded via trail cameras), and I did not find raccoons present during daytime nest checks suggesting that

71

the raccoon(s) swam from the mainland to Turning Point Island. Black-crowned Night-Herons are not likely to re-nest following failure, but re-nesting probability is largely related to the timing of nesting where re-attempts are more likely earlier in the season (Nickell 1966, Henny 1972). From 2007-2017, numbers of night-heron nests at Turning Point ranged from 12-73 (Ohio Department of Natural Resources, unpublished data). Because the number of nesting pairs at Turning Point Island is fairly low, I suggest continued monitoring of raccoon abundance and predation of night-heron nests.

Several studies have noted the negative effects of human disturbance in colonial wading birds (reviewed in Carney and Sydeman 1999) as well as Black-crowned Night-Herons specifically (Tremblay and Ellison 1979, Parsons and Burger 1982, Fernandez-Juricic et al. 2007). When approached, wading bird parents often flush from nests (Conover and Miller 1978, Anderson and Keith 1980), and high amounts of disturbance during the egg phase can cause parents to abandon nests (Dusi and Dusi 1968, Tremblay and Ellison 1979). Juvenile behavior can also be altered through increased vigilance and anti-predator behaviors (Fernandez-Juricic et al. 2007). On two occasions during nest monitoring at Turning Point Island, we noted people walking through the colony. Currently, there is no protection from visitor disturbance on the island. I suggest adding signage at Turning Point Island in warning of the potential effects on the birds during the nesting period.

Within wading bird colonies where many species nest together, the vertical location of nests is related to the body size of the species where nest height increases with

increasing body size (Burger 1979, Park et al. 2011). I found in this study that Black-crowned Night-Herons that nested higher were more likely to have nestlings that survived to fledging age. This is interesting given that Black-crowned Night-Herons are one of the smallest wading birds that nest on the islands. It is possible that night-herons occupy a small niche of nest heights where survival is optimized and aggressive interactions and competition with other species are minimized. At West Sister Island, Shieldcastle and Martin (1997) documented decline in nest numbers along with the shrinking distribution of the Black-crowned Night-Heron nesting area from 1992-1997. The western portion of the island is now managed specifically for night-herons. Habitat restorations began in 1998 with the most recent restoration in 2016, where trees were cut at 4-foot heights in 1-acre increments to provide more availability of nesting sites in the lower canopy (Brewer et al. 2000). The Black-crowned Night-Herons at West Sister occupy these trees 1-2 years post restoration, once they begin to regenerate. Vegetation height seems to regulate the number of nesting night-herons at West Sister Island, as birds typically do not nest above 5 m (Shieldcastle and Martin 1997). Habitat restoration efforts may increase the number of nesting night-herons at West Sister Island, but it will be important to continue to monitor not only the number of nests, but also the rates of nest success and nestling survival because these rates could be related to population density. For example, in studies of Grey Herons (*Ardea cinerea*) and Great Egrets (*Egretta alba*), the number of nestlings surviving to fledge declined as number of nests in the colony increased, suggesting a density-dependent effect (Miller 2001, Takeshi 2013). Expanding monitoring efforts to other breeding colonies throughout the Great Lakes where nest

densities differ may increase our understanding of the nest height, nest density, and nestling survival relationship.

I found some evidence that survival during the post-fledging period may be biased towards males. In some cases, differential survival is related to size differences between males and females where the smaller or larger sex faces greater risks (Anderson et al. 1993, Arroyo 2002). In Black-crowned Night-Herons, males can be larger than females, but in many cases body measurements and mass overlap between sexes (Pyle 1997). Additionally, I did not find any differences in growth rates of males and females during the nestling period. If recruitment is high at the breeding colonies, then the ratio of adult birds could also be biased. An uneven sex ratio of adult birds can limit population size when the ratio is male-biased (Donald 2007). Our sample of adult night-herons in this study was strongly male-biased ($n = 15$ males, $n = 2$ females). However, I cannot ignore the possibility that the sex ratio was related to the capture method (i.e. if males are bolder than females and more likely to enter the trap area). More research is needed to understand the potential effects of sex on survival during different stages in both juvenile and adult night-herons.

Migration - In both spring and autumn, migration strategy was two-fold where some individuals flew to stationary areas nonstop or with few, short stops while others spent considerable time at stopover sites *en route*. Accordingly, individuals differed in their habitat and energy requirements during migration. Night-Herons frequently occupied disturbed habitats on stopover. During an autumn stopover, one night-heron

spent 11 days at a catfish farm in Dallas County, Alabama. Black-crowned Night-Herons are generalist aquatic predators, and are one of many species that utilize aquaculture facilities. Aquaculture ponds provide a constant and sometimes easily accessible food source for wading birds and other aquatic predators. While use of aquaculture facilities may not be common during stopover or nonbreeding, it is important to note because birds using these areas may face unique risks. Permits are required by USDA-APHIS and US Fish and Wildlife Service in order to legally take birds at aquaculture facilities, but growers are encouraged to employ various techniques to exclude or frighten birds from ponds (Gorenzel et al. 1994). Some examples of harassment techniques include pyrotechnics, strobe lights, and broadcasting alarm/distress calls (Gorenzel et al. 1994). Given that habitat availability seems to differ between stopover and nonbreeding areas, additional research incorporating higher resolution tracking technology (e.g. GPS/GSM transmitters) would allow a better understanding of behavior on stopover (e.g. resting versus refueling) as well as habitat utilization during this period.

Our satellite tracking has confirmed that Black-crowned Night-Herons migrate at night, and that migration routes traverse the Appalachian Mountains. Wind turbines are already present in many states spanning the Central Appalachian Mountain region, and wind farms are likely to increase given the attractive location (Appalachian Regional Comission 2006). Wildlife mortality from collisions with turbines can be substantial; a recent study estimates that between 140,000 and 328,000 birds are killed annually in the US from collisions with turbines (Loss et al. 2013), and the total collisions will likely increase as more wind farms are created. Wind energy is also expected in expand in the

75

Lake Erie area in the near future (U.S. Department of Energy 2017). Most Black-crowned Night-Herons in Ohio breed at West Sister Island or Turning Point Island, which are both located off-shore on Lake Erie. At these colonies, Black-crowned Night-Herons nest with other species of wading birds and some songbirds. West Sister Island is located 13 km off-shore and night-herons and other waders must travel back to shore in order to forage and provide food for their young, resulting in much time spent over water. While turbines may be a larger threat to birds during migration, planned development of wind energy within Lake Erie could put breeding birds at risk of collision during daily foraging/provisioning movements as well.

Full annual cycle – One of the ultimate goals of full annual cycle research is to inform integrated population models for a population or species. While there are many types of analyses to examine single demographic parameters (e.g. the Mayfield method for nest success (Mayfield 1961), mark-recapture for survival (White and Burnham 1999, etc.) the goal of integrated population models is to incorporate multiple datasets in a single analysis to estimate population rates as well as population trajectory (Schaub and Abadi 2011). In this study, I provide some key information for building an integrated population model of the Ohio night-heron population with the measures of nestling and post-fledging survival. Therefore, the next step towards informing an integrated population model would be to collect the remaining missing information on juvenile recruitment as well as adult survival rates during each stage of the annual cycle.

Literature Cited

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: the relative importance of time, energy, and safety. In Bird migration. pp. 331–352.

Allen, R. P., and F. P. Mangels (1940). Studies of the nesting behavior of the Black-crowned Night Heron. Proceedings of the Linnean Society of New York 50–51:1–28.

Alves, J. A., T. G. Gunnarsson, D. B. Hayhow, G. F. Appleton, P. M. Potts, W. J. Sutherland, and J. A. Gill (2013). Costs, benefits, and fitness consequences of different migratory strategies. Ecology 94:11–17. doi: 10.1890/12-0737.1

American Wind Energy Association (2017). Economic development impacts of wind projects - jobs and economic impacts resulting from U.S. wind projects 2017-2020.

Anderson, D. J., J. Reeve, J. E. Martinez Gomez, W. W. Weathers, S. Hutson, H. V. Cunningham, and D. M. Bird (1993). Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71:2541 – 2545.

Anderson, D. W., and J. O. Keith (1980). The human influence on seabird nesting success: conservation implications. Biological Conservation 18:65–80. doi: 10.1016/0006-3207(80)90067-1

Anderson, O. R. . J., C. J. Small, J. P. Croxall, E. K. Dunn, B. J. Sullivan, O. Yates, and A. Black (2011). Global seabird bycatch in longline fisheries. Endangered Species Research 14:91–106. doi: 10.3354/esr00347

Appalachian Regional Comission (2006). Energizing Appalachia: A regional blueprint for economic and energy development.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178. doi: 10.2193/2009-367

Arroyo, B. (2002). Sex-biased nestling mortality in the Montagu's harrier Circus pygargus. Journal of Avian Biology 33:455.

Ashoori, A., and A. Barati (2013). Breeding success of Black-crowned Night Heron (Nycticorax nycticorax), Little Egret (Egretta garzetta) and Cattle Egret (Bubulcus ibis) (Aves: Ardeidae) in relation to nest height in the South Caspian Sea. Italian Journal of Zoology 80:149–154. doi: 10.1080/11250003.2012.758784

Auclair, M. M. M., K. A. Ono, and N. G. Perlut (2015). Brood Provisioning And Nest Survival Of Ardea Herodias (Great Blue Heron) in Maine. Northeastern Naturalist

22:307–317.

Ausprey, I. J., and A. D. Rodewald (2011). Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. The Auk 128:293–302. doi: 10.1525/auk.2011.10158

Balogh, A. L., T. B. Ryder, and P. P. Marra (2011). Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. Journal of Ornithology. doi: 10.1007/s10336-011-0648-7

Bancroft, G. T., D. E. Gawlik, and K. Rutchey (2002). Distribution of wading birds relative to vegetation and water depths in the Northern Everglades of Florida, USA. Waterbirds 25:265–277. doi: Doi 10.1675/1524-4695(2002)025[0265:Dowbrt]2.0.Co;2

Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771–785. doi: 10.1111/j.1365-2656.2011.01829.x

Biasutti, M., A. H. Sobel, S. J. Camargo, and T. T. Creyts (2012). Projected changes in the physical climate of the Gulf Coast and Caribbean. Climatic Change 112:819–845. doi: 10.1007/s10584-011-0254-y

Bitton, P.-P., R. D. Dawson, and E. L. O'Brien (2006). Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird. Canadian Journal of Zoology 84:1721–1726. doi: 10.1139/z06-179

Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza (2014). Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. Ecology and Evolution 4:4488–4499. doi: 10.1002/ece3.1139

Blus, L. J., B. A. Rattner, M. J. Melancon, and C. J. Henny (1997). Reproduction of Black-crowned Night-Herons related to predation and contaminants in Oregon and Washington, USA. Colonial Waterbirds 20:185–197.

Borkhataria, R. R., P. C. Frederick, R. A. Keller, and J. A. Collazo (2012). Temporal variation in local wetland hydrology influences postdispersal survival of juvenile Wood Storks (Mycteria americana). The Auk 129:517–528. doi: 10.1525/auk.2012.11244

Bosman, D. S. (2014). Effects of intraclutch variation in egg size and hatching asynchrony on nestling development and survival in semi-precocial Herring Gulls.

Journal of Field Ornithology 85:379–390. doi: 10.1111/jofo.12077

Bosman, D. S., E. W. M. Stienen, and L. Lens (2016). Sex, growth rate, rank order after brood reduction, and hatching date affect first-year survival of long-lived Herring Gulls. Journal of Field Ornithology 0:1–13. doi: 10.1111/jofo.12177

Bregnballe, T., M. Frederiksen, and J. Gregersen (2006). Effects of distance to wintering area on arrival date and breeding performance in Great Cormorants Phalacrocorax carbo. Ardea 94:619–630.

Brewer, D., G. Muehlenhardt, S. Cornelius, S. Dushane, R. Hinkle, J. Hodgins, T. Larson, L. Martin, J. Schomaker, C. Smith, and S. Wells (2000). Management direction. doi: 10.1016/j.ecss.2007.10.010.Nguyen

Brown, D., and G. Miller (2016). Band recoveries reveal alternative migration strategies in American Robins. Animal Migration 3:35–47. doi: 10.1515/ami-2016-0004

Brussee, B. E., P. S. Coates, R. L. Hothem, K. B. Howe, M. L. Casazza, and J. M. Eadie (2016). Nest survival is influenced by parental behaviour and heterospecifics in a mixed-species colony. Ibis 158:315–326. doi: 10.1111/ibi.12351

Brzorad, J. N., A. D. Maccarone, and H. M. Stone (2015). A Telemetry-Based Study of Great Egret (Ardea alba) Nest- Attendance Patterns , Food-Provisioning Rates , and Foraging Activity in Kansas , USA A Telemetry-based Study of Great Egret (Ardea alba). Waterbirds 38:162–172.

Burger, J. (1978). Competition between Cattle Egrets and native North American herons, egrets, and ibises. Condor 80:15–23. doi: 10.2307/1367786

Burger, J. (1979). Resource partitioning: nest site selection in mixed species colonies of herons, egrets and ibises. The American Midland Naturalist 101:191–210.

Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodel inference: a practical information-theoretic approach. In New York: Springer-Verlag.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Bustnes, J. O., B. Moe, M. Helberg, and R. A. Phillips (2013). Rapid long-distance migration in Norwegian Lesser Black-backed Gulls Larus fuscus fuscus along their eastern flyway. Ibis 155:402–406. doi: 10.1111/ibi.12022

Buuren, S. van, and K. Groothuis-Oudshoorn (2011). mice: multivariate imputation by chained equations in R. Journal of Statistical Software 45:1–67.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Carney, K. M., and W. J. Sydeman (1999). A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22:68–79. doi: 10.2307/1521995

Čech, M., and P. Čech (2017). Effect of brood size on food provisioning rate in Common Kingfishers Alcedo atthis. Ardea 105:5–17.

Chapman, B. R., T. L. Grantland, and R. E. Ricklefs. (1981). Growth and development of temperature regulation in nesting Black-Crowned Night Herons. Colonial Waterbirds 4:114–119.

Clark, D. E., K. K. G. Koenen, K. G. Mackenzie, J. W. Pereira, and S. Destefano (2014). Evaluation of a net launcher for capturing urban gulls. Wildlife Society Bulletin 38:605–610. doi: 10.1002/wsb.435

Cleasby, I. R., S. Nakagawa, D. O. S. Gillespie, and T. Burke (2010). The influence of sex and body size on nestling survival and recruitment in the house sparrow. Biological Journal of the Linnean Society 101:680–688.

Clutton-Brock, T. H. (1991). The evolution of parental care. In Princeton University Press.

Conover, M. R., and D. E. Miller (1978). Reaction of ring-billed gulls to predators and human disturbances at their breeding site. Proc. ofthe Colon. Waterbird Group, 2:41–47. Proceedings of the Colonial Waterbird Group 2:41–47.

Conrad, K. F., and R. J. Robertson (1993). Brood size and the cost of provisioning nestlings: interpreting Lack's hypothesis. Oecologia 96:290–292. doi: 10.1007/BF00317744

Cooper, N. W., M. T. Hallworth, and P. P. Marra (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. Journal of Avian Biology 48:209–219. doi: 10.1111/jav.01096

Cox, W. A., F. R. Thompson, A. S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. Journal of Wildlife Management 78:183–193. doi: 10.1002/jwmg.670

Cristol, D. A., M. . Baker, and C. Carbone (1999). Differential migration revisited. In Current Ornithology. pp. 33–88. doi: 10.1007/978-1-4757-9921-7

Currie, D., D. B. A. Thompson, and T. Burke (2000). Patterns of territory settlement and consequences for breeding success in the Northern Wheatear Oenanthe oenanthe. Ibis 142:389–398.

Custer, T. W., and P. C. Frederick (1990). Egg size and laying order of Snowy Egrets, Great Egrets, and Black-crowned Night-Herons. The Condor 92:772–775.

Custer, T. W., and D. W. Peterson Jr. (1991). Growth rates of Great Egret, Snowy Egret and Black-crowned Night-Heron chicks. Colonial Waterbirds 14:46–50.

Dahl, T. E., and C. E. Johnson (1991). Status and trends of wetlands in the conterminous United States mid-1970's to mid 1980's.

Dahlgren, D. K., M. R. Guttery, T. A. Messmer, D. Caudill, R. D. Elmore, R. Chi, and D. N. Koons (2016). Evaluating vital rate contributions to Greater Sage-Grouse population dynamics to inform conservation. Ecosphere 7:1–15. doi: 10.1002/ecs2.1249

Dodson, J. C., N. J. Moy, and L. P. Bulluck (2016). Prothonotary Warbler nestling growth and condition in response to variation in aquatic and terrestrial food availability. Ecology and Evolution 6:7462–7474. doi: 10.1002/ece3.2400

Donald, P. F. (2007). Adult sex ratios in wild bird populations. Ibis 149:671–692. doi: 10.1111/j.1474-919x.2007.00724.x

Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski, and G. Bohrer (2012). Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3:999–1007. doi: 10.1111/j.2041-210X.2012.00245.x

Durant, J. M., D. Ø. Hjermann, G. Ottersen, and N. C. Stenseth (2007). Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

Dusi, J. L., and R. T. Dusi (1968). Ecological factors contributing to nesting failure in a heron colony. 80:458–466.

Dybala, K. E., J. M. Eadie, T. Gardali, N. E. Seavy, and M. P. Herzog (2013). Projecting demographic responses to climate change: Adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. Global Change Biology 19:2688–2697. doi: 10.1111/gcb.12228

Efford, M. G., D. K. Dawson, Y. V. Jhala, and Q. Qureshi (2016). Density-dependent home-range size revealed by spatially explicit capture-recapture. Ecography 39:676–688. doi: 10.1111/ecog.01511

Erwin, R. M., D. F. Brinker, B. D. Watts, G. R. Costanzo, and D. D. Morton (2011). Islands at bay: rising seas, eroding islands, and waterbird habitat loss in Chesapeake Bay (USA). Journal of Coastal Conservation 15:51–60. doi: 10.1007/s11852-010-0119-y

Erwin, R. M., J. G. Haig, D. B. Stotts, and J. S. Hatfield (1996a). Dispersal and habitat use by post-fledging juvenile Snowy Egrets and Black-crowned Night-Herons. Wilson Bulletin 108:342–356.

Erwin, R. M., J. G. Haig, D. B. Stotts, and J. S. Hatfield (1996b). Reproductive success, growth and survival of Black-crowned Night-Heron (Nycticorax nycticorax) and Snowy Egret (Egretta thula) chicks in coastal Virginia. The Auk 113:119–130. doi: 10.2307/4088940

Etezadifar, F., and A. Barati (2015). Factors affecting offspring growth and daily nest survival rates in the coastal breeding western reef heron (egretta gularis) in the persian gulf. Marine Ecology 36:379–388. doi: 10.1111/maec.12147

Etterson, M. A., S. N. Ellis-Felege, D. Evers, G. Gauthier, J. A. Grzybowski, B. J. Mattsson, L. R. Nagy, B. J. Olsen, C. M. Pease, M. P. van der Burg, and A. Potvien (2011). Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments. Ecological Modelling 222:2178–2190. doi: 10.1016/j.ecolmodel.2010.10.013

Fasola, M., Y. Zhang, D. Zhao, Y. Dong, and H. Wang (2001). Age-assortative mating related to reproductive success in Black-crowned Night Herons. Waterbirds: The International Journal of Waterbird Biology 24:272–276. doi: 10.2307/1522041

Fernandez-Juricic, E., P. A. Zollner, C. Leblanc, and L. M. Westphal (2007). Responses of nestling Black-crowned Night Herons (Nycticorax nycticorax) to aquatic and terrestrial recreational activities : a manipulative study. Waterbirds 30:554–565.

Finch, T., S. J. Butler, A. M. A. Franco, and W. Cresswell (2017). Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86:662–673. doi: 10.1111/1365-2656.12635

Frederick, P. C., R. Bjork, G. T. Bancroft, and G. V. N. Powell (1992). Reproductive success of three species of herons relative to habitat in southern Florida. Colonial Waterbirds 15:192–201.

Fujioka, M. (1985). Food delivery and sibling competition in experimentally even-aged broods of the Cattle Egret. Behavioral Ecology and Sociobiology 17:67–74. doi: 10.1007/BF00299431

Gawlik, D. E. (2002). The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329–346. doi: 10.1890/0012-9615(2002)072[0329:TEOPAO]2.0.CO;2

Geary, B., M. C. Green, and B. M. Ballard (2015). Movements and survival of juvenile Reddish Egrets Egretta rufescens on the Gulf of Mexico coast. Endangered Species Research 28:123–133. doi: 10.3354/esr00682

Gebhardt-Henrich, S., and H. Richner (1998). Causes of growth variation and its consequences for fitness. In Avian growth and development: Evolution within the altricial-precocial spectrum. pp. 324–339.

Gilbert, N. I., R. A. Correia, J. P. Silva, C. Pacheco, I. Catry, P. W. Atkinson, J. A. Gill, and A. M. A. Franco (2016). Are White Storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident White Storks (Ciconia ciconia) from a partially migratory population. Movement Ecology 4:1–13. doi: 10.1186/s40462-016-0070-0

Gilliland, S. G., C. D. Ankney, and G. J. Robertson (2016). Effect of brood size on nestling growth and survival of Great Black-backed Gull (Larus marinus) chicks. Waterbirds 39:246–252. doi: 10.1675/063.039.sp122

González-Medina, E., J. A. Castillo-Guerrero, and E. Mellink (2010). Parental and chick responses of Laughing Gulls (Leucophaeus atricilla) to increase of flight costs and brood size. Journal of Ornithology 151:219–225. doi: 10.1007/s10336-009-0448-5

Goodenough, A. E., D. G. Coker, M. J. Wood, and S. L. Rogers (2017). Overwintering habitat links to summer reproductive success: intercontinental carry-over effects in a declining migratory bird revealed using stable isotope analysis. Bird Study 64:433–444.

Gorenzel, W. P., F. S. Conte, and T. P. Salmon (1994). Bird damage at aquaculture facilities. In The Handbook: Prevention and Control of Wildlife Damage. p. E-5-E-18.

Gow, E. A., A. B. Musgrove, and K. L. Wiebe (2013). Brood age and size influence sex-specific parental provisioning patterns in a sex-role reversed species. Journal of Ornithology 154:525–535. doi: 10.1007/s10336-012-0923-2

Grüebler, M. U., and B. Naef-Daenzer (2008). Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. Ecology 89:2736–2745. doi: 10.1890/07-0786.1

Hafner, H., Y. Kayser, V. Boy, M. Fasola, A.-C. Julliard, R. Pradel, and F. Cezily (1998). Local survival, natal dispersal, and recruitment in Little Egrets Egretta garzetta. Journal of Avian Biology 29:216–227. doi: 10.2307/3677103

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18. doi: 10.1111/j.1365-2656.2010.01740.x

Hewson, C. M., K. Thorup, J. W. Pearce-Higgins, and P. W. Atkinson (2016). Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7:1–8. doi: 10.1038/ncomms12296

Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. W. Coulston, N. Herold, J. Wickham, and K. Megown (2015). Completion of the 2011 National Land Cover Database for the conterminous United States - Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:346–

354.

Hothem, R. L., B. E. Brussee, and W. E. Davis Jr. (2010). Black-crowned Night-Heron (Nycticorax nycticorax). *The Birds of North America Online*.

Hothem, R. L., and D. Hatch (2004). Reproductive success of the Black-crowned Night Heron at Alcatraz Island, San Francisco Bay, California, 1990-2002. Waterbirds 27:112–125.

Hötker, H. (2002). Arrival of Pied Avocets Recurvirostra avosetta at the breeding site: Effects of winter quarters and consequences for reproductive success. Ardea:379–387.

Hunt, V. M. (2016). Reproductive success and habitat selection in Black-crowned Night-Herons (Nycticorax nycticorax) in a city park. American Midland Naturalist 175:168–182. doi: 10.1674/0003-0031-175.2.168

Huschle, G., J. E. Toepfer, and D. C. Douglas (2013). Migration and wintering areas of American Bitterns (Botaurus lentiginosus) that summer in central North America as determined by satellite and radio telemetry, 1998 – 2003. Waterbirds 36:300–309. doi: 10.1675/063.036.0307

Hylton, R., P. C. Frederick, T. E. De La Fuente, and M. G. Spalding (2006). Effects of nestling health on postfledging survival of Wood Storks. The Condor 108:97–106. doi: http://dx.doi.org/10.1650/0010-5422(2006)108[0097:EONHOP]2.0.CO;2

Janiszewski, T., P. Minias, and Z. Wojciechowski (2013). Reproductive consequences of early arrival at breeding grounds in the White Stork Ciconia ciconia. Bird Study 60:280–284. doi: 10.1080/00063657.2013.778227

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra (2006). Assessing habtiat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology 20:1433–1444.

Jones, A. W., and D. M. Post (2016). Does intraspecific competition promote variation ? A test via synthesis. doi: 10.1002/ece3.1991

Jones, T. M., M. P. Ward, T. J. Benson, and J. D. Brawn (2017). Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. Journal of Avian Biology 48:439–447. doi: 10.1111/jav.01143

Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.

Jungsoo, K., and K. Tae-Hoe (2007). Clutch size, reproductive success, and growth rate of Black-crowned Night Herons Nycticorax nycticorax. Waterbirds 30:129–132. doi: 10.1675/1524-4695(2007)030[0129:CSRSAG]2.0.CO;2

Kalmbach, E., and P. H. Becker (2005). Growth and survival of Neotropic Cormorant (Phalacrocorax brasilianus) chicks in relation to hatching order and brood size. Journal of Ornithology 146:91–98. doi: 10.1007/s10336-004-0061-6

Kalmbach, E., and M. M. Benito (2007). Sexual size dimorphism and offspring vulnerability in birds. In Oxford University Press.

Keedwell, R. J. (2003). Does fledging equal success? Post-fledging mortality in the Black-Fronted Tern. Journal of Field Ornithology 74:217–221.

Kelly, J. P., H. M. Pratt, and P. L. Greene (1993). The distribution, reproductive success, and habitat characteristics of heron and egret breeding colonies in the San Francisco Bay area. Colonial Waterbirds 16:18–27. doi: 10.2307/1521552

Kilner, R., and R. A. Johnstone (1997). Begging the question: are offspring solocitation behaviours signals of need? Trends in Ecology & Evolution 12:11–15. doi: 10.1016/S0169-5347(96)10061-6

Kim, J., and T.-H. Koo (2009). Nest Site Selection and Reproductive Success of Herons and Egrets in Pyeongtaek Heronry, Korea. Waterbirds 32:116–122. doi: 10.1675/063.032.0113

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Alerstam (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176–184. doi: 10.1111/1365-2656.12135

Klug, H., and M. B. Bonsall (2014). What are the benefits of parental care? the importance of parental effects on developmental rate. Ecology and Evolution 4:2330–2351. doi: 10.1002/ece3.1083

Kochert, M. N., M. R. Fuller, L. S. Schueck, L. Bond, M. J. Bechard, B. Woodbridge, G. L. Holroyd, M. S. Martell, and U. Banasch (2011). Migration patterns, use of stopover areas, and austral summer movements of Swainson's Hawks. The Condor 113:89–106. doi: 10.1525/cond.2011.090243

Koczur, L. M., G. M. Kent, B. M. Ballard, K. D. Meyer, and M. C. Green (2018). Space use and movements of adult Reddish Egrets (Egretta rufescens) during winter. Waterbirds 41:1–15.

Kölliker, M., H. Richner, I. Werner, and P. Heeb (1998). Begging signals and biparental care: nestling choice between parental feeding locations. Animal Behaviour 55:215–222. doi: 10.1006/anbe.1997.0571

Kölzsch, A., G. J. D. M. Müskens, H. Kruckenberg, P. Glazov, R. Weinzierl, B. A. Nolet, and M. Wikelski (2016). Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover

use and departure. Oikos 125:1496–1507. doi: 10.1111/oik.03121

Kranstauber, B., R. Weinzierl, M. Wikelski, and K. Safi (2015). Global aerial flyways allow efficient travelling. Ecology Letters 18:1338–1345. doi: 10.1111/ele.12528

Kushlan, J. A., M. J. Steinkamp, K. C. Parsons, J. Capp, M. Acosta-Cruz, M. Coulter, I. Davidson, L. Dickson, N. Edelson, R. Elliot, R. M. Erwin, et al. (2002). Waterbird conservation for the Americas: the North American waterbird conservation plan.

Laake, J. L. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep:1–25.

Lack, D. L. (1947). The significance of clutch- size. Ibis 89:302–352.

Lack, D. L. (1954). The natural regulation of animal numbers. In The Clarendon Press, Oxford.

Lack, D. L. (1968). Ecological adaptations for breeding in birds. In Methuen, London.

Ledwón, M., and J. Betleja (2015). Post-breeding migration of Night Herons Nycticorax nycticorax tracked by GPS/GSM transmitters. Journal of Ornithology 156:313–316. doi: 10.1007/s10336-014-1131-z

Lescroël, A., G. Ballard, V. Toniolo, K. J. Barton, P. R. Wilson, P. O. Lyver, and Ainl (2010). Working less to gain more: when breeding quality relates to foraging efficiency. Ecology 91:2044–2055.

Littlefield, C. D., and J. E. Cornely (1984). Fall migration of birds at Malheur National Wildlife Refuge, Oregon. Western Birds 15:15–22.

López-López, P. (2016). Individual-based tracking systems in ornithology: welcome to the era of big data. Ardeola 63:103–136. doi: 10.13157/arla.63.1.2016.rp5

Loss, S. R., T. Will, and P. P. Marra (2013). Estimates of bird collision mortality at wind facilities in the contiguous United States. Biological Conservation 168:201–209. doi: 10.1016/j.biocon.2013.10.007

Maness, T. J., and D. J. Anderson (2013). Predictors of juvenile survival in birds. In Ornithological Monographs. doi: 10.1525/om.2013.78.1.1.1

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:1–4. doi: 10.1098/rsbl.2015.0552

Marra, P. P., L. A. Culp, A. L. Scarpignato, and E. B. Cohen (2014). Full annual cycle climate change vulnerability assessment for migratory birds of the Upper Midwest and Great Lakes Region.

Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable carbon isotopes. *Science*.

Martin, C. A., J. C. Alonso, J. A. Alonso, C. Palacin, M. Magana, and B. Martin (2007). Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard Otis tarda. Journal of Avian Biology 38:335–346. doi: 10.1111/j.2007.0908-8857.03811.x

Martinez-Meyer, E., A. T. Peterson, and A. G. Navarro-Siguenza (2004). Evolution of seasonal ecological niches in the Passerina buntings (Aves: Cardinalidae). Proceedings of the Royal Society B: Biological Sciences 271:1151–1157.

Mayfield, H. (1961). Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Mayfield, H. (1975). Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

McKinnon, E. A., C. M. Macdonald, H. G. Gilchrist, and O. P. Love (2016). Spring and fall migration phenology of an Arctic-breeding passerine. Journal of Ornithology 157:681–693. doi: 10.1007/s10336-016-1333-7

Mikuska, T., J. A. Kushlan, and S. Hartley (1998). Key areas for wintering North American herons. Colonial Waterbirds 21:125–134.

Miller, C. (2001). Long-term monitoring of a breeding colony of white herons (Egretta alba) on the Waitangiroto river, South Westland, New Zealand. Notornis 48:157–163.

Mills, A. M. (2005). Protogyny in autumn migration: Do male birds "play chicken"? The Auk 122:71–81.

Mock, D. W. (1985). Siblicidal brood reduction: the prey-size hypothesis. The American Naturalist 125:327–343.

Mock, D. W., and G. A. Parker (1986). Advantages and disadvantages of egret and heron brood reduction. Evolution 40:459–470.

Mock, D. W., and G. A. Parker (1997). The evolution of sibling rivalry. In Oxford University Press.

Morbey, Y. E., and R. C. Ydenberg (2001). Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673. doi: 10.1046/j.1461-0248.2001.00265.x

Morrison, R. I. G., and K. A. Hobson (2004). Use of body stores in shorebirds after arrival on High-Arctic breeding grounds. The Auk 121:333–344. doi: 10.1642/0004-8038(2004)121[0333:UOBSIS]2.0.CO;2

Musgrove, A. B., and K. L. Wiebe (2014). Northern Flickers increase provisioning rates to raise more but poorer quality offspring when given experimentally enlarged broods. The Auk 131:571–582. doi: 10.1642/AUK-14-51.1

Naef-Daenzer, B., F. Widmer, and M. Nuber (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal Ecology 70:730–738.

Naef-Daenzer, L., B. Naef-Daenzer, and R. G. Nager (2000). Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. Journal of Avian Biology 31:206–214.

Nakagawa, S. (2015). Missing data: mechanisms , methods, and messages. In Ecological Statistics: Contemporary Theory and Application. pp. 81–105.

Nakagawa, S., and R. P. Freckleton (2011). Model averaging, missing data and multiple imputation: a case study for behavioural ecology. Behavioral Ecology and Sociobiology 65:103–116. doi: 10.1007/s00265-010-1044-7

Newton, I. (2008). The migration ecology of birds. In Academic Press, Oxford, UK.

Nielson, R. M., H. Sawyer, and T. L. McDonald (2013). BBMM: Brownian bridge movement model.

Nilsson, C., R. H. G. Klaassen, and T. Alerstam (2013). Differences in speed and duration of bird migration between spring and autumn. The American Naturalist 181:837–845. doi: 10.1086/670335

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59–64. doi: 10.1098/rspb.2003.2569

O'Connor, C. M., D. R. Norrid, G. T. Crossin, and S. J. Cooke (2014). Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere 5:1–11.

Ohio Department of Natural Resources (2017). Ohio's listed species. *5356*.

Oppel, S., A. N. Powell, and D. L. Dickson (2008). Timing and distance of King Eider migration and winter movements. The Condor 110:296–305. doi: 10.1525/cond.2008.8502

Ouwehand, J., and C. Both (2016). African departure rather than migration speed determines variation in spring arrival in Pied Flycatchers. Journal of Animal Ecology 86:88–87. doi: 10.1111/1365-2656.12599

Park, S., K. Kim, H. Chung, Y. Choi, and H.-C. Sung (2011). Vertical nest stratification and breeding success in a six mixed-species heronry in Taeseong, Chungbuk, Korea. Animal Cells and Systems 15:85–90. doi: 10.1080/19768354.2011.555119

Parsons, K. C., and J. Burger (1982). Human disturbance and nestling behavior in Black-crowned Night Herons. The Condor 84:184–187. doi: 10.2307/1367667

Paxton, K. L., and F. R. Moore (2015). Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. Journal of Avian Biology 46:495–506. doi: 10.1111/jav.00614

Pérez, J. H., J. S. Krause, H. E. Chmura, S. Bowman, M. McGuigan, A. L. Asmus, S. L. Meddle, K. E. Hunt, L. Gough, N. T. Boelman, and J. C. Wingfield (2016). Nestling growth rates in relation to food abundance and weather in the Arctic. The Auk 133:261–272. doi: 10.1642/AUK-15-111.1

Pyle, P. (1997). Identification guide to North American birds, part 1: Columbidae to Ploceidae. In Slate Creek Press.

R Core Development Team (2018). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*.

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe (2009). Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B: Biological Sciences 276:1619–1626. doi: 10.1098/rspb.2008.1452

Ricklefs, R. E. (1968). Patterns of growth in birds. Ibis 110:419–451. doi: 10.1111/j.1474-919X.1968.tb00058.x

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48. doi: 10.5479/si.00810282.9

Ricklefs, R. E. (1984). The optimization of growth rate in altricial birds. Ecology 65:1602–1616.

Rodewald, P. G., M. B. Shumar, A. T. Boone, D. L. Slager, and J. McCormac (2016). The Second Atlas of Breeding Birds in Ohio. In Pennsylvania State University.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016). Partners in flight landbird conservation plan: 2016 revision for Canada and Continental United States. *Partners in Flight Science Committee*.

Rush, S. A., C. Pekarik, D. V. Weseloh, F. Cuthbert, D. Moore, and L. Wires (2015). Changes in heron and egret populations on the Laurentian Great Lakes and connecting channels, 1977-2009. Avian Conservation and Ecology 10:1–17.

Rushing, C. S., T. B. Ryder, J. F. Saracco, and P. P. Marra (2013). Assessing migratory connectivity for a long-distance migratory bird using multiple intrinsic makers. Ecological Applications 24:445–456. doi: 10.1890/13-1091.1

Ryder, T. B., J. W. Fox, and P. P. Marra (2011). Estimating migratory connectivity of Gray Catbirds (Dumetella carolinensis) using geolocator and mark–recapture data. The Auk 128:448–453. doi: 10.1525/auk.2011.128.4.810

Saino, N., P. Ninni, M. Incagli, S. Calza, R. Sacchi, and A. Moller (2000). Begging and parental care in relation to offspring need and condition in the Barn Swallow (Hirundo rustica). The American Naturalist 156:637–649.

Saunders, S. P., T. W. Arnold, E. A. Roche, and F. J. Cuthbert (2014). Age-specific survival and recruitment of piping plovers Charadrius melodus in the Great Lakes region. Journal of Avian Biology 45:437–449. doi: 10.1111/jav.00319

Schaub, M., and F. Abadi (2011). Integrated population models: A novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152:S227–S237. doi: 10.1007/s10336-010-0632-7

Schreiber, E. A. (1996). Experimental Manipulation of Feeding in Red-Tailed Tropicbird Chicks. Colonial Waterbirds 19:45–55. doi: 10.2307/1521806

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen (1999). Effects of sample size on kernal home range estimates. Journal of Wildlife Management 63:739–747.

Sénéchal, É., J. Bêty, H. G. Gilchrist, K. A. Hobson, and S. E. Jamieson (2011). Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165:593–604.

Shieldcastle, M. C., and L. Martin (1997). Colonial Waterbird Nesting on West Sister Island National Wildlife Refuge and the Arrival of Double-Crested Cormorants. In Symposium on Double-Crested Cormorants: Population Status and Management Issues in the Midwest. pp. 115–120.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smiseth, P. T., C. T. Darwell, and A. J. Moore (2003). Partial begging: an empirical model for the early evolution of offspring signalling. Proceedings of the Royal Society B: Biological Sciences 270:1773–1777. doi: 10.1098/rspb.2003.2444

Smith, A. D., and S. R. McWilliams (2014). What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behavioral Ecology 25:1423–1435. doi: 10.1093/beheco/aru148

Smith, R. J., and F. R. Moore (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology & Sociobiology 57:231–239. doi: 10.1007/s00265-004-0855-9

Sprent, J., and S. C. Nicol (2012). Influence of habitat on home-range size in the short-beaked echidna. Australian Journal of Zoology 60:46–53. doi: 10.1071/ZO11098

Stier, A., A. Ricardou, S. Uriot, N. De Pracontal, and J. A. Kushlan (2017). Breeding season home range and migration of the Agami Heron (Agamia agami). Waterbirds 40:289–296.

Stirrat, S. C. (2003). Seasonal changes in home-range area and habitat use by the agile wallaby (Macropus agilis). Wildlife Research 30:593–600.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. Macpherson, J. W. Fox, and V. Afanasyev (2010). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B: Biological Sciences 278:131–137. doi: 10.1098/rspb.2010.1220

Stutchbury, B. J. M., R. Siddiqui, K. Applegate, G. T. Hvenegaard, P. Mammenga, N. Mickle, M. Pearman, J. D. Ray, A. Savage, T. Shaheen, and K. C. Fraser (2016). Ecological Causes and Consequences of Intratropical Migration in Temperate-Breeding Migratory Birds. The American Naturalist 188:S28–S40. doi: 10.1086/687531

Takeshi, S. (2013). Colony Development and Density-Dependent Processes in Breeding Grey Herons. International Journal of Zoology:1–10.

Taylor, M. A., D. B. Enfield, and A. A. Chen (2002). Influence of the tropical Atlantic versus the tropical pacific on caribbean rainfall. Journal of Geophysical Research 107:1–14.

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:1–11.

Therneau, T. (2015). A package for purvival analysis in S.

Thomas, K., and D. Shutler (2001). Ectoparasites, nestling growth, parental feeding rates, and begging intensity of tree swallows. Canadian Journal of Zoology 79:346–353. doi: 10.1139/cjz-79-2-346

Thompson, S. P., C. D. Littlefield, and R. Y. Ryder (1979). Historical review and status of colonial nesting birds on Malheur National Wildlife Refuge, Oregon. Proceedings of the Colonial Waterbird Group 3:156–164.

Tremblay, J., and L. N. Ellison (1979). Effects of human disturbance on breeding of Black-crowned Night Herons. The Auk 96:364–369. doi: 10.2307/4085315

U.S. Department of Energy (2017). Lake Erie Energy Development Corporation (LEEDCo) Project Icebreaker Draft Environmental Assessment (DOE/EA-2045). Cleveland, OH.

U.S. Fish and Wildlife Service, and Canadian Wildlife Service (2012). North American Waterfowl Management Plan. North American Waterfowl Management Plan 2012 – People Conserving Waterfowl and Wetlands.

Walter, W. D., D. P. Onorato, and J. W. Fischer (2015). Is there a single best estimator? Selection of home range estimators using area-under-the-curve. Movement Ecology 3:1–11. doi: 10.1186/s40462-015-0039-4

Wang, Z., X. Zhou, Q. Lin, W. Fang, and X. Chen (2011). New primers for sex identification in the Chinese Egret and other ardeid species. Molecular Ecology Resources 11:176–179. doi: 10.1111/j.1755-0998.2010.02879.x

Warnock, N. (2010). Stopping vs. staging: The difference between a hop and a jump. Journal of Avian Biology 41:621–626. doi: 10.1111/j.1600-048X.2010.05155.x

Webster, M. S., and P. P. Marra (2005). The importance of understanding migratory connectivity and seasonal interactions. In Birds of Two Worlds: The Ecology and Evolution of Migration. pp. 199–209.

Weimerskirch, H., K. Delord, A. Guitteaud, R. A. Phillips, and P. Pinet (2015). Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Scientific Reports 5:1–7. doi: 10.1038/srep08853

White, G. C., and K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120-139.

Wilcox, C., E. Van Sebille, and B. D. Hardesty (2015). Threat of plastic pollution to seabirds is global, pervasive, and increasing. Proceedings of the National Academy of Sciences 112:11899–11904. doi: 10.1073/pnas.1502108112

Van Wilgenburg, S. L., and K. A. Hobson (2011). Combining stable-isotope (D) and band recovery data to improve probabilistic assignment of migratory birds to origin. Ecological Applications 21:1340–1351. doi: 10.1890/09-2047.1

Wilson, Jr., W. H., A. R. Savage, and R. E. Zierzow (1996). Arrival dates of migratory

breeding birds in Maine: results from a volunteer network. Northeastern Naturalist 4:83–92.

van der Winden, J., M. J. M. Poot, and P. W. van Horssen (2010). Large birds can migrate fast: The post-breeding flight of the Purple Heron Ardea purpurea to the Sahel. Ardea 98:395–402. doi: 10.5253/078.098.0313

Wolford, J. W., and D. A. Boag (1971). Food habits of Black-crowned Night Herons in southern Alberta. Auk 88:435–437.

Woodin, M. C., M. K. Skoruppa, J. W. Edwardson, and J. E. Austin (2012). Evaluation of capture techniques for Long-billed Curlews wintering in Texas. Bulletin of the Texas Ornithology 45:13–22.

Woodworth, B. K., A. E. M. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright, and D. R. Norris (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia 181:413–422. doi: 10.1007/s00442-015-3527-8

Wyman, K. E., and F. J. Cuthbert (2017). Black Tern (Chlidonias niger) breeding site abandonment in U.S. Great Lakes coastal wetlands is predicted by historical abundance and patterns of emergent vegetation. Wetlands Ecology and Management 25:583–596. doi: 10.1007/s11273-017-9537-z

Yosef, R., and A. Wineman (2010). Differential stopover of Blackcap (Sylvia atricapilla) by sex and age at Eilat , Israel. Journal of Arid Environments 74:360–367. doi: 10.1016/j.jaridenv.2009.09.004

Appendix A: Chapter 1 Supplementary Materials

Figure A.1. Driving route used to search for nanotagged fledgling Black-crowned Night-Herons in Lake Erie, Ohio from June to November in 2016 and 2017.

Figure A.2. Example flight path used to search for nanotagged fledgling Black-crowned

Night-Herons in Lake Erie, Ohio from June to November in 2016 and 2017.

Table A.1. Mass, wing, culmen, and tarsus daily growth rates (mean ± SD) for Black-crowned Night-Heron chicks by rank in brood from Lake Erie, Ohio, in 2016 and 2017.

Chick rank	*n*	Year	Mass (g/day)	Wing (mm/day)	Culmen (mm/day)	Tarsus (mm/day)
A	16	2016	35.48 ± 11.20	9.06 ± 11.76	2.10 ± 11.57	3.20 ± 17.78
	5	2017	38.38 ± 6.98	9.34 ± 23.30	2.25 ± 23.10	3.34 ± 0.99
B	16	2016	36.03 ± 1.21	9.26 ± 1.96	2.27 ± 2.84	3.50 ± 2.64
	4	2017	23.60 ± 0.93	8.61 ± 0.81	1.83 ± 3.81	3.03 ± 1.21
C	13	2016	30.89 ± 0.45	7.30 ± 0.53	2.56 ± 0.78	3.51 ± 0.57
	3	2017	15.16 ± 0.63	6.08 ± 0.94	1.80 ± 0.42	2.38 ± 0.85
D	4	2016	25.54 ± 1.04	6.63 ± 0.61	2.20 ± 1.13	3.24 ± 0.98
	1	2017	27.82	5.27	2.13	2.82