2014

Rise of a Floater Class: Behavioral Adjustments by Breeding Bald Eagles in a Population Approaching Saturation

Courtney L. Turrin
College of William & Mary - Arts & Sciences

Rise of a floater class: Behavioral adjustments by breeding Bald Eagles in a
population approaching saturation

Courtney L. Turrin

New City, NY

BS, Bucknell University, 2011

A Thesis presented to the Graduate Faculty
of the College of William and Mary in Candidacy for the Degree of
Master of Science
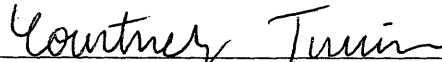
Department of Biology

The College of William and Mary
January 2014

APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

_____
Courtney L. Turrin

Approved by the Committee, October 2013

_____
Committee Chair
Mitchell A. Byrd Research Professor of Conservation Biology Bryan D. Watts, Biology
The College of William and Mary

_____
Professor John Swaddle, Biology
The College of William and Mary

_____
Assistant Professor Matthias Leu, Biology
The College of William and Mary

COMPLIANCE PAGE

Research approved by

W&M Institutional Animal Care and Use Committee

Protocol number(s): IACUC-2010-12-20-7056-mdwils

Date(s) of approval: 2010-12-20 through 2013-12-20

ABSTRACT

The Bald Eagle (*Haliaeetus luecocephalus*) population within the Chesapeake Bay has been growing rapidly for more than 40 years and is now approaching saturation. As the population reaches capacity, density-dependent mechanisms are expected to constrain reproductive options for birds of recruitment age, leading to the formation and expansion of a floater class. Negative feedback from these non-breeding, non-territorial adults has been shown to impact reproductive success of breeders in raptor species, providing a behavioral mechanism that slows population growth. However, little is known about the nature of interactions between floaters and established breeders during the reproductive period. Despite their presence in many populations and species, floaters remain an enigmatic aspect of population biology.

We estimated the growth of the floater pool from 1990 to 2013 using reproductive data from aerial surveys and a closed BIDE model. We assessed long-term changes in breeder nest guarding patterns from 1994 – 2002 compared to 2013 to gauge the response of breeding pairs to increasing floater numbers. We used reproductive survey data (2006 – 2013) to identify the period during development when Bald Eagle broods are most at risk of failure to determine when intrusion poses the greatest threat to nest success. During observation sessions conducted in the 2012 and 2013 breeding seasons, we quantified intruder pressure at Bald Eagle nests, characterized the behaviors involved in conspecific encounters, and examined nest guarding behaviors of breeders.

We found that nearly 100% of newly mature birds were recruited annually into the breeding population in the early 1990's, but by 2011, less than 1 in 5 birds became breeders in their first year after attaining adult plumage. In concert with the decline in the assimilation of new breeders, the floater pool has increased over 5-fold since 1990 with an average doubling time of 2.8 years. We identified the first two to three weeks after hatching as the critical period for Bald Eagle nest success in the lower Chesapeake Bay, with the probability of nest failure steadily decreasing from 27% for 1-week-old broods to 7% of for broods beyond the three-week threshold. The average territorial intrusion rate during the reproductive period was 0.28 ± 0.32 intrusions/hr. Juvenile intrusions occurred closer to the nest than adult intrusions, but breeders showed higher response rates toward adult intruders. Breeders responded to intruders more frequently and more aggressively when in the presence of their mates. Nests in the post-hatching stage were guarded significantly more often than during pre-laying or incubation periods. Aerial surveys indicated that the frequency of nest guarding by the second adult during the critical period has doubled from 1994 - 2002 to 2013. These findings suggest that floater pressure on breeding pairs is increasing as the population approaches saturation and that pairs are responding with behavioral adjustments.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

This thesis is dedicated to Barbara, who has worn many hats, including grandmother, mentor, and friend.

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

BALD EAGLES ADJUST NEST GUARDING BEHAVIOR IN RESPONSE TO INCREASING FLOATER POOL

Abstract. Floaters arise in populations when competition for limited resources results in breeding pairs preventing other mature individuals from establishing breeding territories. Bald Eagles in the lower Chesapeake Bay are approaching saturation and the range of opportunities for birds of recruitment age is narrowing. Focusing on two major tributaries of the Bay (James and Rappahannock Rivers), we used reproductive survey data to calculate the annual recruitment of 5-year-old Bald Eagles into the breeding population and to estimate the number of recruitment-age birds that joined the floater population each year from 1990 to 2013. The annual growth of the floater pool increased exponentially from an average of 11 adults in the 1990's to over 550 birds in 2013, with an average doubling time of 2.6 years. Assimilation of new breeders decreased from nearly 100% of transitioning birds to less than 17% over the 24-year study period. Based on these estimates, we compared nest guarding behavior from 1994 to 2002, when floater numbers were relatively low, to nest guarding in 2013 to determine whether breeding adults nesting in the lower Chesapeake Bay have adjusted defensive behavior to cope with increasing floater pressure. Concurrent with the expansion of the floater pool was a shift in nest guarding behavior; breeding adults doubled nest guarding effort in the early post-hatching period in 2013 compared to the earlier time period. The results

suggest that breeding pairs may adjust reproductive time budgets in response to increasing floater pressure.

INTRODUCTION

Floaters are reproductively mature birds that have not established a nesting territory (Brown 1969). Floaters are often non-breeders, though in some species and populations floaters may account for a considerable portion of the copulations (Smith and Arcese 1989). A floater class forms when resources are limited in comparison to the number of reproductive-age birds in the population (Brown 1969, Newton 1998). Under such conditions, breeding pairs prevent other reproductively mature individuals from establishing breeding territories in order to maximize their own fitness (Brown 1969, Newton 1992, Penteriani et al. 2011).

In some species, floaters may play a role in regulating population size and growth rate. The interference competition hypothesis suggests that population size is regulated through density-dependent competition for food (eg. Furness and Birkhead 1984, Martin 1987, Houston and Schmutz 1995, Newton 1998) and nesting sites (Newton 1998). In territorial species, the availability of suitable nesting space may provide the ultimate limit to population size (Newton 1979; Hunt 1998; Newton 1998; López-Sepulcre and Kokko 2005). As available nesting territory becomes limiting, contests among floaters and established breeders contribute to the stabilization of population growth by increasing adult mortality (Newton 1979, 1998) and negatively impacting breeding pairs' reproductive

2

success (Hunt 1998, Carrete et al. 2005, López-Sepulcre and Kokko 2005, Bretagnolle et al. 2008, Penteriani et al. 2011).

As the Bald Eagle (*Haliaeetus leucocephalus*) population in the Chesapeake Bay approaches carrying capacity (Watts et al. 2007), available nesting territory is becoming limiting and the range of opportunities for birds of recruitment age is narrowing. Territorial interactions at active nests are expected to become more frequent as the floater to breeder ratio and competition for nesting opportunities increase within the population (Newton 1979, Hunt 1998, López-Sepulcre and Kokko 2005). In raptor species, the ensuing fights between breeders and floaters can lead to injury or death (Jenkins and Jackman 1993, Hunt 1995). Intruding conspecifics may also attack chicks, resulting in nest failure (Markham and Watts 2007). In addition, floater pressure has been shown to impair breeding pairs' ability to provide for and protect broods (Bretagnolle et al. 2008; Penteriani et al. 2011). The increasing threat of territorial intrusion by floaters may result in adjusted reproductive time budgets, with breeding pairs increasing vigilance and nest guarding behaviors in order to maintain nesting territories and protect young from intruders.

The objectives of this study are to estimate long-term (1990 – 2013) changes in the size of the Bald Eagle floater pool in the lower Chesapeake Bay and to test for behavioral adjustments by breeding adults to floater pressure. We will assess changes in the assimilation of recruitment-age birds into the breeding population over time. In addition, we will examine long-term (1994 - 2002

compared to 2013) and within-season (2013) shifts in the frequency of nest

guarding to gauge the response of breeding adults to increasing floater numbers.

METHODS

We surveyed Bald Eagle nests along the James and Rappahannock Rivers in

Virginia from 1985 to 2013. We followed a standard two-flight approach including

a survey flight and a productivity flight (Fraser et al. 1983; Watts et al. 2006,

2008). The survey flights were conducted from late February to early March with

the purpose of finding new nests, checking known nests, and documenting

breeding attempts. Productivity flights were conducted from late April to mid-May

with the intention of determining nesting success, the number of offspring

produced, and brood age (Watts et al. 2006, 2008).

Growth of the Floater Pool. We used reproductive data and a multi-year BIDE

model (Bailey 1964, Cohen 1969, Pulliam 1988) with an assumption of a closed

population to estimate the size of recruitment-age cohorts, assimilation rates, and

the annual growth of the floater class. We estimated age-specific survival rates

using data from studies that have used transmitters to track mortality within

populations assumed to exhibit normal demographics (Table 1.1). We weighted

survivorship estimates based on the number of birds tracked in each study

relative to the total number of tracked birds in all studies. Collectively, the

estimated post-fledging survivorship based on these studies was 80.5% in the

first year and 90% in subsequent years, such that approximately 55.7% (95%

4

confidence interval, 54.1 – 57.4%) of fledged birds survive to reproductive age.

We applied these mortality rates to the number of chicks produced in each year's

cohort (1985 – 2008) to estimate the number of individuals that survived from

fledging through to breeding age each year from 1990 to 2013.

We determined the number of available birds of recruitment age that were

assimilated into the breeding population (Eq. 1). We applied an annual mortality

rate of 0.10 to the breeding adult population (P_{t-1}) to determine the replacement

demand for recruitment-aged birds within the breeding population. We used the

number of new breeding territories established each year (E_t) to estimate the

number of recruits forming such territories under the assumption that all

territories were formed by birds that were breeding for the first time. We

considered annual recruitment (A_t) to be the sum of the replacement demand and

the number of recruits on newly established territories. Finally, we calculated the

number of new floaters in each year of the study as the difference between the

estimated number of recruitment-age individuals (R_t) and the annual recruitment

of new breeders (A_t).

Equation 1. $A_t = (0.1 * P_{t-1}) + (E_t * 2)$

Equation 2.   Floater Pool Growth $= R_t - A_t$

We assessed the rate of increase in floater numbers by determining the

average time required for the floater population to double in size. Average

doubling time was calculated using the growth equation $N_t = N_0 e^{rt}$ where $t_{double} =$

ln(2)/*r* (Watts et al. 2006). N_0 was the number of floaters in the first year of the study (1990), and N_t was the number of floaters in the final year (2013).

Nest guarding. Nest guarding behavior was recorded during aerial surveys. Nest guarding is a type of defensive behavior that breeders use to deter potential predation (Slack 1976, Woodard and Murphy 1999), brood parasitism (Møller 1987, Gowaty et al. 1989), and territorial or mate takeover attempts (Nice 1941, Slagsvold et al. 1994, Mougeot 2000). Observations of nests in this population indicate that 80% of nest guarding occurs within 100 meters of the nest (Chapter 4). Thus, for the purposes of this study, we defined nest guarding as a member of the breeding pair attending the nest area within 100 meters of the nest structure, with the exception of individuals engaged in brooding, incubation, or feeding.

We were interested in the stage of brood development and the number of breeding adults attending nests. Incubation and post-hatching periods were distinguished by assessing nest contents and adult behavior. Chick age was determined during flights using degree of feather development and body size as indicators. We recorded whether one, both, or neither breeding adult was in attendance at the time of the survey. We assumed that adult eagles perched within 100 meters of the nest were breeding adults and the territory holders. This assumption is consistent with direct behavioral observations of breeding pairs at active nests in the lower Chesapeake Bay population (Chapter 4). We were primarily interested in the behavior of the second adult, as this individual would

6

be the adult to guard the nest while the other performs parental care activities in the nest.

We grouped nest guarding data into an early (1994 – 2002) and late (2013) time period for comparison. The early time period was selected because 1994 was the earliest year that guarding data were collected during aerial surveys, and after 2002, the estimated floater population began to increase exponentially. Between 2005 and 2012, nest guarding data were not collected during reproductive surveys. We focused comparisons on incubation and the first three weeks after hatching because sample size of broods representing the older age classes was limited. The early time period included n = 1247 nests in incubation and n = 54 nests in the post-hatching period. The late time period included n = 123 nests in incubation and n = 49 nests in the post-hatch period. In addition to examining long-term changes in guarding behavior, we also assessed shifts in nest guarding coverage over the course of the reproductive period during the 2013 breeding season (n = 358).

Statistical analyses. We used a chi square test to compare the frequency of nest guarding by the second breeding adult in the early and late time periods. We also conducted chi square analyses to examine whether there were any within-season (2013) age-dependent trends in nest attendance and nest guarding using brood age in weeks. Finally, we assessed the influence of reproductive stage on nest guarding behavior. Reproductive stages included incubation; early post-hatching (EPH), which we defined as the first 3 weeks after hatching; and late

post-hatching (LPH), which included broods older than 3 weeks and up to 10 weeks old.

RESULTS

Growth of the Floater Pool. Estimated annual growth of the floater pool has increased exponentially since the 1990's with an average doubling time of 2.6 years (Figure 1.1). In the 1990's, an average of 11 transitioning adults became floaters each year. The estimated number of nonbreeding adults began rapidly increasing in 2003. By 2013, the annual addition to the floater pool was more than 550 recruitment-age birds. Over the study period the number of floaters per breeding pair increased from less than 0.25 in the late 1990's to 1.5 in 2013.

The percentage of recruitment-age birds being assimilated into the breeding pool has changed over time. In the early 1990's, nearly 100% of recruitment-age birds were assimilating into the breeding faction of the population, either to replace lost breeders or by establishing new breeding territories (Figure 1.2). Over the 23-year study period, assimilation rates have decreased by more than 5-fold, with only 17% of birds reaching reproductive age becoming breeders in 2013.

Nest guarding. Nest guarding behavior was significantly more common in the later time period compared to the early period. Particularly at nests with hatched young, the frequency of nest guarding by the second breeding adult was higher in 2013 than from 1994 to 2002 (χ^2 = 14.27, P < 0.001; Figure 1.3). In 2013, 1- to

8

3-week-old broods were guarded by the second adult twice as often as broods in the first three weeks of hatching in the early time period.

Within-season analyses indicate that breeder attendance at active nests was significantly related to chick age and reproductive stage (Figure 1.4). The frequency of unattended nests was lower in the first four weeks after hatching and higher in each subsequent week than we would expect if the frequency of unattended nests was consistent throughout the post-hatching period ($\chi^2 = 39.03$, $P < 0.0001$). Adults rarely left nests unattended during incubation and in the EPH period, but sightings of unattended nests were significantly more frequent in the LPH period ($\chi^2 = 112.5$, $P < 0.0001$).

Nest guarding by the second breeding adult decreased significantly with increasing brood age (Figure 1.4). Nest guarding was observed in weeks 1 through 3 more frequently than expected and less frequently than expected in weeks 6 through 10 ($\chi^2 = 86.41$, $P < 0.0001$). When we assessed the results by reproductive stage, 53.1% of observed EPH nests were guarded by the second adult, compared to 21.2% of nests in the incubation period, and 2.2% of nests in the LPH period ($\chi^2 = 65.48$, $P < 0.0001$).

DISCUSSION

We estimate that the annual growth of the floater pool in the Chesapeake Bay Bald Eagle population increased over 5-fold from 2003 to 2013. The increase in floaters is a consequence of the reduction in per capita establishment of new breeding territories. Though the breeding portion of the population is approaching

9

saturation (Watts et al. 2007), estimates from the past 24 years indicate that the floater portion of the population is currently in a period of exponential growth. The floater pool is expected to continue growing until the population size stabilizes near carrying capacity (Hunt 1998).

Increases in the number of nonbreeders of reproductive age may have negative impacts on territory holders. Our results suggest that breeding adults have increased nest guarding effort during the first three weeks of the post-hatching period, a time that is critical to the survival of Bald Eagle broods in the Chesapeake Bay (Chapter 2). The high frequency of guarding observed in 2013 indicates a behavioral shift, as breeders in the same population guarded nests half as often 1 to 2 decades prior (1994 – 2002). The earlier time frame corresponds to a period when floater numbers were comparatively low; thus, intrusion pressure from floaters was less intense. The increased rates of nest guarding observed in the later time period may be a behavioral response to increasing floater pressure on breeding pairs.

Floaters have been shown to influence breeder fitness in a number of ways. Pressure from floaters can lead to declines in feeding rates (Davies and Houston 1981), increased stress on breeding adults (Praw and Grant 1999), nest disturbance (Komdeur 1996), declines in hatching success, and declines in productivity (Bretagnolle et al. 2008). In this population, we have documented an increase in nest guarding effort concurrent with a period of rapid increase in floater numbers. Dedicating more time and energy to nest guarding may affect the ability of breeding adults to successfully care for young. Though the average

10

productivity of Bald Eagle nests in the lower Chesapeake Bay has not shown indications of decline as a result of increasing floater numbers (Watts et al. 2006, unpublished data), we expect that there is a threshold level of floater pressure that breeding pairs can withstand (Hunt 1998). When this threshold is reached, floater pressure on breeding adults may lead to evident declines in reproductive success.

Our estimation of the size of the annual cohort of transitioning birds is contingent on the assumption that the population is closed to movement (Bailey 1964, Cohen 1969, Pulliam 1988). Though it is unlikely that emigration and immigration never occur in the Chesapeake Bay Bald Eagle population, evidence suggests that movement into and out of the population during the study period was limited. The Center for Conservation Biology has used satellite transmitters to track the movements of over 45 resident Bald Eagles representing a cross section of age classes (Watts and Mojica 2012). To date, all of these individuals have home ranges within the Chesapeake Bay, and those that have begun breeding have established territories within the bay (Watts and Mojica, unpublished data). Furthermore, there are only a handful of known cases of birds immigrating into the Chesapeake Bay population (B.D. Watts, pers. comm.). Because evidence suggests that emigration and immigration have relatively minor influences on the current population, the annual floater pool growth estimates presented here likely approximate actual floater numbers fairly accurately.

The Bald Eagle population in the lower Chesapeake Bay is expected to reach saturation within the next decade (Watts et al. 2007). When this occurs, all suitable nesting space will be occupied. Studies of other species have documented adjustments by breeding adults in response to increasingly intense competition for nesting territory, including constricted territory size (Norton et al. 1982, Ridley et al. 2004), increased mate guarding behavior (Birkhead 1982, Mougeot et al. 2002), reduced food provisioning, and reduced copulation rate (Mougeot et al. 2002). The results of this study provide evidence that breeding pairs may also respond to floater pressure with increased nest guarding focused on the post-hatching period, a behavioral adaptation for which there is little prior evidence. Bald Eagles in the lower Chesapeake Bay may further modify behavior to cope with increasing stress and threats to nesting territories and brood survival as the floater population continues to grow.

Table 1.1. Several studies have used transmitters to determine age-specific mortality rates in Bald Eagles. The number of birds tracked and the number that survived the first year after fledging are listed for each study. The results were pooled to estimate post-fledging mortality rate in the first year to be 19.5%. In subsequent years, mortality declined to 10%.

Birds Tracked	Birds Survived	Source
39	39	Buehler et al. 1991
44	28	Wood 1992
13	10	Jenkins et al. 1999
11	10	McClelland et al. 1996
15	13	Harmata et al. 1999
8	4	Hodges et al. 1987
70	57	Millsap et al. 2004
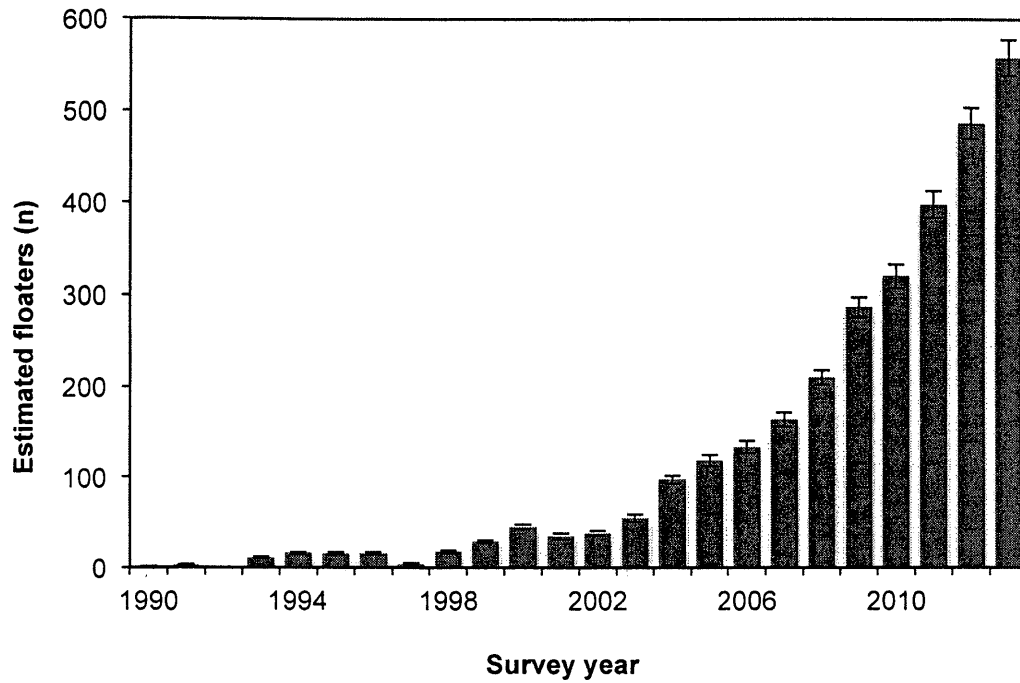
Figure 1.1. The annual growth of the floater pool was estimated from 1990 –

2013 using a closed BIDE model and data from reproductive surveys of Bald

Eagles in the lower Chesapeake Bay. Over the 24-year study period, annual

assimilation of recruitment-age birds into the floater pool increased over 5-fold.
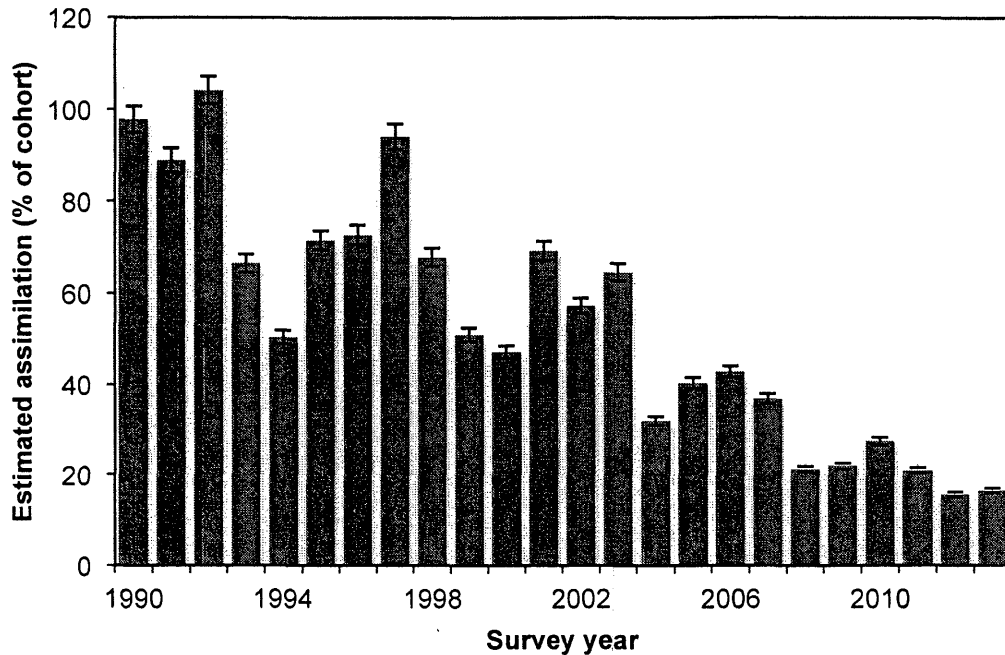
Figure 1.2. Assimilation into the breeding faction of the Bald Eagle population in the lower Chesapeake Bay was estimated (1990 – 2013) using a closed BIDE model and data from reproductive surveys of nests in the population. Assimilation was calculated as the percent of each recruitment-age cohort that gained a nesting territory, either by replacing mortality of pre-existing breeders or by establishing new territories. Annual recruitment of new breeders fell from nearly 100% of recruitment-age birds in the early 1990's to less than 20% after 2011.
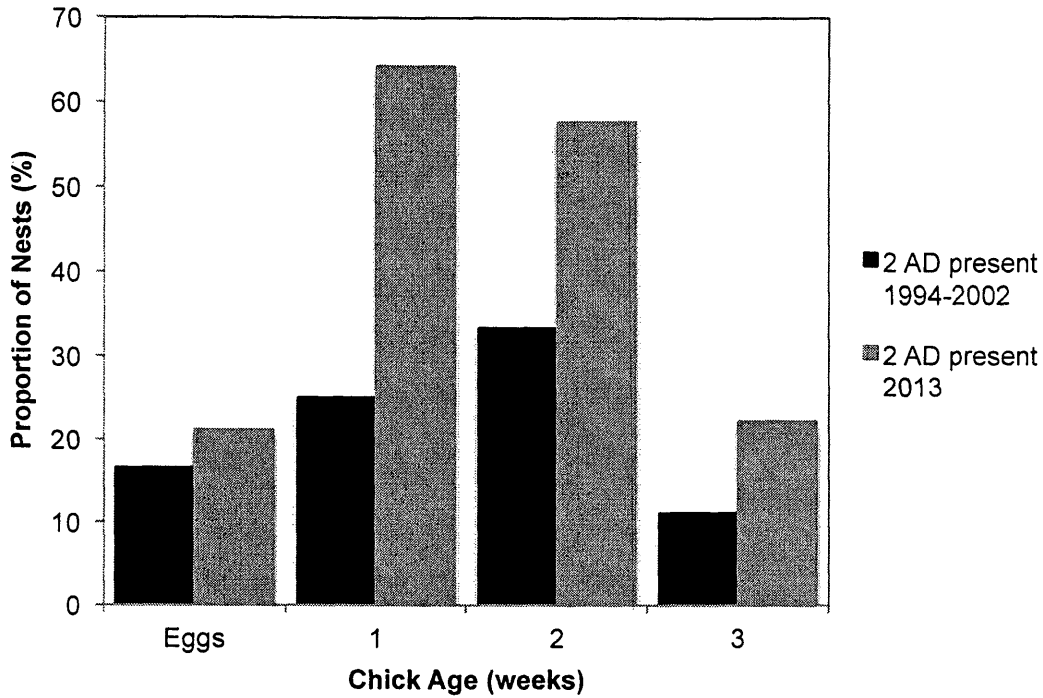
Figure 1.3. Proportion of the total nests surveyed in each developmental stage (incubation through 3 weeks post-hatching) from 1994 – 2002 and in 2013 that were attended by both breeding adults. Data were collected during aerial reproductive surveys of Bald Eagles in the lower Chesapeake Bay. From 1994 - 2002, the frequency of nest guarding by the second adult in the first 3 weeks of the post-hatching period was 50% lower than in 2013.
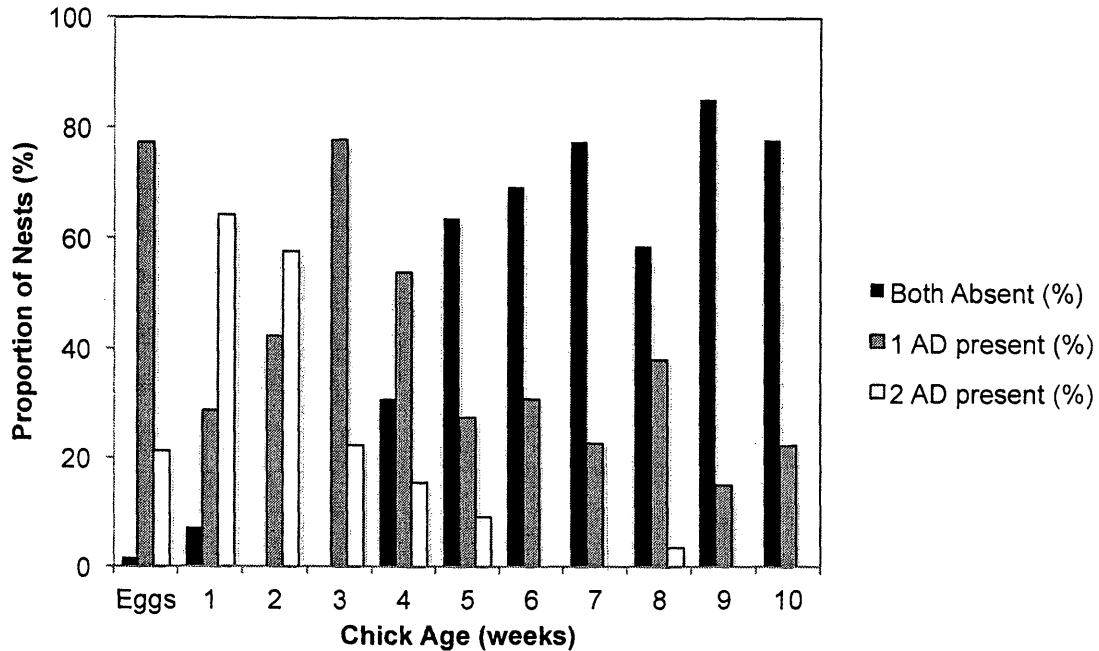
Figure 1.4. During aerial surveys of the lower Chesapeake Bay (2013), breeder attendance at nests was recorded as a percent of the total nests surveyed at different developmental time points (incubation through 10 weeks post-hatching). When compared to an even distribution, nests were guarded by both breeding adults more often than expected in weeks 1 - 3 and less often than expected in weeks 6 - 10. In the first 3 weeks after hatching, 53.1% of nests were attended by both adults, compared to 21.2% of nests in the incubation period, and 2.2% of nests 4 weeks and older.

CHAPTER 2

TIMING OF BROOD FAILURE IN CHESAPEAKE BAY BALD EAGLES

Abstract.

The risk of nest failure is influenced by environmental factors and the ability of adults to meet the demands of the brood throughout development. Changes in the vulnerability of the chicks and competing demands for adult time allocation lead to temporal patterns in the occurrence of nest failure. Using reproductive surveys of active Bald Eagle nests in the lower Chesapeake Bay (2006 – 2013), we determined the critical period when nests are most susceptible to failure. A nest survival analysis in Program MARK indicated that the probability of brood failure declined over the post-hatching period from 27.0% in the first week to 17.0% in the second week, 11.2% in week three, and 7.2% for broods that were 4 weeks and older. Post-hoc comparisons showed that broods 4-weeks and older had a significantly greater probability of survival than 1-week-old broods, and there was a strong trend towards higher survivorship in 3-week-old broods than in 1-week-old broods. The results suggest that the critical period for Bald Eagle nests is in the first two to three weeks after hatching.

INTRODUCTION

Brood failure in birds has been attributed to a variety of environmental stressors, including a lack of resources and depredation of nestlings. For Bald Eagles (*Haliaeetus leucocephalus*) and other raptors, the most important of these threats

18

is often insufficient food resources, which may cause nest failure at any point in the post-hatching period (Hagan 1986, Wiehn and Korpimäki 1997, Dykstra et al. 1998, Gill and Elliot 2003). The death of one of the breeding adults often results in nest failure, particularly when it occurs early in the post-hatching period, because the various roles required to successfully raise a brood are difficult for a single adult to accomplish (Purger 1997, Markham and Watts 2007). Predation is also an important cause of brood failure in raptors (Marchesi et al. 2002, Sergio et al. 2003, Sunde 2005). Though adult Bald Eagles have no natural predators, eagles are vulnerable to predation in the nestling stage. Predators of Bald Eagle chicks include Northern Raccoons (*Procyon lotor*; Nash et al. 1980, Fyfe and Olendorf 1976) and other eagles (Markham and Watts 2007).

Nest failure patterns in the Chesapeake Bay Bald Eagle population have changed over the past 50 years. Throughout the 1960s and 1970s, the majority of nest failures were caused by environmental contaminants and occurred predominately during the incubation stage, when the bioaccumulation of these chemicals rendered eggs inviable (Cooke 1973, Wiemeyer et al. 1984, Clark et al. 1998). Since the banning of DDT and other organochlorine pesticides, contaminants are no longer a major cause of nest failure in the population (Watts et al. 2006, 2007, 2008). Evaluating the frequency and timing of brood failures in recent years will provide insight into what factors currently influence nest success in Bald Eagles nesting in the lower Chesapeake Bay.

We are interested specifically in assessing post-hatching failure patterns. Our aim is to use reproductive survey data (2006 – 2013) to identify the critical

19

period of development when Bald Eagle nests in the lower Chesapeake Bay are most susceptible to failure. We will determine the probability of survival to fledging age for broods surveyed at different ages to assess the risk of nest failure over time.

METHODS

We surveyed nesting Bald Eagles within the lower Chesapeake Bay and the lower Delmarva Peninsula (2006 - 2013) to examine failure patterns. We followed a standard two-flight approach including a survey flight and a productivity flight (Watts et al. 2008). Survey flights were conducted from late February to early March with the purpose of finding new nests, checking known nests, and documenting breeding attempts. Productivity flights were conducted from late April to mid-May and were intended to determine nesting success and productivity (Watts et al. 2008).

We defined nest failure as a nest in which at least one chick was observed during the first aerial survey, but no chicks were present during the second survey of the season. The first survey was timed to the peak period of incubation to maximize detection of breeding attempts. Variation in breeding phenology of reproductive pairs allowed for the observation of nests in different stages of development. We assumed that these nests are representative of the population. Chick age was determined during flights based on the degree of feather development and body size. We excluded nests whose estimated brood age at the time of the second survey was 77 days or older, since we could not

20

determine if empty nests at this stage were indicative of fledging or failure. We were able to evaluate nest failure frequencies for broods surveyed at hatching age through eight weeks post-hatching.

Statistical Analysis. We tested for age-related trends in nest failure patterns using Mayfield's estimator for nest survival (Mayfield 1961) in Program MARK (White and Burnham 1999). This method was chosen because it accounts for variation in exposure time among surveyed nests. Because brood age data were collected during aerial surveys, the temporal resolution of the data did not allow for an accurate assessment of age in days. Instead, we stratified nests by age in weeks, resulting in four groups: 1-week-old (n = 145), 2-weeks-old (n = 202), 3-weeks-old (n = 95), and 4-weeks and older (n = 47). Broods that were 4-weeks and older were grouped together because there were fewer older nests sampled due to the timing of the surveys. We modeled nest survival for each group using a logit link function and assuming constant daily survival rate (DSR) within groups.

We assessed the influence of development stage on failure using a one-way analysis of variance (ANOVA) test with age as the grouping parameter. Post-hoc comparisons of survivorship among age groupings were made using Tukey's honestly significant difference (HSD) test. Alpha was set at $\alpha = 0.05$ when determining significance of pairwise comparisons. All statistical analyses were conducted using R software (R Development Group 2008).

RESULTS

The probability of nest success was lowest for broods surveyed within one week of hatching and steadily increased with brood age (Figure 2.1). Of all documented brood failures, 44% occurred in nests surveyed within 1 week of hatching, though only 29.7% of total nests were in this group. Nests surveyed at 2 weeks of age made up 41.3% of total study nests and 42% of nest failures. 12% of nest failures occurred in broods surveyed at 3-weeks-old, and 2% of failures occurred in broods 4-weeks and older, though 3- and 4-week-old broods made up 19.4% and 9.6%, respectively, of total nests in the study. The DSR increased in the weeks after hatching from 0.996 +/- 0.010 (mean +/- standard devation) for 1-week-old broods to 0.998 +/- 0.007 for 2-week-old broods and to 0.999 +/- 0.006 for broods that were 3-weeks and older.

The results of an ANOVA test indicated that brood age had a significant influence on the probability of nest success (Table 2.1). Post-hoc Tukey's HSD comparisons showed that broods 4-weeks and older had a significantly greater probability of survival than 1-week-old broods (P < 0.01). All other comparisons were not significant at α = 0.05. However, there was a strong trend towards higher survivorship in 3-week-old broods than in 1-week-old broods (P = 0.060).

DISCUSSION

The results indicate that there is a bottleneck effect influencing brood survival in the early post-hatching period. 86% of brood failures occurred within 2 weeks of hatching and 98% occurred within 3 weeks of hatching, with the number of

broods surveyed at these ages making up 71% and 89%, respectively, of total nests surveyed. Though the only significant difference in survivorship among age groupings was between 1-week-old broods and broods 4-weeks and older, the probability of nest failure in surveyed nests decreased from 27.0% for 1-week-old broods to 17.0% for 2-week-old broods and to 11.2% for 3-week-old broods. A developmental threshold seems to exist at 3 weeks post-hatch, beyond which Bald Eagle survivorship increased to 0.928 +/- 0.049. The results suggest that the critical stage for Bald Eagle nests in the lower Chesapeake is in the first 2 to 3 weeks after hatching, with the risk of brood failure declining steadily over this time period.

Our analysis was based on an assumption that the nests we surveyed are representative of the population. Because the reproductive survey is timed to maximize detection of breeding attempts, the sample is biased to early breeders. Pairs that breed early in the season tend to be older, experienced pairs (Watts and Byrd, unpublished data), and therefore, may not be representative of the breeding population as a whole. As the population transitions from a rapidly growing to a stable population, the age of breeders is advancing and the population will reach a stable age distribution (Hunt 1998). The data presented likely reflects the older age classes and may or may not reflect patterns in younger age classes that breed later.

There are several factors that may cause nest failure rates to peak in the early post-hatching period. Bald Eagles produce altricial young that are unable to regulate their own body temperatures. Chicks must be brooded constantly by one

23

of the adults until they are able to thermoregulate at approximately 15 days old (Bortolotti 1984). Following this time period, adults may continue to brood until chicks are 5 weeks old (Warnke et al. 2002). Because chicks are vulnerable to cold, hypothermia brought on by cold and wet early spring weather is one of the most common causes of brood mortality in the Chesapeake Bay population (B.D. Watts, pers. comm.).

In addition to brooding, breeding pairs must also provide sufficient food for nestling growth and development. The availability of food is a major cause of nest failure and brood reduction in birds, and in raptor species specifically (Lack 1966, Bechard 1983, Mock 1985, Martin 1987, Wiehn and Korpimäki 1997, Amar et al. 2003). Bald Eagle chicks grow rapidly in the early period after hatching and require consistent provisioning effort (Bortolotti 1984, Bortolotti 1988, Warnke et al. 2002, Markham and Watts 2008). Depending upon the size of the brood, prey delivery rates for Bald Eagle nests in the lower Chesapeake are between 1.9 +/- 0.63 and 3.2 +/- 1.7 deliveries/10 h, with the peak in provisioning demand likely occurring 4 or 5 weeks after hatching (Markham 2004). The energetic demands of the brood coupled with environmental stresses leads to a critical period in the early post-hatching stage of development during which nests are most susceptible to failure.

Conspecific intrusion contributes to the stress on breeding pairs and may also influence nest failure patterns by directly threatening chick survival. Though documented cases of intruding Bald Eagles killing nestlings are rare, infanticide has been recorded by nest cameras at sites on the James River in 2002

(Markham and Watts 2007); at Turtle Bay in Redding, CA, in 2013 (unpublished); at Aberdeen Proving Ground in 2009 (unpublished), and at Blackwater National Wildlife Refuge in Maryland in 2012 (unpublished). Nest failures at two nests in New York have also been attributed to infanticide committed by an intruder (P. Nye pers. comm., Markham and Watts 2007). In five of these instances, the attacks occurred during the period of highest nest failure identified here. The James River chicks were killed at 13 and 15 days old (Markham and Watts 2007), the Turtle Bay chicks were newly hatched when killed, the Aberdeen chicks were 10-12 days old, the Blackwater chicks were approximately 10 days old, and the chick at one of the nests in New York was 1 week old (P. Nye pers. comm., Markham and Watts 2007). The other New York infanticide incident occurred when the eaglet was 4 weeks old (P. Nye pers. comm., Markham and Watts 2007) and therefore beyond the critical period. Collectively, these anecdotes suggest that conspecific intrusion and infanticide may be a factor contributing to the temporal pattern of brood loss.

It is likely that cold, wet weather; inadequate provisioning; and intrusion leading to infanticide are all factors affecting the patterns of brood failure described here. Further research is necessary to assess the relative influence of each factor on brood failure rates in the Chesapeake Bay Bald Eagle population. Future study should focus on quantifying the proportion of brood failures that can be attributed to each of the aforementioned factors. Because floater numbers and, subsequently, competition for nesting territory are increasing in the lower Chesapeake Bay (Chapter 1), intrusion and infanticide may become a more

important cause of brood loss as the Bald Eagle population approaches saturation.

Table 2.1. Results of a one-way ANOVA for the influence of brood age on nest success in the lower Chesapeake Bay (2006-2013). Factor tested is brood age with levels including 1 week, 2 weeks, 3 weeks, and 4 – 8 weeks old. The results indicate that brood age significantly influenced the probability of nest success.

Source	df	SS	MS	F	P
Brood age	3	2.1872	0.7291	2.9816	0.031
Mean-squared error	485	118.5947	0.2445		
Total error	488	120.7819			
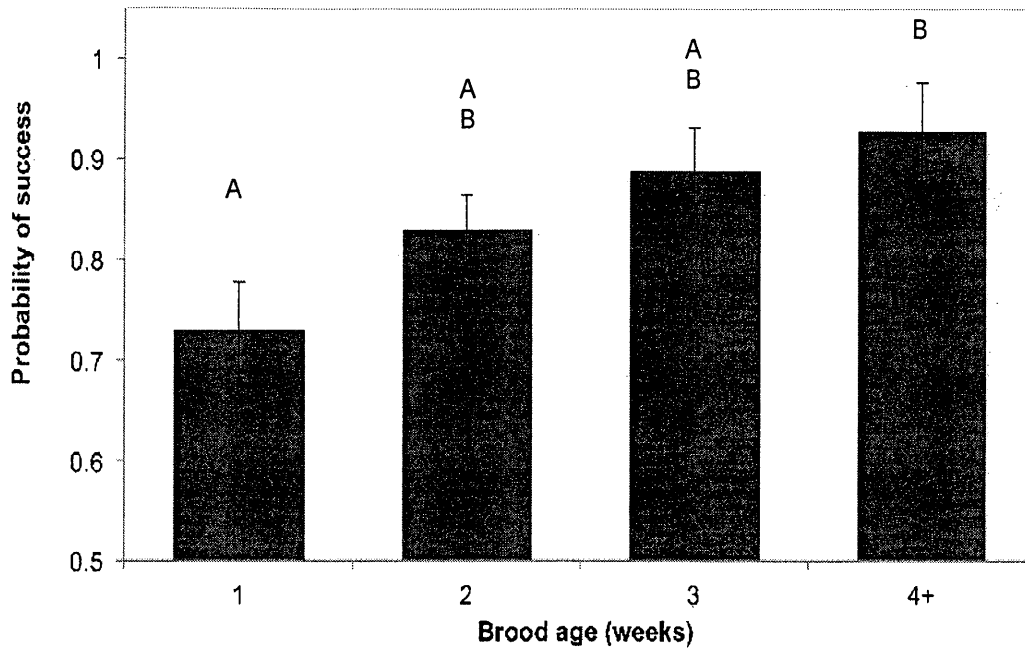
Figure 2.1. We surveyed Bald Eagle nests in the lower Chesapeake Bay (2006 –

2013), and calculated the probability of nest success for broods of varying age. If

chicks survived to fledging age, the nest was considered successful. The

probability of nest failure decreased steadily from 27% for broods surveyed within

one week of hatching to 7.2% for broods surveyed at 4-weeks-old or older.

CHAPTER 3

INTRASPECIFIC INTRUSION AT BALD EAGLE NESTS

Abstract. Competition for nesting territory has been shown to act as a density-dependent feedback mechanism influencing population growth rate. However, little is known about the nature of territorial interactions between established breeders and floaters. We examined territorial intrusion rates and associated behaviors at 31 active Bald Eagle nests in the lower Chesapeake Bay during the 2012 and 2013 breeding seasons. The average intrusion rate experienced at these nests during the reproductive period was 0.28 ± 0.32 intrusions/hr. Variance in intrusion rate was high and there was no apparent predictive pattern to these events. Juvenile intrusions occurred closer to the nest than adult intrusions, but breeders showed higher response rates toward adults, with 78% of adult intruders eliciting a response compared to 47% of juveniles. Breeding adults responded to intruders more often and more aggressively when in the presence of their mate. Because the presence of both breeders allows pairs to respond to intruders more effectively, increasing intrusion rates may force pairs to allocate more time to nest defense at the expense of other parental care behaviors.

INTRODUCTION

Factors that contribute to population regulation have been the focus of ecological study for decades (eg. Brown 1969, Pulliam 1988, Murdoch 1994). One

prominent type of population regulator is density dependence (Newton 1998, Sibly et al. 2005, Brook and Bradshaw 2006). Population size is limited by density-dependent competition for critical resources, including food (eg. Furness and Birkhead 1984, Martin 1987, Houston and Schmutz 1995, Newton 1998) and breeding sites (Newton 1998, López-Sepulcre and Kokko 2005). For territorial species like the Bald Eagle, competition for breeding sites often provides the ultimate limit to population size (Newton 1979, Hunt 1998, Newton 1998, López-Sepulcre and Kokko 2005). As populations approach saturation, space needed to establish new territories becomes limiting and increasing numbers of nonbreeding floaters result (Newton 1979, Hunt 1998, López-Sepulcre and Kokko 2005). Contests for breeding space may act as a density-dependent regulator of population growth by increasing adult mortality (Newton 1979, 1998) and reducing reproductive rates by impairing breeding pairs' ability to provide for or protect broods (Bretagnolle et al. 2008, Penteriani et al. 2011).

Competition among Bald Eagles for nesting space in the lower Chesapeake Bay is increasing. The population has been growing exponentially for over 30 years (Watts et al. 2006), and evidence suggests that floater numbers have been increasing in the last decade. A comparison between the number of birds reaching recruitment age and the rate of territory formation suggests that nearly 100% of reproductively mature birds were assimilating into the breeding population in the early 1990's. By 2013, that percentage had fallen to 17%, indicating that 4 out of every 5 transitioning birds are becoming floaters (Chapter 1). Data from tracked birds in the Chesapeake Bay population (Watts and Mojica

30

2012) provides further evidence of floaters, having documented an increase in age-to-first-reproduction (Watts and Mojica, unpublished data).

Little is known about the nature of interactions between established breeders and floaters. Though numerous studies have addressed territoriality in Bald Eagles, most document interspecific encounters, including interactions with other raptors (Ogdon 1975, Morrison et al. 2006). Studies addressing intraspecific territorial conflicts have described interactions with juvenile Bald Eagles (Kimball 2009), reactions to decoys (Mahaffy and Frenzel 1987), or anecdotes (Gerrard et al. 1980, Gerrard and Bortolotti 1988); however, there is little known about how adult eagles interact during intraspecific territorial encounters in the reproductive period. Examining the frequency of intrusion and the behaviors associated with these interactions will provide insight into how individuals cope as populations approach carrying capacity.

Our objectives are to quantify conspecific intrusion pressure on breeding Bald Eagles and to characterize behavioral responses by breeders to intruders. We will assess the frequency of intrusion by juvenile and adult-plumaged birds, the proximity of intruder approaches to the nest, and responses by territory holders in different situational contexts. We suspect that intruding floaters are motivated by the desire to obtain nesting territories. Thus, we expect that the rate of intrusion by adult-plumaged birds may vary throughout the reproductive period to reflect times of greatest nest vulnerability. We expect territory holders to respond more frequently to adult-plumaged intruders than to juvenile intruders. We also suspect that the frequency of breeder response increases with closer

31

proximity of the intruder to the nest and when the mate is present to assist in the defensive effort.

METHODS

Study sites. We observed Bald Eagle nests (Figure 3.1) located along James River (n = 21), Pamunkey River (n = 2), Pagan River (n = 2), Lynnhaven River (n = 2), Nansemond River (n = 2), Elizabeth River (n = 1), and the Southwest Branch Back River (n = 1). In 2012, we selected 12 nest sites that were monitored throughout the reproductive period from pre-laying through fledging. In 2013, we selected 19 nests for observation focused on the critical period for nest success, which has been identified as the 3-week period following hatching (Chapter 2). This time frame is when nests are most vulnerable and therefore when intrusion has the greatest potential to impact nesting success. In this paper, we will refer to this period as "the sensitive window".

Direct Observation Sessions. We conducted three-hour focal animal observation sessions at each nest using a continuous sampling technique (Altmann 1974). In 2012, nests were observed during 1 to 3 sessions in the pre-laying period and 2 to 5 sessions in the incubation period, with the exception of two nests that were not observed prior to egg laying. All study nests were observed during 3 to 5 sessions in the post-hatching period. Nests were observed during morning (6:00 to 10:00) and early afternoon (11:00 to 15:00) sessions. To improve efficiency, nests were paired for observations according to

proximity, and the observation order within each pairing was alternated to disperse any time of day bias. Behaviors were noted in accordance with a pre-established set of definitions (Table 3.1).

Intrusion - An intrusion was defined as a Bald Eagle that is not a member of the breeding pair approaching within 500 meters of the nest. Mahaffy and Frenzel (1987) examined territorial response distances of Bald Eagles in Chippewa National Forest in Minnesota and determined average response distance to be 0.59 ± 0.26 km for all reproductive periods. We used a conservative definition of intrusion limited to approaches within 500m of the nest because of constraints on visibility in the field.

We examined the influence of intruder age class and approach distance on breeder response to intrusion. Immature Bald Eagles go through a series of distinct plumage changes from Basic I through definitive plumage, attained when they reach sexual maturity at five years of age (McCollough 1989). We classified intruders as either adults or juveniles, which included second-year through fourth-year birds, according to the plumage criteria outlined by McCollough (1989). We estimated distances to nests using the location of the individual relative to designated landmarks, such as specific trees or other permanent landscape features. The distance from each landmark to the nest was calculated using U.S. Geological Survey topographic maps, a laser rangefinder, or Google Earth software. For individuals within 50m of the nest, distances were estimated to the nearest 5m. Rounding units increased incrementally, to the nearest 10m

when an individual was 51- to 100-m from the nest and to the nearest 50-m for

an individual 101- to 500-m from the nest, to reflect diminishing accuracy as

distance from the nest increased.

Breeder Response – We characterized the context and strength of responses by

breeding adults to intruders. Contextual data included whether one or both

breeding adults were present at the time of intrusion, whether one or both

breeders responded, and the duration of the response. In 2012, we also recorded

the specific behaviors exhibited by breeding pairs, including vocalizing, chasing,

attacking, circling, returning to the nest, and perching by the nest. We assessed

whether intruder age class, intruder approach distance, and mate presence

during intrusion events influenced breeder response rates. We categorized

responses to intrusion as strong, weak, or non-response. We defined a strong

response as one involving chasing or attacking an intruder. We defined a weak

response as calling, postural display, returning to or circling the nest area, or

perching in the nest area. We defined a non-response as a breeder present at

the time of intrusion showing no behavioral changes, or looking in the direction of

the intruder but exhibiting no further reaction. We did not consider intrusion

events that occurred in the absence of breeding adults within the response

framework.

Statistical Analysis. We used frequency comparisons to assess intruder age

and approach distance, and we assessed breeder responses to intrusion using

G-tests of independence. Intruder approach distances to the nest and corresponding response frequencies were assessed using Pearson's chi-squared test. Because accuracy of distance estimates declines with increasing distance from the nest, measurements were grouped into the following categories for analysis: 0-25, 26-50, 51-100, 101-150, 151-250, and 251-500 meters. We calculated the expected frequency of adult intrusions based on the proportion of juvenile intrusions in each distance category. We used the G-test of independence to compare the proportion of intrusions eliciting a breeder response when the mate was present and when the mate was absent at the time of intrusion. We also assessed the influence of intruder age on the probability of breeder response using a G-test of independence. Statistical analyses were completed using R software (R Development Group 2008).

Sensitivity analyses were conducted to evaluate the influence of intruders of unknown age on results. We assigned all unknown-aged intruders to the adult age class. We then re-ran tests that incorporated intruder age class as a factor of influence and re-evaluated the significance. Finally, we assigned all unknown-aged intruders to the juvenile age class and again re-ran all relevant statistical analyses to assess the influence of unknown-aged intruders on the results.

RESULTS

Intraspecific Intrusion. In over 540 hours of nest observation, 163 intraspecific intrusion events were observed, translating into an average intrusion rate of 0.28 ± 0.32 intrusions/hr (mean ± standard deviation). The intrusion rate of adult-

plumaged birds was 0.12 ± 0.12 intrusions/hr, and the intrusion rate of juvenile-plumaged birds was 0.17 ± 0.26 intrusions/hr. There was considerable variation in intrusion rates among nests, ranging from 0 to 20 intrusion events in 12 hours of observation during the post-hatching period.

Intrusion patterns in the sensitive window were similar to those observed outside of the critical period. During 340 hours of observation in the sensitive window, 92 intrusions occurred, while 71 intrusions occurred during the 200 observation hours falling outside of the critical period. The average intrusion rate in the sensitive window was 0.30 ± 0.37 intrusions/hr, compared to 0.38 ± 0.22 intrusions/hr outside of the sensitive window. Adult intruders did not target the sensitive window, as intrusions by adults occurred at a rate of 0.12 ± 0.14 intrusions/hr during this period and 0.15 ± 0.15 intrusions/hr during the other study time. Intrusions by juveniles during the sensitive window occurred at a rate of 0.18 ± 0.30 intrusions/hr, compared to 0.23 ± 0.18 intrusions/hr outside of the sensitive window.

Intrusions were not the result of random movement over the landscape. Intruders were attracted to the nest structures during both the entire reproductive period (χ^2 = 2384, P < 0.0001; Figure 3.2) and during the sensitive window (χ^2 = 1645, P < 0.0001). Juveniles approached closer to nests compared to adult-plumaged intruders during the entire observation period (χ^2 = 24.245, P = 0.0002; Figure 3.3) and sensitive window (χ^2 = 23.682, P = 0.0002). A sensitivity analysis revealed that unknown-aged intruders had no significant influence on frequency

36

comparisons for either approach distance or intruder age (all χ^2 > 22.5, P < 0.001).

Breeder Response. Intrusions elicited a variety of responses from breeding pairs. Responses included looking in the direction of the intruder but taking no further action (23.5%), vocalizing (21.4%), attacking and/or chasing the intruder (17.3%), circling the nest area (8.2%), and returning to the nest area and perching (5.1%). Breeders did not respond to 24.5% of intrusion events. Breeder response rate was not significantly related to intruder approach distance (χ^2 = 6.004, P = 0.306). Breeders showed a significantly higher response rate toward adult intruders, with 78% of adult intruders eliciting a response compared to 47% of juvenile intruders (G-statistic = 9.931, P = 0.002).

Though there were relatively few intruders of unknown age, a sensitivity analysis indicated that these unknowns may influence the results concerning breeder response to intrusion. Of the intruders of unknown age, 4 elicited responses from breeders and 6 did not. A sensitivity analysis indicated that the relationship between breeder response rate and intruder age would no longer be significant if the 4 intruders of unknown age that elicited a response were juveniles and the 6 intruders of unknown age that did not elicit a response were adults (G-statistic = 3.234, P = 0.072). If all unknowns were juveniles, there would be no effect on significance (G-statistic = 11.064, P < 0.001). Likewise, if all unknowns were adults, the difference in breeder response to juvenile and adult intruders would remain significant (G-statistic = 6.062, P = 0.014).

37

Mate presence at the time of intrusion influenced response rate. Eighty-four percent of intrusions occurring in the presence of both breeding adults elicited a response, while 49% of intrusions that occurred in the presence of one breeder elicited a response (G-statistic = 12.693, P = 0.0004). Of the intrusions that occurred in the presence of both adults, one adult responded alone more often than both adults responded together (χ^2 = 16.8919, P < 0.0001; Figure 3.4). There was no significant difference in the response rates of male and female breeders when both were present (χ^2 = 3.1622, P = 0.075; Figure 3.4).

As with response rates, the strength of response to an intruder was also influenced by mate presence. Of the total responses to intrusion observed when both breeders were present, 62% were strong responses. Of total responses to intrusion observed when only one breeder was present, only 17% of responses were strong. The G-test of independence indicated that there was a significant relationship between strength of response and mate presence (G-statistic = 9.641, P = 0.002; Figure 3.5).

There was a significant influence of breeder sex on the probability of calling during an intrusion event. Females present during intrusion events called significantly more in response to intrusion than males that were present during intrusion events (χ^2 = 5.158, P = 0.023). A sensitivity analysis indicated that the single occurrence of a breeder of unknown sex calling during an intrusion did not affect the result (all χ^2 > 4.333, P < 0.037). When intrusions were not occurring, females seemed to call less frequently to their mates than males did, but the difference was not significant (χ^2 = 1.653, P = 0.199).

38

DISCUSSION

Conspecific intrusion represents a frequent and unpredictable threat to Bald Eagle nests in the lower Chesapeake Bay. Intraspecific intrusions at nest sites occurred on average approximately every 3.5 hours, with an adult-plumaged bird intruding every 8.3 hours. Variance among nests was high, however, with no intrusions observed during observations at 8 of our 31 study nests and with 4 of our 31 study nests experiencing intrusion rates that were more than twice the average. The episodic nature of these events may make it difficult for breeding pairs to anticipate and defend against intrusions.

When both adults were present at the time of intrusion, breeding pairs responded more often and more aggressively than when only one breeder was present, suggesting that more frequent nest attendance by both breeders may increase success of defensive efforts. When one adult, more frequently the female, is the sole breeder at the nest site, the adult must either remain on the nest to protect the offspring or leave the nest unprotected to chase off the intruder. When the mate is present, the female is able to stay with the chicks while the male chases or attacks the intruder. The percentage of observation time that one adult attended the nest was comparable to that documented by Steidl and Anthony (2000) in an Alaskan sub-population along the Gulkana River Basin (59% and 59.2%, respectively). However, the percent of observation time that both adults were in attendance was more than twice as high for nests in our study (36%) than for nests in Alaska (13.5%, Steidl and Anthony 2000). The reason for this discrepancy is unclear, but one possible explanation is that pairs

39

nesting in the lower Chesapeake Bay may adjust attendance behavior in response to floater pressure.

The type of response exhibited by breeders during intrusion may be influenced by other factors in addition to mate presence. Mahaffy and Frenzel (1987) documented breeding pairs responding to a mounted Bald Eagle and to a tethered live eagle by circling and calling, but pairs never chased or attacked the decoys. Kimball (2009), however, observed breeders attacking conspecific juvenile intruders on multiple occasions. The differences in response type observed in these studies suggest that the behavior of intruders may affect breeder response behavior. Breeding pairs may also habituate to consistent activity near the nest (Watson et al. 1999, Steidl and Anthony 2000). Pairs subject to frequent conspecific intrusions may become accustomed to intruders in their territories and may respond less aggressively. In addition, familiarity of specific intruders may influence response. Breeders often become accustomed to neighboring pairs (Galeotti and Pavan 1993, Hardouin et al. 2006) and perceive these familiar individuals as less threatening than strangers once territorial boundaries are established (Temeles 1994, Briefer et al. 2008). If breeding pairs respond less frequently or less aggressively toward neighbors than toward unknown adult birds, then our estimates of the frequency and strength of response by breeders toward adult intruders are likely conservative.

Another potential influence on breeder response is whether the intrusion event is solitary or concurrent with other intrusions. There were several occasions during which multiple intrusions occurred simultaneously. For the

40

purposes of our analyses, simultaneous intrusions were considered to be one event. In one instance, four juveniles intruded concurrently. By default, the female breeder could only choose whether to respond to one of these intruders. Her lack of response may have been influenced by the fact that chasing off one of the intruders would leave the nest vulnerable to attack by the other intruding birds. Increasing floater numbers and population density in the lower Chesapeake Bay may lead to more frequent multiple intrusion events.

Our results indicate that intrusions are intentional and not the result of random movement over the landscape, but the motivation for intrusion remains unclear. The higher probability of response by breeders to adult intruders (0.78) compared to juvenile intruders (0.47) suggests that breeders' perception of threat may be different for adult and juvenile intruders. One explanation for this observation concerns possible differences in adults' and juveniles' incentives for intrusion. In some avian populations, juvenile and subadult birds have been shown to remain in their natal territory, acting as helpers at the nest and learning parental care skills and information about nest site quality (Skutch 1935, 1961; Emlen 1982; Hunter 1987; Woolfenden and Fitzpatrick 1990; Hatchwell 1999). Breeding adults increase fitness by allowing offspring to assist with chick rearing, and juveniles benefit via inclusive fitness and from the skills learned while helping (Hamilton 1964). It is possible that breeding Bald Eagles tolerate juvenile intruders when they are offspring from previous years; however, the Bald Eagle is a well-studied species and there is no known evidence of helping behavior, even in populations that are thought to be at saturation (eg. Hansen and Hodges

1985; Bowman et al. 1995, 1997; Stinson et al. 2001). More likely, the differential response toward juvenile and adult intruders relates to the motive of the latter age group. Nest failure has been linked to subsequent territory abandonment in birds (eg. Darley et al. 1977, Harvey et al. 1979, Weatherhead and Boak 1986, Haas 1998, Catlin et al. 2005). If an adult intruder causes nest failure, the intruder may have a chance at a territorial takeover. It is less likely that juvenile intruders are motivated by the possibility of territorial takeover, as they will not have use for a breeding territory until they reach reproductive maturity. For Bald Eagles, the probability of nest failure is highest in the first two to three weeks after hatching (Chapter 2); therefore, we would expect intrusions during this critical period to pose the greatest threat to nest success. Interestingly, there was no apparent difference in intrusion rates of adult- and juvenile-plumaged birds during the sensitive window, and there was no difference in adult intrusion rates during the sensitive window compared to rest of the reproductive period. The results suggest that adult intruders are not specifically targeting the critical period. Further research on the aftermath of nest failure is necessary to examine territorial takeover as a potential motivator of adult intruders.

Table 3.1. Description of behaviors documented during continuous focal animal observations of 31 active Bald Eagle nests in the lower Chesapeake Bay during the 2012 and 2013 breeding seasons.

Behavior	Definition
CA	Emits a call or call note
NT	Approaches, attacks, or perches in nest tree
PE	Perches in any location other than the nest tree
CH	Chases, pursues another individual
AT	Attacks another individual with physical contact
FL	Continuous directional flight
CI	Circles the nest area
SO	Soars
Breeder-Specific Behaviors	
RE	Breeder returns to nest in response to an intrusion event
NO	No discernable response
AB	Breeder is absent at time of intrusion
LO	Breeder looks in direction of intruder or calling mate
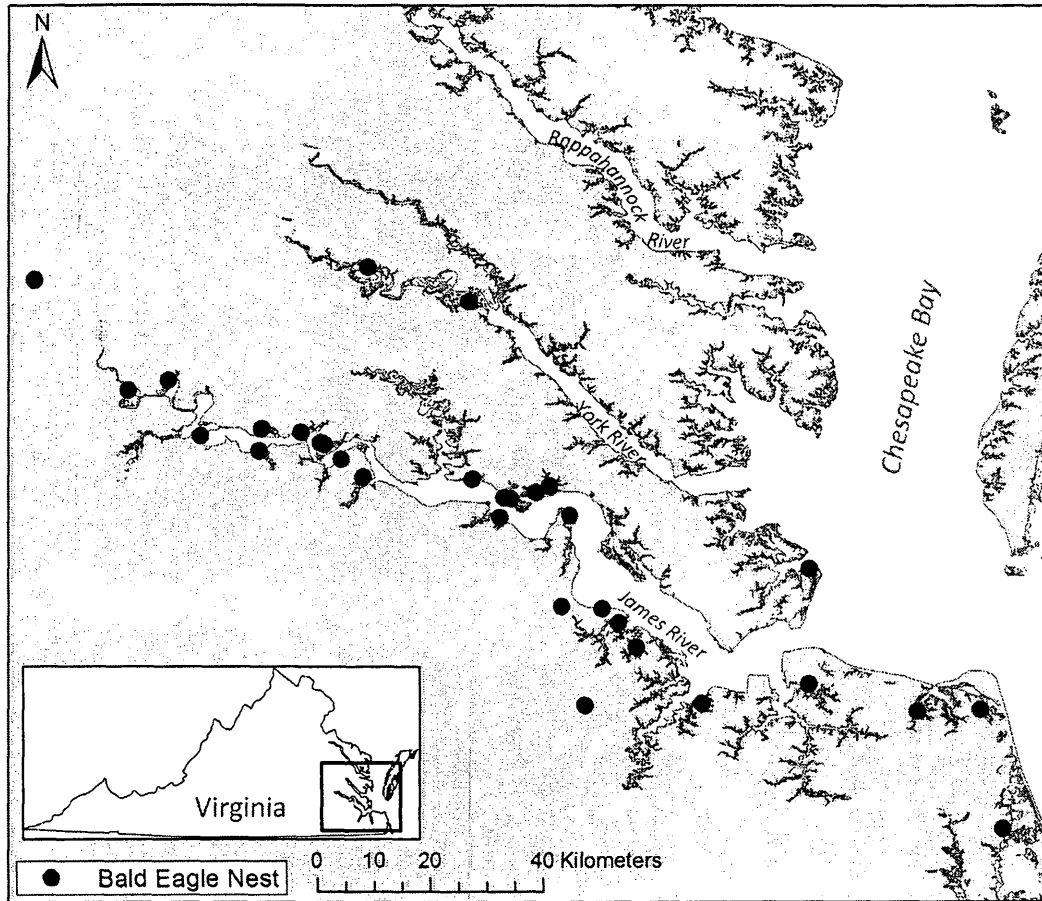
Figure 3.1. Locations of nests in the lower Chesapeake Bay used in observational monitoring study (2012-2013).
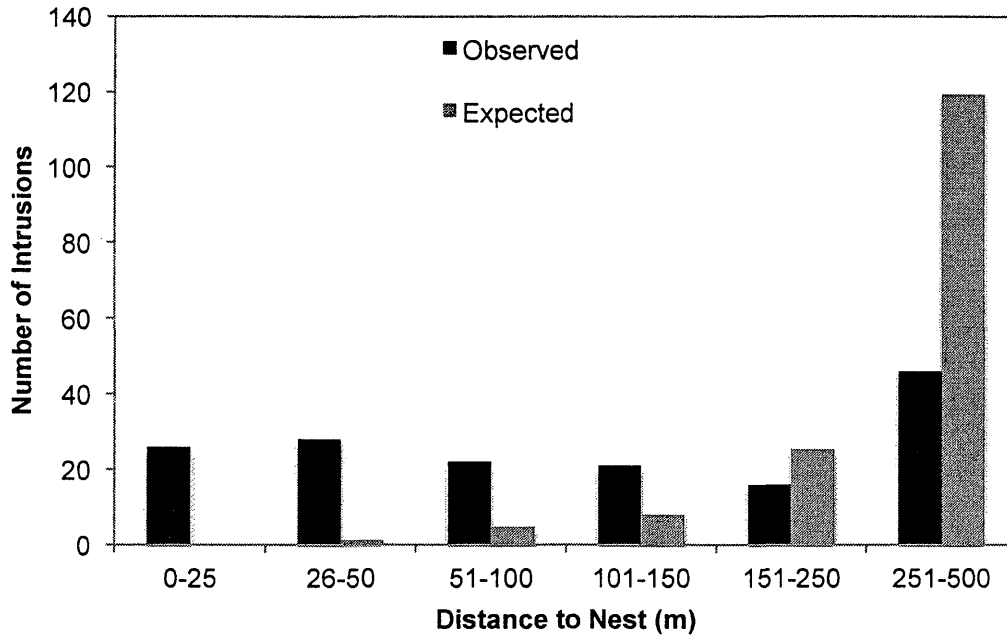
Figure 3.2. Approach distances of intraspecific intruders to nest sites of breeding

Bald Eagles in the lower Chesapeake Bay (2012 and 2013 breeding seasons).

Expected frequencies were calculated based on relative area within each

distance category to represent a random distribution of intrusions. Intruders were

attracted to the nest structures and were not moving randomly over the

landscape.
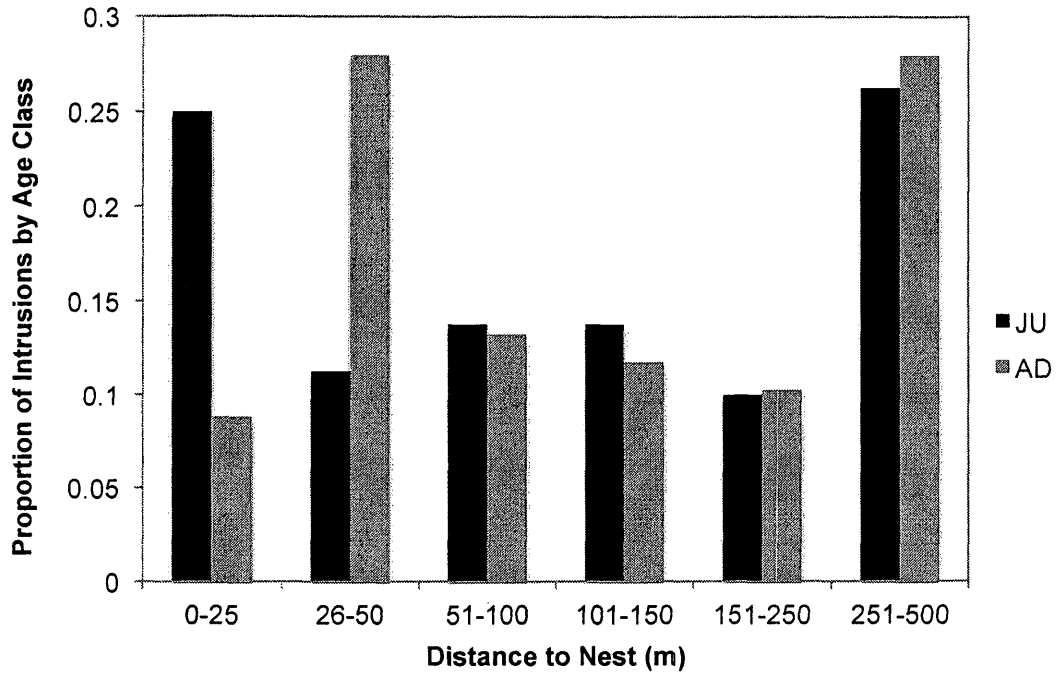
Figure 3.3. Approach distances of juvenile and adult intruders around nests of breeding Bald Eagles in the lower Chesapeake Bay (2012 and 2013 breeding seasons) as proportions of the total intrusions by each age class. Juvenile intrusions occurred closer to the nest than adult intrusions.
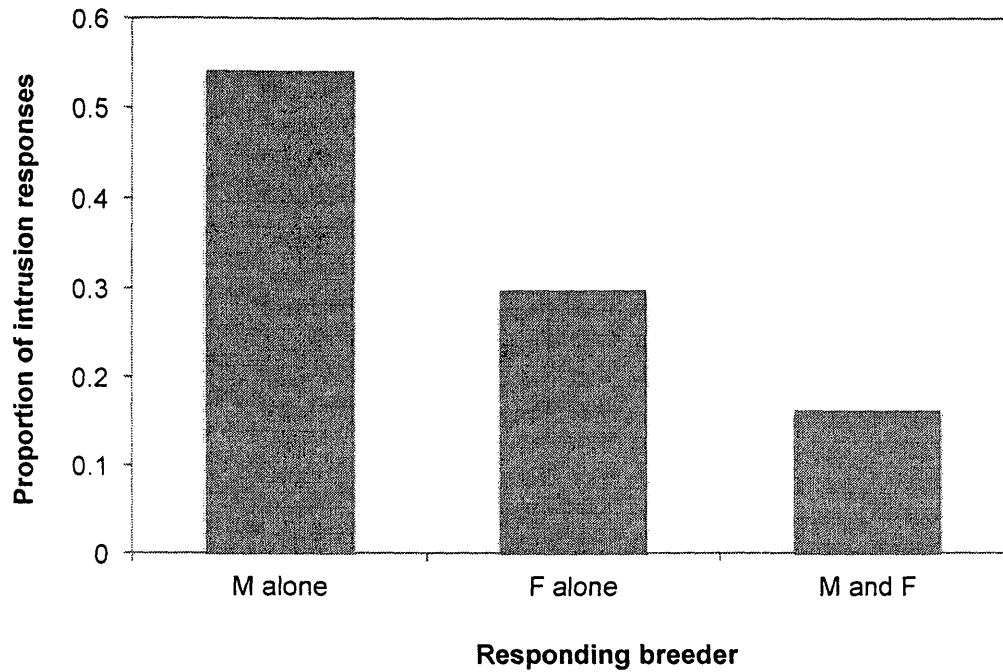
Figure 3.4. Proportion of intraspecific intrusions occurring in the presence of both

breeders that elicited a response by breeding males alone, by breeding females

alone, and by both breeding adults at Bald Eagle nests in the lower Chesapeake

Bay (2012 and 2013 breeding seasons). In 84% of intrusions, a single breeder

responded, while both adults responded together to only 16% of intrusion events.
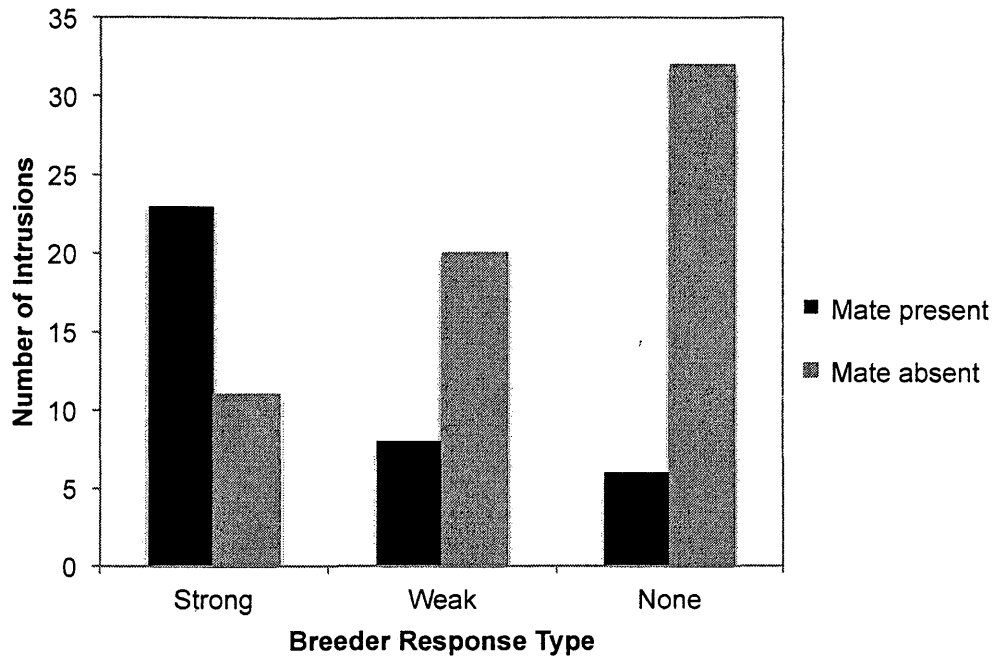
Figure 3.5. Response type (strong, weak, or no response) by breeding Bald

Eagles in the lower Chesapeake Bay (2012 ad 2013 breeding seasons) given

mate presence. Strong responses involved chasing or attacking intruders, while

weak responses involved calling, watching the intruder, or exhibiting a defensive

posture. Sixty-two percent of intrusions occurring in the presence of both adults

evoked strong responses, while only 17% of intrusions occurring when one

breeding adult was present evoked a strong response by breeders.

CHAPTER 4

BALD EAGLES FOCUS NEST GUARDING EFFORT ON POST-HATCHING PERIOD

Abstract. As the Chesapeake Bay Bald Eagle population approaches saturation, competition for breeding territories appears to be intensifying. Frequent territorial interactions may force breeders to adjust nest guarding behavior to deter potential takeover attempts and protect chicks. We examined nest guarding behavior of Bald Eagles in the lower Chesapeake Bay during the 2012 and 2013 breeding seasons. Nests were guarded in the post-hatching period three times as often as in the pre-laying period and over five times more often than during the incubation period. Though females were in attendance for 80% of observation time compared to males' 51%, male breeders guarded nests nearly twice as often as females. Adults guarded preferentially within 25-m of the nest from a perch in an adjacent tree or the nest tree, excluding in the nest itself, possibly to maximize visibility and response time. If increasing rates of conspecific territorial interaction force males to allocate more time to nest guarding, a tradeoff may become apparent, with males dividing time between guarding the nest and foraging for food to provision offspring.

INTRODUCTION

Investments in nest guarding behavior are expected to reflect fitness tradeoffs between risks to eggs or broods and other duties required for successful brood rearing. For example, guarding may reduce productivity losses to potential

predators (Slack 1976, Woodard and Murphy 1999) or brood parasites (Møller 1987, Gowaty et al. 1989) at the expense of time dedicated to brooding and provisioning of young. Guarding is also important for territory maintenance in repelling territorial or mate takeover attempts by nonbreeding adult floaters (Nice 1941, Slagsvold et al. 1994, Mougeot 2000). As Bald Eagles in the Chesapeake Bay approach saturation (Watts et al. 2008), the floater portion of the population is growing, creating more competition for nesting sites. An analysis of annual recruitment rates of new breeders showed that nearly 100% of reproductively mature birds were assimilating into the breeding portion of the population in the early 1990's. By 2013, that percentage had fallen to 17%, indicating that 4 out of every 5 transitioning birds are excluded from breeding locally and may become floaters (Chapter 1).

As a surplus of adult birds vies for a limited number of breeding territories, territorial interactions become increasingly frequent (Newton 1979, Hunt 1998, López-Sepulcre and Kokko 2005). Fitness tradeoffs may shift in response to increasing floater pressure as nest guarding becomes more essential to reproductive success. Though documented accounts are rare, conspecific intruders have been shown to kill young Bald Eagle chicks (Markham and Watts 2007). More frequently, intrusion indirectly effects reproductive success by creating additional stresses on breeders (Penteriani et al. 2011). These stresses include forcing adults to allocate time and energy to chasing off intruders (Sunde and Bølstad 2004); pressuring adults to constrain territories to a more defensible size (Norton et al. 1982, Mougeot et al. 2003, Ridley et al. 2004); wounding or

50

killing one of the breeding adults, leaving the other to attempt to care for chicks alone (Newton 1979); and forcing adults to spend more time guarding the nest at the expense of other parental care activities.

Nest guarding behavior in Bald Eagles is poorly described. Our aim is to examine parental attendance and nest guarding by breeding Bald Eagles in the lower Chesapeake Bay. We will determine whether nest guarding coverage changes over the course of the reproductive period. We will assess the relative contributions by male and female breeders to total nest guarding effort. We will also describe the types of locations that breeders choose when nest guarding and the distance between guarding locations and the nest. We hypothesize that guarding effort is focused on the post-hatching period when nests are most vulnerable to failure (Chapter 2). We suspect that there is a sex bias in nest guarding roles, as is evident in other parental care behaviors in Bald Eagles (eg. Gerrard and Bortolotti 1988, Cain 1998, Bryan et al. 2005). Finally, we hypothesize that preferred guarding locations optimize visibility of the nest area for effective surveillance.

METHODS

Study Sites. We selected Bald Eagle nest sites (Figure 3.1) in Virginia along the James River (n = 21), Pamunkey River (n = 2), Pagan River (n = 2), Lynnhaven River (n = 2), Nansemond River (n = 2), Elizabeth River (n = 1), and the Southwest Branch Back River (n = 1). We observed nests during the 2012 (n = 12) and 2013 (n = 19) breeding seasons. In 2012, nests were observed

throughout the breeding season from pre-laying through fledging. In 2013, we refined our observation period to more intensively cover the first three weeks after hatching, as this is the critical period for Bald Eagle nest success in the Chesapeake Bay (Chapter 2).

Direct Observations. We conducted three-hour focal animal observation sessions at each nest using a continuous sampling technique (Altmann 1974). In 2012, nests were observed during 1 to 3 sessions in the pre-laying period and 2 to 5 sessions in the incubation period, with the exception of two early nests that were not observed prior to egg laying. All study nests were observed during 3 to 5 sessions in the post-hatching period. Nests were observed during morning (between 6:00 and 10:00) and early afternoon (between 11:00 and 15:00) sessions. To improve efficiency, nests were paired for observations according to proximity, and the observation order within each pairing was alternated to disperse any time of day bias.

We were interested in breeder attendance and nest guarding behavior. Mahaffy and Frenzel (1987) determined the average radius of the defended area around Bald Eagle nests in Minnesota's Chippewa National Forest to be 0.59 ± 0.26 km during the reproductive period. Because of constraints on visibility in the field, we used a conservative estimate of 500 meters as the radius of the defended territory around active nests. We documented the total time that each adult was present within 500 meters of the nest. We recorded nest guarding, defined as a member of the breeding pair being within 500 meters of the nest

with the exception of individuals engaged in brooding, incubation, feeding, or other mutually exclusive activities. We excluded nest guarding performed by adults that were attending the nest alone, since the motivation for solitary adults to nest guard is different than that of adults whose mate is present. We also recorded additional data related to nest guarding, including bout length, breeder sex, distance to the nest, and location. We estimated distances to nests using the location of the individual relative to designated landmarks, such as specific trees or other permanent landscape features. We determined the distance from each landmark to the nest using U.S. Geological Survey topographic maps, a laser rangefinder, or Google Earth software. For individuals within 50-m of the nest, distances were estimated to the nearest 5-m. Rounding units increased incrementally, to the nearest 10-m when an individual was 51- to 100-m from the nest and to the nearest 50-m for an individual 101- to 500-m from the nest, to reflect diminishing accuracy as distance from the nest increased.

Statistical Analysis. We evaluated the relationship between reproductive period and nest guarding behavior using a one-way analysis of variance (ANOVA) test. We compared male and female contributions to nest guarding using Welch's t test to account for unequal variances. We compared the distribution of nest guarding locations to a random distribution using Pearson's chi squared tests. Because accuracy of distance estimates declines with increasing distance to the nest, measurements were grouped into the following categories for analysis: 0-

25, 26-50, 51-100, 101-150, 151-250, and 251-500 meters. Statistical analyses were completed using R software (R Development Group 2008).

Sensitivity analyses were conducted to account for observations in which breeder sex could not be determined. We performed these analyses by re-running statistical tests as if all unknowns were of the same sex and assessing whether the results remained significant at the designated alpha value of 0.05.

RESULTS

During the 2012 and 2013 nesting seasons, nests were observed for 540.8 hours. Females attended the nest area for significantly more time (t = -5.3439, df = 30.9, P < 0.0001; Figure 4.1) and for longer average bouts of time than males (t = -6.3818, df = 140.524, P < 0.0001) in the post-hatching period. Observations for which breeder sex was unknown comprised 0.8% of total attendance events, and a sensitivity analysis indicated that these observations had no effect on the results (all t > -5.1108, P < 0.0001). Nests were left unattended during 5% of the total observation time, and the average length of time that neither adult was present was 8.65 ± 9.57 min (mean ± standard deviation).

Nest guarding varied with reproductive stage. Nests were guarded in the post-hatching period three times more often than in the pre-laying period and five times more often than during the incubation period (ANOVA, $F_{(2, 52)}$ = 18.438, P < 0.0001). In the analysis of nest guarding after hatching (2012 and 2013 breeding seasons), males guarded nests for more total time (t = 2.7349, df = 21.994, P = 0.012, Figure 4.2a) and for longer bouts of time than females (t = 2.3488, df =

20.348, P = 0.029; Figure 4.2b). Nests were guarded by a single adult more often than by both breeders simultaneously (t = -9.1226, df = 26.197, P < 0.0001).

Adults guarded broods preferentially from locations within 25 meters of the nest (χ^2 = 30185, P < 0.0001; Figure 4.3). Adults engaged in nest guarding behavior also showed substrate preferences (χ^2 = 109.3, P < 0.0001), guarding primarily from an adjacent tree (43.6% of guarding events). Excluding guarding by adults perched in the nest itself, 24.2% of guarding events were conducted from a perch in the nest tree. Nest guarding from a position in the nest and aerial guarding while circling the nest site comprised 16.3% and 15.9% of guarding events, respectively.

DISCUSSION

Nest guarding rates were highest in the post-hatching period, particularly in the first three weeks. On average, nests were guarded during 37.6% of post-hatching observation time, 11.5% of pre-laying observation time, and only 6.8% of observation time in the incubation period. Adults guarded preferentially within 25-m of the nest from a perch in an adjacent tree or the nest tree, excluding in the nest itself, possibly to maximize response time and visibility for effective surveillance and nest defense.

Because the motivation for nest guarding differs in each stage of the reproductive period, the results offer insight into the environmental pressures that force pairs to nest guard. Guarding in the pre-laying period is often intended to guard the mate to deter extra-pair copulation (Korpimäki et al. 1996, Mougeot et

55

al. 2002) or to ward off potential territorial takeover attempts. The latter is more likely for this species, as Bald Eagles form persistent pair bonds and are considered monogamous (Stalmaster 1987, Jenkins and Jackman 1993). Furthermore, the prevalence of floaters in the population translates to a high risk of territorial takeover attempts early in the breeding season when non-territory holders compete for breeding opportunities. Though passerines often guard nests during incubation to deter nest parasitism and predators (Slack 1976, Woodard and Murphy 1999), Bald Eagle nest guarding rates were lowest during the incubation period, and, moreover, the second adult was rarely in attendance during incubation. This is likely because eagles do not face the same nest parasitism threats as passerines. In addition, adult Bald Eagles have no true predators in this ecosystem, so the incubating adult may be able to protect the eggs without significant risk to their own survival. Nest guarding in the post-hatching period, particularly in the first 3 weeks, is most critical to protecting altricial young from potential predators. This was the predominant type of nest guarding in which breeding Bald Eagle pairs engaged.

The timing of peak nest guarding activity necessitates the presence of both breeders at the nest, with one adult brooding chicks and the other perched nearby to guard the nest. Past nest defense studies have focused on the nest guarding role performed by males in the absence of females (Ricklefs 1969, Slack 1976, Greig-Smith 1980, Hayes and Robertson 1989, Martin 1992, Markman et al. 1995, Komdeur and Kats 1999) or on nest guarding by sentinels in cooperative breeding systems (Skutch 1935, McGowan and Woolfenden 1989,

Hailman et al. 1994, Burton and Yasukawa 2001, Wright et al. 2001). Our

observations of Bald Eagle nests in the lower Chesapeake indicate that the

second adult, generally the male, plays an important role in nest defense by

acting as a sentinel to guard against potential threats while the first adult broods

chicks. This may suggest that the female is vulnerable during brooding (Burton

and Yasukawa 2001, Wilson 2008) or that both adults are essential in warding off

intruders so as not to leave chicks unattended. There is evidence supporting the

latter explanation, as simultaneous intrusions were observed in multiple

instances with as many as four birds intruding at once, and breeders responded

more often and more aggressively to intruders when both members of the

breeding pair were present at the time of the intrusion event (Chapter 3). The

absence of the second adult at nests with older chicks suggests that reproductive

tradeoffs shift for adults with older broods, possibly because chicks are more

vulnerable to potential predators in the early post-hatching period.

As the Bald Eagle population in the Chesapeake Bay continues to grow,

breeders may reinforce nest guarding efforts in response to the increasing risk of

intraspecific intrusion (Chapter 1). Time allocated to nest guarding detracts from

the time breeding adults have for other fundamental parental care behaviors,

including provisioning. If the quantity and quality of food provided to chicks is

compromised, nestling growth rates and the rate of mass gain may be negatively

affected (Bortolotti 1989, Markham and Watts 2008). Alternatively, if adults do

not adjust time budgets to allow for more nest guarding coverage, pairs may face

a greater risk of nest failure resulting from an intrusion event. Infanticide and

cannibalism have been documented in Bald Eagles in the Chesapeake Bay

(Markham and Watts 2007).
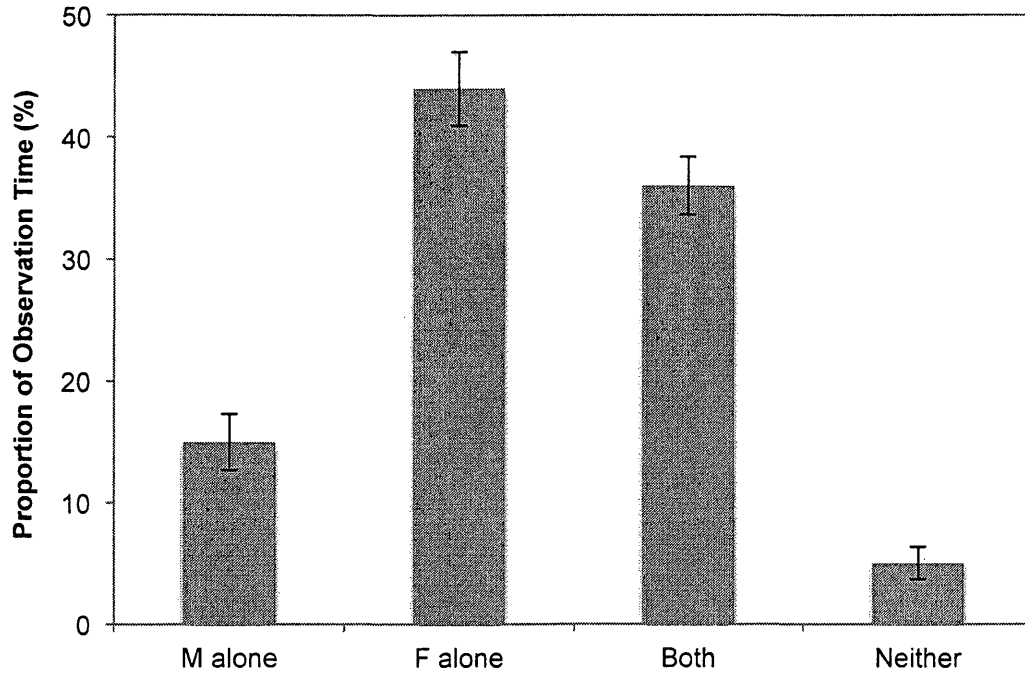
Figure 4.1. We documented nest attendance by male and female breeding Bald Eagles during the first 3 weeks after hatching in the lower Chesapeake Bay (2012 and 2013 breeding seasons). Female breeders attended nests significantly more often than males (80% and 51%, respectively). When males were in attendance, their mates were also present 71% of the time.
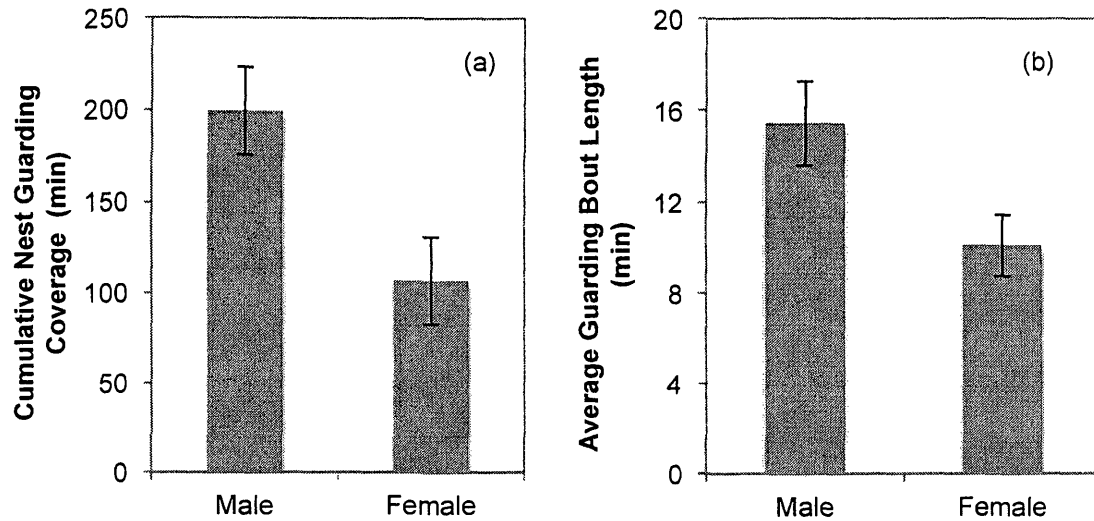
Figure 4.2. We present (a) total nest guarding coverage and (b) average bout length of nest guarding behavior exhibited by male and female Bald Eagles in the lower Chesapeake Bay (2012 and 2013 breeding seasons). Male breeders performed the majority of the nest guarding effort, guarding nests for nearly twice as much total time as females during guarding bouts that were 50% longer on average than those of females.
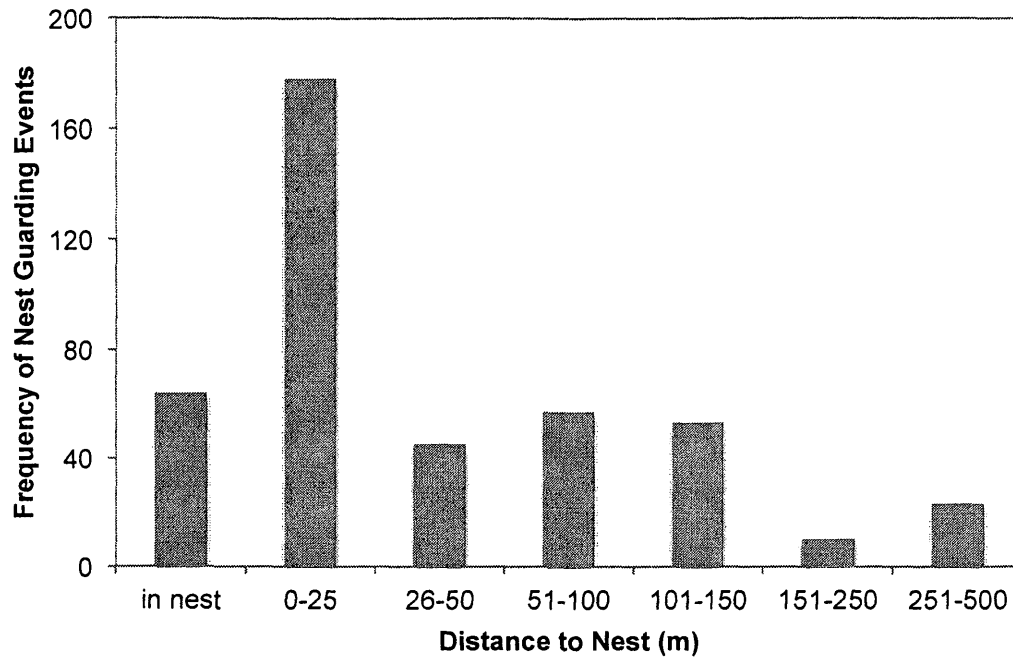
Figure 4.3. We recorded breeder distance to the nest during nest guarding bouts of Bald Eagle pairs in the lower Chesapeake Bay (2012 and 2013 breeding seasons). Pairs exhibited preferences for guarding close to the nest, with 56% of nest guarding activity occurring within 25-m of the nest, including in the nest itself, and 80% of nest guarding occurring within 100-m of the nest.

REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227-267.

Amar A., S. Redpath, and S. Thirgood. 2003. Evidence for food limitation in the declining hen harrier population on the Orkney Islands, Scotland. Biological Conservation 111(3): 377-384.

Bailey, N.T.J. 1964. The elements of stochastic processes with applications to the natural sciences. Wiley, New York.

Bechard, M.J. 1983. Food supply and the occurrence of brood reduction in Swainson's Hawk. Wilson Bulletin 95(2): 233-242.

Birkhead, T.R. 1982. Timing and duration of mate guarding in magpies, *Pica pica*. Animal Behaviour 30: 227-283.

Bortolotti, G.R. 1984. Physical development of nestling Bald Eagles with emphasis on the timing of growth events. Wilson Bulletin 96(4): 524-542.

Bortolotti, G.R. 1988. Factors influencing the growth of Bald Eagles in north central Saskatchewan. Canadian Journal of Zoology 67(3): 606-611.

Bortolotti, G.R. 1989. Factors influencing the growth of Bald Eagles in north central Saskatchewan. Canadian Journal of Zoology 67: 606-611.

Bowman, T.D., P.F. Schempf, and J.A. Bernatowicz. 1995. Bald Eagle survival and population dynamics in Alaska after the Exxon Valdez oil spill. The Journal of Wildlife Management 59(2): 317-324.

Bowman, T.D., P.F. Schempf, and J.I. Hodges. 1997. Bald eagle population in

Prince William Sound after the Exxon Valdez oil spill. The Journal of

Wildlife Management 61(3): 962-967.

Bretagnolle, V., F. Mougeot, and J.C. Thibault. 2008. Density dependence in a

recovering osprey population: demographic and behavioural processes.

Journal of Animal Ecology 77(5): 998-1007.

Briefer, E., F. Rybak, and T. Aubin. 2008. When to be a dear enemy: flexible

acoustic relationships of neighbouring skylarks, *Alauda arvensis*. Animal

Behaviour 76(4): 1319-1325.

Brook, B.W., and C.J.A. Bradshaw. 2006. Strength of evidence for density

dependence in abundance time series of 1198 species. Ecology 87(6):

1445-1451.

Brown, J.L. 1969. Territorial behavior and population regulation in birds: a review

and re-evaluation. Wilson Bulletin 81(3): 293-329.

Bryan, A.L., Jr., L.B. Hopkins, C.S. Eldridge, I.L. Brisbin, Jr., and C.H. Jagoe.

2005. Behavior and food habits at a Bald Eagle nest in inland South

Carolina. Southeastern Naturalist 4(3): 459-468.

Buehler, D. A., J. D. Fraser, J. K. D. Seegar, G. D. Therres, and M. A. Byrd.

1991. Survival rates and population dynamics of Bald Eagles on

Chesapeake Bay. Journal of Wildlife Management 55: 608-613.

Burton, N., and K. Yasukawa. 2001. The "predator early warning system" of red-

winged blackbirds. Journal of Field Ornithology 72: 106-112.

Cain, S.L. 1998. Time budgets and behavior of nesting Bald Eagles. p.73-94, *in*

B.A. Wright and P.F. Schempf, eds. Bald Eagles in Alaska. Bald Eagle

Research Institute, Juneau, Alaska, 434 p.

Carrete, M., J.A. Sanchez-Zapata, J.F. Calvo, and R. Lande. 2005. Demography

and habitat availability in territorial occupancy of two competing species.

Oikos 108: 125–136.

Catlin, D.H., D.K. Rosenberg, and K.L. Haley. 2005. The effects of nesting

success and mate fidelity on breeding dispersal in burrowing owls.

Canadian Journal of Zoology 83(12): 1574-1580.

Clark, K.E., L.J. Niles, and W. Stansley. 1998. Environmental contaminants

associated with reproductive failure in bald eagle (*Haliaeetus*

leucocephalus) eggs in New Jersey. Bulletin of Environmental

Contamination and Toxicology 61(2): 247-254.

Cohen, J.E. 1969. Natural Primate Troops and a Stochastic Population Model.

The American Naturalist 103(933): 455-477.

Cooke, A.S. 1973. Shell thinning in avian eggs by environmental pollutants.

Environmental Pollution 4(2): 85-152.

Darley, J.A., D.M. Scott, and N.K. Taylor. 1977. Effects of age, sex, and breeding

success on site fidelity of gray catbirds. Bird-Banding 48(2): 145-151.

Davies, N.B., and A.I. Houston. 1981. Owners and satellites: the economics of

territory defence in the pied wagtail, *Motacilla alba*. The Journal of Animal

Ecology 50: 157-180.

Dykstra, C.R., M.W. Meyer, D.K. Warnke, W.H. Karasov, D.E. Andersen, W.W. Bowerman IV, and J.P. Giesy. 1998. Low reproductive rates of Lake Superior bald eagles: low food delivery rates or environmental contaminants? Journal of Great Lakes Research 24(1): 32-44.

Emlen, S.T. 1982. The evolution of helping. I. An ecological constraints model. American Naturalist 119(1): 29-39.

Fraser, J.D., L.D. Frenzel, J.E. Mathisen, F. Martin, and M.E. Shough. 1983. Scheduling bald eagle reproductive surveys. Wildlife Society Bulletin 11: 13-16.

Furness, R.W., and T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311(5987): 655-656.

Fyfe, R.W., and R.R. Olendorf. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Canadian Wildlife Service, Occasional Paper no. 23.

Galeotti, P., and G. Pavan. 1993. Differential responses of territorial Tawny Owls *Strix aluco* to the hooting of neighbours and strangers. Ibis 135(3): 300-304.

Gerrard, J.M., P.N. Gerrard, and D.W.A. Whitfield. 1980. Behavior in a non-breeding Bald Eagle. Canadian Field Naturalist 94(4): 391-397.

Gerrard, J.M. and G.R. Bortolotti. 1988. The Bald Eagle. Smithsonian Institution, Washington, 155 p.

Gill, C.E., and J.E. Elliott. 2003. Influence of food supply and chlorinated

hydrocarbon contaminants on breeding success of bald eagles.

Ecotoxicology 12: 95-111.

Gowaty, P.A., J.H. Plissner, and T.G. Williams. 1989. Behavioural correlates of

uncertain parentage: mate guarding and nest guarding by eastern

bluebirds, *Sialia sialis*. Animal Behaviour 38(2): 272-284.

Greig-Smith, P.W. 1980. Parental investment in nest defence by stonechats

(*Saxicola torquata*). Animal Behaviour 28: 604-619.

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding

dispersal: an experimental approach. The Auk 115(4): 929-936.

Hailman, J.P., K.J. McGowan, and G.E. Woolfenden. 1994. Role of helpers in the

sentinel behaviour of the Florida scrub jay (*Aphelocoma c. coerulescens*).

Ethology 97: 119–140.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. II. Journal of

Theoretical Biology 7(1): 17-52.

Hansen, A.J., and J.I. Hodges. 1985. High rates of nonbreeding adult Bald

Eagles in Southeastern Alaska. Journal of Wildlife Management 49(2):

454-458.

Hardouin, L.A., P. Tabel, and V. Bretagnolle. 2006. Neighbour–stranger

discrimination in the little owl, *Athene noctua*. Animal Behaviour 72(1):

105-112.

Harmata, A. R., G. J. Montopoli, B. Oakleaf, P. J. Harmata, and M. Restani. 1999. Movements and survival of Bald Eagles banded in greater Yellowstone ecosystem. Journal of Wildlife Management 63:781-793.

Harvey, P.H., P.J. Greenwood, and C.M. Perrins. 1979. Breeding area fidelity of Great Tits (Parus Major). Journal of Animal Ecology 48: 305-313.

Hatchwell, B.J., A.F. Russell, M.K. Fowlie, and D.J. Ross. 1999. Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. The Auk 116(2): 355-363.

Hayes P.A., and R.J. Robertson. 1989. The impact of male parental care on female eastern kingbird reproductive success. Wilson Bulletin 101: 462-467.

Hodges, J. I., E. L. Boeker, and A. J. Hansen. 1987. Movements of radio-tagged Bald Eagles Haliaeetus leucocephalus, in and from southwestern Alaska. Canadian Field Naturalist 101:136-140.

Houston, C., and J. Schmutz. 1995. Declining reproduction among Swainson's Hawks in prairie Canada. Journal of Raptor Research 29: 198–201.

Hunt, G. 1995. A pilot golden eagle population study in the Altamont Pass Wind Resource Area, California. No. NREL/TP--441-7821. National Renewable Energy Lab., Golden, CO (United States); California Univ., Santa Cruz, CA (United States). Predatory Bird Research Group.

Hunt, W.G. 1998. Raptor floaters at Moffat's equilibrium. Oikos, 82: 191-197.

Hunter, L.A. 1987. Acquisition of territories by floaters in cooperatively breeding purple gallinules. Animal Behaviour 35(2): 402-410.

Jenkins, J.M., and R.E. Jackman. 1993. Mate and nest site fidelity in a resident population of Bald Eagles. The Condor 95(4): 1053-1056.

Jenkins, J. M., R. E. Jackman, and W. G. Hunt. 1999. Survival and movements of immature Bald Eagles fledged in northern California. Journal of Raptor Research 33:81-86.

Kimball, S.A. 2009. Behavioral interactions of breeding Bald Eagles (*Haliaeetus leucocephalus*) at Lake Cascade, Idaho. M.S. thesis, Boise State University, Boise, ID.

Komdeur, J. 1996. Breeding of the Seychelles magpie robin *Copsychus sechellarum* and implications for its conservation. Ibis 138(3): 485-498.

Komdeur, J., and R.K.H. Kats. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. Behavioral Ecology 10(6): 648-658.

Korpimäki, E., K. Lahti, C.A. May, D.T. Parkin, G.B. Powell, P. Tolonen, and J.H. Wetton. 1996. Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. Animal Behaviour 51(4): 945-955.

Lack, D. 1966. Population studies of birds. Oxford: Clarendon Press.

López-Sepulcre, A. and H. Kokko, 2005. Territorial defense, territory size, and population regulation. American Naturalist 166(3): 317-329.

Mahaffy, M.S., and L.D. Frenzel. 1987. Elicited territorial responses of northern Bald Eagles near active nests. Journal of Wildlife Management 51(3): 551-554.

Marchesi, L., P. Pedrini, and F. Sergio. 2002. Biases associated with diet study methods in the Eurasian eagle owl. Journal of Raptor Research 36(1): 11-16.

Markham, A.C., and B.D. Watts. 2007. Documentation of infanticide and cannibalism in Bald Eagles. Journal of Raptor Research 41(1): 41-44.

Markham, A.C., and B.D. Watts. 2008. The influence of salinity on provisioning rates and nestling growth in bald eagles in the lower Chesapeake Bay. The Condor 110(1): 183-187.

Markman, S., Y. Yom-Tov, and J. Wright. 1995. Parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. Animal Behaviour 50: 655-669.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18: 453-487.

Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology 9: 163-197.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73(3): 255-261.

McClelland, B. R., P. T. McClelland, R. E. Yates, E. L. Caton, and M. E. McFadden. 1996. Fledging and migration of juvenile Bald Eagles from Glacier National Park, Montana. Journal of Raptor Research 30:79-89.

McCollough, M.A. 1989. Molting sequence and aging of Bald Eagles. The Wilson Bulletin 101: 1-10.

McGowan, K.J., and G.E. Woolfenden. 1989. A sentinel system in the Florida scrub jay. Animal Behaviour 37: 1000-1006.

Millsap, B., T. Breen, E. McConnell, T. Steffer, L. Phillips, N. Douglass, and S. Taylor. 2004. Comparative fecundity and survival of Bald Eagles fledged from suburban and rural natal areas in Florida. Journal of Wildlife Management 68(4): 1018-1031.

Mock, D.W. 1985. Siblicidal brood reduction: the prey-size hypothesis. American Naturalist 125(3): 327-343.

Møller, A.P. 1987. Intraspecific nest parasitism and anti-parasite behaviour in swallows, *Hirundo rustica*. Animal Behaviour 35(1): 247-254.

Morrison, J.L., M. Terry, and P.L. Kennedy. 2006. Potential factors influencing nest defense in diurnal North American raptors. Journal of Raptor Research 40(2): 98-110.

Mougeot, F. 2000. Territorial intrusions and copulation patterns in red kites, *Milvus milvus*, in relation to breeding density. Animal Behaviour 59(3): 633-642.

Mougeot, F., J.-C. Thibault, and V. Bretagnolle. 2002. Effects of territorial intrusions, courtship feedings and mate fidelity on the copulation behaviour of the osprey. Animal Behaviour 64: 759–769.

Mougeot, F., S.M. Redpath, F. Leckie, and P.J. Hudson. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. Nature 421(6924): 737-739.

Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology 75(2): 271-287.

Nash, C., M. Pruett-Jones, and G.T. Allen. 1980. The San Juan Islands bald eagle nesting survey. p.105-115, *in* R.L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen, *eds.* Proceedings of the Washington Bald Eagle Symposium, 14-15 June, 1980, Seattle, Washington, USA. 254 p.

Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. Biol. Rev. 67: 129–173.

Newton, I. 1998. Population limitation in birds. Buteo Books, Vermillion, SD.

Nice, M.M. 1941. The role of territory in bird life. American Midland Naturalist 26(3): 441-487.

Norton, M.E., P. Arcese, and P.W. Ewald. 1982. Effect of intrusion pressure on territory size in black-chinned hummingbirds (*Archilochus alexandri*). The Auk 99(4): 761-764.

Ogdon, J.C. 1975. Effects of Bald Eagle territoriality on nesting ospreys. The Wilson Bulletin 87(4): 496-505.

Penteriani, V., M. Ferrer, and M.M. Delgado. 2011. Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. Animal Conservation 14(3): 233-241.

Praw, J.C., and J.W.A. Grant. 1999. Optimal territory size in the Convict Cichlid.

Behaviour 136(10/11): 1347-1363.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American

Naturalist 132(5): 652-661.

Purger, J.J. 1997. Accidental death of adult Red-looted Falcons *Falco*

vespertinus and its effect on breeding success. Vogelwelt-Berlin 118: 325-

328.

Ricklefs R.E. 1969. An analysis of nesting mortality in birds. Smithsonian

Contributions to Zoology 9: 1-48.

Ridley, J., J. Komdeur, and W.J. Sutherland. 2004. Incorporating territory

compression into population models. Oikos 105(1): 101-108.

Sergio, F., L. Marchesi, and P. Pedrini. 2003. Spatial refugia and the coexistence

of a diurnal raptor with its intraguild owl predator. Journal of Animal

Ecology 72(2)L 232-245.

Sibly, R., D. Barker, M. Denham, J. Hone, and M. Pagel. 2005. On the regulation

of populations of mammals, birds, fish, and insects. Science 309: 607-

610.

Skutch, A.F. 1935. Helpers at the nest. The Auk 52(3): 257-273.

Skutch, A.F. 1961. Helpers among birds. The Condor 63(3): 198-226.

Slack, R. D. 1976. Nest guarding behavior by male Gray Catbirds. The Auk

93(2): 292-300.

Slagsvold, T., S. Dale, and G.P. Sætre. 1994. Dawn singing in the great tit
(*Parus major*): mate attraction, mate guarding, or territorial defence?
Behaviour 131: 115-138.

Smith, J.N., and P. Arcese. 1989. How fit are floaters? Consequences of
alternative territorial behaviors in a nonmigratory sparrow. American
Naturalist 133(6): 830-845.

Stalmaster, M. 1987. The Bald Eagle. Universe Books, New York.

Steidl, R.J., and R.G. Anthony. 2000. Experimental effects of human activity on
breeding Bald Eagles. Ecological Applications 10: 258-268.

Stinson, D.W., J.W. Watson, and K.R. McAllister. 2001. Washington state status
report for the bald eagle. Washington Department of Fish and Wildlife,
Olympia. 92 p.

Sunde, P. 2005. Predators control post-fledging mortality in tawny owls, *Strix
aluco*. Oikos 110(3): 461-472.

Temeles, E.J. 1994. The role of neighbours in territorial systems: when are they
'dear enemies'?. Animal Behaviour 47(2): 339-350.

Warnke, D.K., D.E. Andersen, C.R. Dykstra, M.W. Meyer, and W.H. Karasov.
2002. Provisioning rates and time budgets of adult and nestling Bald
Eagles at inland Wisconsin nests. Journal of Raptor Research 36(2): 121-
127.

Watson, J.W., D.J. Pierce, and B.C. Cunningham. 1999. An active Bald Eagle
nest associated with unusually close human activity. Northwestern
Naturalist 80(2): 71-74.

Watts, B.D., A.C. Markham, and M.A. Byrd. 2006. Salinity and population

parameters of Bald Eagles (Haliaeetus leucocephalus) in the lower

Chesapeake Bay. The Auk 123(2): 393-404.

Watts, B.D., G.D. Therres, and M.A. Byrd. 2007. Status, distribution, and the

future of Bald Eagles in the Chesapeake Bay area. Waterbirds 30: 25-38.

Watts, B.D., G.D. Therres, and M.A. Byrd. 2008. Recovery of the Chesapeake

Bay Bald Eagle nesting population. Journal of Wildlife Management 72:

152-158.

Watts, B.D., and E.K. Mojica. 2012. Use of satellite transmitters to delineate Bald

Eagle communal roosts within the upper Chesapeake Bay. Journal of

Raptor Research 46(1): 120-127.

Weatherhead, P.J., and K.A. Boak. 1986. Site infidelity in song sparrows. Animal

Behaviour 34(5): 1299-1310.

Wiehn, J. and E. Korpimäki. 1997. Food limitation on brood size: experimental

evidence in the Eurasian kestrel. Ecology 78(7): 2043-2050.

Wiemeyer, S.N., C.M. Bunck, and C.J. Stafford. 1993. Environmental

contaminants in bald eagle eggs—1980–84—and further interpretations of

relationships to productivity and shell thickness. Archives of Environmental

Contamination and Toxicology 24(2): 213-227.

Wood, P. B. 1992. Habitat use, movements, migration patterns, and survival of

subadult Bald Eagles in north Florida. Unpublished Ph.D. Dissertation.

University of Florida, Gainsville.

Woodard, J.D., & M.T. Murphy. 1999. Sex roles, parental experience and

   reproductive success of eastern kingbirds, *Tyrannus tyrannus*. Animal

   Behaviour 57(1): 105-115.

Woolfenden, G.E., and J.W. Fitzpatrick. 1990. Florida scrub jays: a synopsis after

   18 years of study. p. 241-266, *in* P.B. Stacey and W.D. Koenig, eds.

   Cooperative breeding in birds: long-term studies of ecology and behavior.

   Cambridge University Press, Cambridge, 617 p.

Wright, J., E. Berg, S.R. De Kort, V. Khazin, and A.A. Maklakov. 2001.

   Cooperative sentinel behavior in the Arabian babbler. Animal Behaviour

   62(5): 973-979.

VITA

Courtney Turrin was born in Concord, California. She graduated as salutatorian of Clarkstown South High School in 2007 and earned her Bachelor of Science in Biology from Bucknell University, graduating *summa cum laude* in 2011.

Courtney's research experiences range broadly from exploring the role of the cytoskeleton in diatom motility to examining impacts of native and invasive crayfish species on the declining American eel population in the Hudson River tributaries. After graduating from Bucknell, she interned at the Acopian Center for Conservation Learning at Hawk Mountain Sanctuary, where she conducted research on dispersal behavior in American kestrels and co-authored and illustrated an educational coloring book entitled *Kestrels of the World*.

In 2011, Courtney began her thesis research with Dr. Bryan Watts and the Center for Conservation Biology. She completed the requirements for the Master of Science degree at the College of William and Mary in January of 2014.