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NEST GUARDING IN CHESAPEAKE BAY BALD EAGLES

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ABSTRACT.—As Bald Eagle (*Haliaeetus leucocephalus*) populations approach carrying capacity in the Chesapeake Bay, competition for breeding territories appears to be intensifying. Frequent territorial interactions may force breeders to adjust nest-guarding behavior. We examined nest-guarding behaviors at active Bald Eagle nests in the lower Chesapeake Bay during the nesting season (2012 and 2013). Guarding coverage was $13.7 \pm 4.2\%$ of total observation time during the pre-laying period, $6.8 \pm 2.2\%$ of observation time in the incubation period, and $26.3 \pm 3.2\%$ of observation time in the nestling period. Females were present in the nest area for $80.0 \pm 2.7\%$ of the nestling period. Although males were present only $51.2 \pm 2.8\%$ of the nestling period, male breeders guarded nests twice as often as females. Adults guarded most often from perches in adjacent trees and within 25 m of the nest. If increasing rates of conspecific interactions force males to allocate more time to nest guarding, a tradeoff may occur, with males dividing time between guarding the nest and foraging for food to provision offspring.

KEY WORDS: *Bald Eagle*; *Haliaeetus leucocephalus*; *nest defense*; *nest guarding*; *parental roles*.

CUSTODIA DE NIDOS POR *HALIAEETUS LEUCOCEPHALUS* EN CHESAPEAKE

RESUMEN.—A medida que las poblaciones de *Haliaeetus leucocephalus* se acercan a la capacidad de carga en Chesapeake Bay, parece intensificarse la competencia por los territorios de cría. Las interacciones territoriales frecuentes pueden forzar a las parejas reproductivas a adaptar su comportamiento de custodia de los nidos. Examinamos diversos comportamientos de custodia de nidos activos de *H. leucocephalus* en la región baja de Chesapeake Bay durante la época de cría (2012 y 2013). El comportamiento de custodia ocupó el $13.7 \pm 4.2\%$ del tiempo total de observación durante el periodo previo a la puesta, el $6.8 \pm 2.2\%$ del tiempo de observación en el periodo de incubación y el $26.3 \pm 3.2\%$ del tiempo de observación en el periodo de estancia de los pollos en el nido. Las hembras estuvieron presentes en el área del nido durante el $80.0 \pm 2.7\%$ del periodo de estancia de los pollos en el nido. Aunque los machos estuvieron presentes sólo el $51.2 \pm 2.8\%$ del periodo de estancia de los pollos en el nido, los machos reproductores protegieron sus nidos el doble de veces que las hembras. Los adultos desplegaron comportamientos de protección con mayor frecuencia desde posaderos ubicados en los árboles adyacentes al nido y en un radio de 25 m alrededor del mismo. Si las crecientes tasas de interacción intra-específicas obligan a los machos a emplear más tiempo en la protección del nido, esto puede resultar en un compromiso en el que los machos tengan que dividir su tiempo entre la protección del nido y la búsqueda de comida para la provisión de su prole.

[Traducción del equipo editorial]

Motivations for breeding adults to guard nests change throughout the nesting season. Investments in nest guarding are expected to reflect fitness trade-offs between risks to territory, eggs, or brood and other duties required for successful brood-rearing (e.g., Markman et al. 1995). Guarding in the pre-laying stage may be intended to deter extra-pair copulation and ensure paternity (Korpimäki et al. 1996, Mougeot 2000, Mougeot et al. 2002). In territorial species, guarding prior to egg-laying may also advertise that the territory is occupied and help to ward off

competition (Nice 1941, Mougeot 2000, Margalida and Bertran 2005). In species subject to brood parasitism, nest guarding during the incubation stage prevents parasitic species from laying eggs in the nest (Møller 1987, Gowaty et al. 1989). Guarding also deters potential predators of eggs or chicks (Slack 1976, Woodard and Murphy 1999). In the event of a predation attempt, guarding adults are better prepared to defend the nest by chasing or attacking intruders (Turrin and Watts 2014). Nest guarding likely fulfills multiple purposes simultaneously.

Nest sites are a limiting resource for Bald Eagles (*Haliaeetus leucocephalus*) in the Chesapeake Bay

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area in the eastern U.S.A. (Watts et al. 2008). As the population approaches regional carrying capacity, the number of floaters is growing disproportionately and competition for nesting sites is increasing. An analysis of annual recruitment rates of new breeders showed that nearly 100% of reproductively mature eagles were assimilated into the breeding portion of the population in the early 1990s. By 2013, that proportion had fallen to 17%, indicating that most young adult birds were excluded from breeding locally (Turrin 2013). These birds may disperse out of the Chesapeake Bay or may become floaters until they attain a breeding opportunity.

As a surplus of adult birds competes for a limited number of nesting territories, territorial interactions may become increasingly frequent (Newton 1979, Hunt 1998, López-Sepulcre and Kokko 2005). Adult mortality resulting from intraspecific conflict can be important in regulating raptor populations near carrying capacity (Newton 1979, 1998) and has been documented in adult Bald Eagles (Jenkins and Jackman 1993, Elliott et al. 2011). A recent investigation of territorial interactions in Bald Eagles in the Chesapeake Bay found that intraspecific intrusions around active nests are common during the nesting season (Turrin and Watts 2014). Though documented accounts are rare, there is anecdotal evidence in Bald Eagles of conspecific intruders killing nestlings (Markham and Watts 2007). More frequently, intrusion indirectly affects reproductive success by creating additional stresses on breeders (Kauffman et al. 2004, Bretagnolle et al. 2008). These stresses include the allocation of time and energy to chasing off intruders (Sunde and Bølstad 2004); the constraint of the territory to a more defensible size (Norton et al. 1982, Mougeot et al. 2003, Ridley et al. 2004); conflicts resulting in the wounding or killing of a breeding adult, which leaves the mate to care for the young alone (Newton 1979); and may include the allocation of more time to nest guarding at the expense of other parental care activities.

Nest-guarding behavior in Bald Eagles is poorly described. Our objective was to examine parental attendance and nest guarding by breeding Bald Eagles in the lower Chesapeake Bay. We attempted to determine whether nest-guarding coverage changed over the course of the nesting period and whether male and female breeders contributed equally to nest attendance and guarding effort. We also described the types of locations that breeders chose when nest guarding. We predicted that (1) guard-

ing coverage would change throughout the stages of the nesting season. We expect adults to adjust nest guarding in response to shifts in time demands of the reproductive stages and changes in the risks associated with intrusions in different stages of the nesting season. We hypothesized that (2) there would be a sex bias in total nest attendance and (3) in nest-guarding effort during the nesting period. Sex biases in parental roles have been demonstrated for a variety of parental care behaviors in Bald Eagles (e.g., Gerrard and Bortolotti 1988, Cain 1998, Bryan et al. 2005). Because female breeders' time budgets are dominated by incubation and brooding, particularly in the early post-hatching period, we expected females to spend more time at the nest overall but to have less time available to dedicate specifically to guarding. Though males are responsible for the majority of provisioning, males' time budgets seem to have more room for flexibility; thus, we expected males to guard nests more than females. Finally, we hypothesized that (4) breeding adults would use some types of nest-guarding locations more often than others.

METHODS

Study Sites. We studied Bald Eagles at active nest sites 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 ($n = 1$; Fig. 1). We chose nests located along the salinity gradient characteristic of the major tributaries of the Chesapeake Bay in order to examine a sample that was representative of the population. Nests were selected based on accessibility and visibility of the site, our observation of breeding activity such as nest maintenance and presence of the breeding pair early in the breeding season, permission to access the property, and proximity to another suitable study nest to allow for two observation sessions to be conducted in succession each day.

Direct Observations. We observed each nest for one breeding season in either 2012 ($n = 12$) or 2013 ($n = 19$) during repeated 3-hr focal animal observation sessions using a continuous sampling technique (Altmann 1974). Nests were observed during equal numbers of morning (0600–1000 H) and early afternoon (1100–1500 H) sessions to minimize any time of day bias. Sessions were distributed as evenly across the total observation window for each nest as time and other factors allowed.

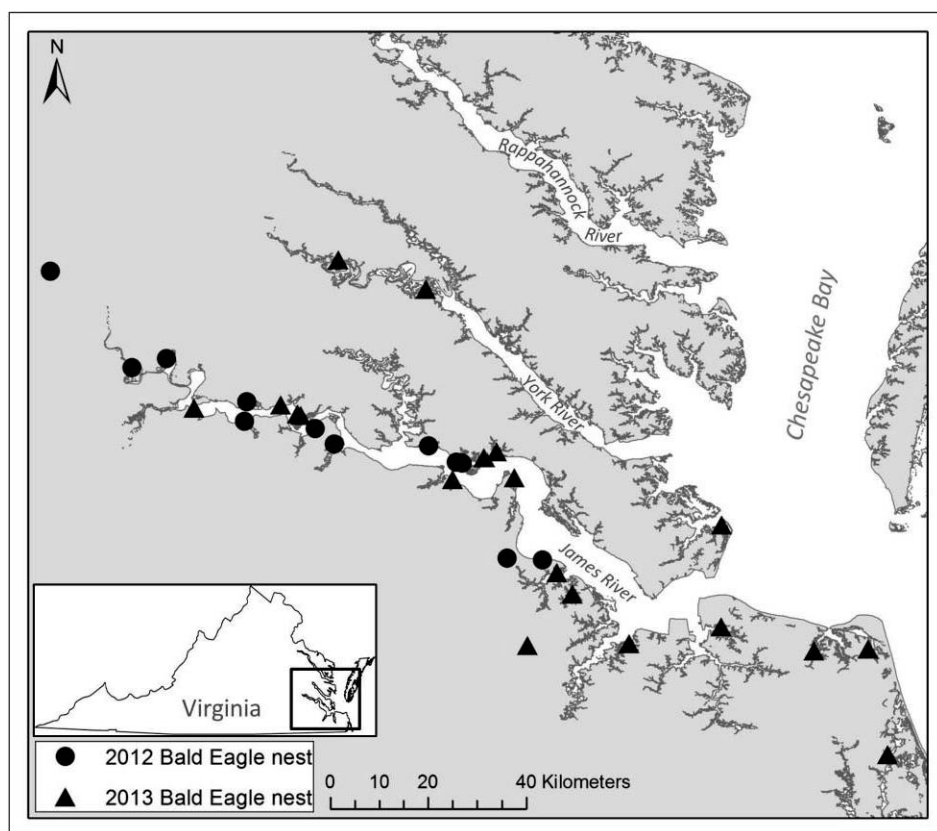


Figure 1. Locations of study nests in the lower Chesapeake Bay where nest-guarding behavior of breeding Bald Eagles was observed (2012–2013).

In 2012, observations were conducted throughout the nesting season in order to assess changes in guarding behavior across nesting phases. Nests were observed for one to three sessions in the pre-laying period and two to five sessions in the incubation period, with the exception of two nests that were not observed prior to egg-laying. All 2012 nests were observed during three to five sessions within the first 5 wk of the nestling period. In 2013, we refined our observation period to more intensively cover the early nestling period, as this had been identified as a critical period for nest success (Turrin 2013). All 2013 observations occurred during the first 3 wk after hatching, during which nests were observed for four or five sessions each.

We were interested primarily in 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 nesting period. This is

supported by Jones's (2009) suggestion that radii of defended areas are at least 250 m at nests in the Pacific Northwest. Based on these studies and constraints on visibility in the field, we used an estimate of 500 m as the radius of the defended territory around nests. We estimated distances to nests using the location of the individual bird 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 51–100 m from the nest and to the nearest 50 m for an individual 101–500 m from the nest, to reflect diminishing accuracy as distance from the nest increased.

We defined nest guarding as a state in which both breeders were within 500 m of the nest, and at least

one of the breeders was not engaged in brooding, incubation, or feeding. We excluded nest guarding by adults that were attending the nest alone for several reasons. First, when a solitary adult is present, it is often difficult to distinguish brooding, incubating, and feeding from guarding, particularly because these behaviors may occur simultaneously. Second, the motivations of and costs to solitary adults to nest guard likely differ from those of adults whose mates are present. Although an individual that is brooding, incubating, or feeding may be engaged in some form of guarding, presumably this individual would be in attendance at the nest regardless of guarding in order to perform these other parental care behaviors. There is a greater cost for the second adult, as spending time at the nest for the sole purpose of guarding introduces an additional stress on the adult's time budget, detracting from time available for other activities. While females perform the majority of the incubation and brooding effort, males are primarily responsible for provisioning. Time that males spend guarding at the nest may affect time available for foraging and may subsequently affect provisioning. Finally, guarding by a solitary and second adult are different in terms of the defensive options available if an intrusion occurs. An adult is more likely to chase or attack intruders when its mate is present at the time of the intrusion than when it is absent, and solitary adults more often exhibit weak and likely less effective responses, including calling, postural display, or circling the nest area (Turrin and Watts 2014).

In addition to nest-guarding coverage data, which were collected in both years of the study, in 2013 we also recorded parental attendance and additional data related to nest guarding, including bout length, breeder sex, distance to the nest, and location or perching substrate. We defined nest attendance as the total time the adult was present within 500 m of the nest. Sex was determined based on the relative size of the adults within each pair. Subtle plumage differences between breeders were evident in some pairs, and because nests were watched in multiple sessions, individuals were subsequently distinguished based on unique plumage. In some observations, sex could not be identified, and these events were excluded from the analyses.

Statistical Analyses. To avoid pseudoreplication, we considered nests or individual male and female breeders as sample units. We evaluated the relationship between nesting stage (pre-laying, incubation, and nestling) and guarding effort in the 2012

breeding season using a one-way analysis of variance (ANOVA) test. Using data from the 2013 nesting season, we calculated the proportion of observation time that each nest was attended and guarded by breeders. We found average bout lengths of attendance and nest-guarding behaviors at each nest. We compared female and male attendance and nest-guarding behaviors using Welch's *t*-tests to account for unequal variances. We assessed variation in distance to the nest and type of location used by adults engaged in guarding using one-way ANOVA tests. For each nest, we calculated the proportion of guarding events in each distance or location category. We averaged these values across nests and performed ANOVA tests. Because accuracy of distance estimates declined 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 m. We included only perched guarding events in the distance ANOVA analysis, as distance could be estimated with confidence in only 59% of aerial guarding events. Where ANOVA tests were significant, *post-hoc* evaluations were conducted using Tukey's honestly significant difference test. Statistical analyses were completed using R software (R Core Team 2013). All tests were two-tailed, and all values are reported as means \pm standard error.

We conducted sensitivity analyses to account for observations in which the sex of the breeder could not be accurately determined. We performed these analyses by rerunning 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. We used Spearman's rank correlation to test the data for a systematic bias related to observation effort (i.e., the total number of hours observed per nest) to determine whether there was an effect of differences in observation time across nests.

RESULTS

During the 2012 and 2013 nesting seasons, we monitored 31 Bald Eagle nests located along tributaries of the lower Chesapeake Bay. Total observation time was 540.8 hr. In 2012, nests were observed for 4.6 ± 0.7 hr in the pre-laying period, 10.4 ± 0.7 hr during incubation, and 10.7 ± 0.6 hr in the nestling period, on average. In 2013, observation time averaged 12.7 ± 0.4 hr per nest during the nestling period.

Nest-guarding effort varied with nesting stage. On average, nests were guarded during $13.7 \pm 4.2\%$ of

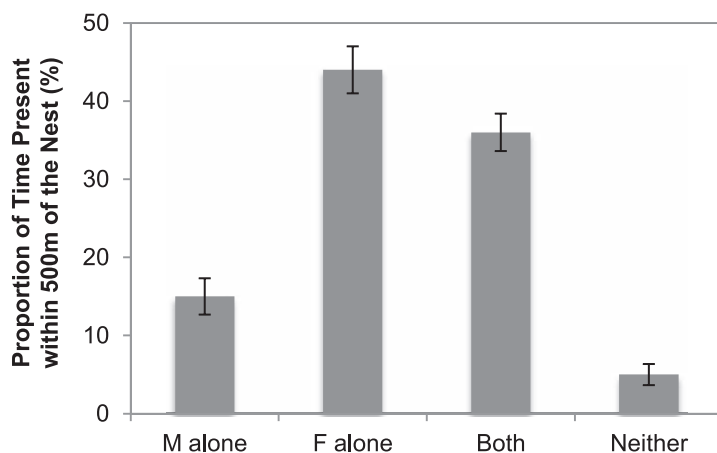


Figure 2. Mean nest attendance \pm SE by male (M) and female (F) breeding Bald Eagles at 19 nests in the lower Chesapeake Bay during the first 3 wk of the nestling period (2013). Nest attendance was defined as the proportion of time a breeding adult was present within 500 m of the nest.

the pre-laying period, $6.8 \pm 2.2\%$ of the incubation stage, and $21.9 \pm 5.2\%$ of the nestling period during the 2012 breeding season (one-way ANOVA: $F_{2,31} = 3.611$, $P = 0.039$). Pairwise *post-hoc* comparisons indicated that guarding coverage was significantly higher in the nestling period than during incubation ($P = 0.030$). All other pairwise tests were nonsignificant (all $P > 0.364$). There was no effect of observation effort within each nesting stage on observed guarding coverage ($r_s = 0.060$, $n = 34$, $P = 0.736$). The study-wide (2012 and 2013) average nest-guarding coverage during the nestling period was $26.3 \pm 3.2\%$.

During the 2013 nestling period, females attended the nest area more often ($t = -5.344$, $P < 0.001$, $df = 30.9$; Fig. 2) and for longer average bouts of time than males ($t = -6.271$, $P < 0.001$, $df = 25.2$). Observations for which breeder sex was unknown made up 0.8% of total attendance events, and a sensitivity analysis indicated that these observations had no effect on the results (all $t > -5.111$, $P < 0.001$). We found no effect of differences in observation time across nests on average attendance bout length of male ($r_s = -0.081$, $n = 19$, $P = 0.741$) and female ($r_s = 0.034$, $n = 19$, $P = 0.889$) breeders at individual study nests. The proportion of time that females attended nests was positively correlated with observation time ($r_s = 0.562$, $n = 19$, $P = 0.012$), while male attendance was not ($r_s = 0.353$, $n = 19$, $P = 0.137$). On average, nests were left unattended during $5.0 \pm 1.4\%$ of observation time in 2013. Two nests were never observed unattended. At other study nests, the aver-

age bout length of nonattendance was 6.9 ± 1.2 min ($n = 17$).

Males guarded nests more than females during the nestling stage ($t = 4.281$, $P < 0.001$, $df = 35.8$; Fig. 3A). The difference between male and female guarding bout lengths was not significant ($t = 1.733$, $P = 0.092$, $df = 36.0$; Fig. 3B). There was no effect of observation effort on the proportion of time nests were guarded by male and female breeders ($r_s = 0.172$, $n = 19$, $P = 0.481$; $r_s = 0.268$, $n = 19$, $P = 0.268$, respectively). There was no correlation between observation effort and average male guarding bout length ($r_s = 0.313$, $n = 19$, $P = 0.192$), but female guarding bout length was positively correlated with observation time ($r_s = 0.568$, $n = 19$, $P = 0.011$).

In 2013, adults guarded broods most often from perches within 25 m of the nest but not in the nest itself (one-way ANOVA: $F_{6,126} = 7.676$, $P < 0.001$; Fig. 4). Pairwise tests showed that guarding in the 0–25 m distance category was significantly higher than in all other distance categories (all $P < 0.004$) except for in the nest, though that relationship approached significance ($P = 0.052$). All other pairwise comparisons were nonsignificant (all $P > 0.064$). Adults engaged in nest-guarding behavior guarded most often from an adjacent tree ($43.6 \pm 5.7\%$ of guarding events; one-way ANOVA: $F_{3,72} = 9.054$, $P < 0.001$). Of total guarding events, $24.2 \pm 5.0\%$ were conducted from a perch in the nest tree but not in the nest itself. Nest guarding from a position in the nest and aerial guarding while circling or soaring over the

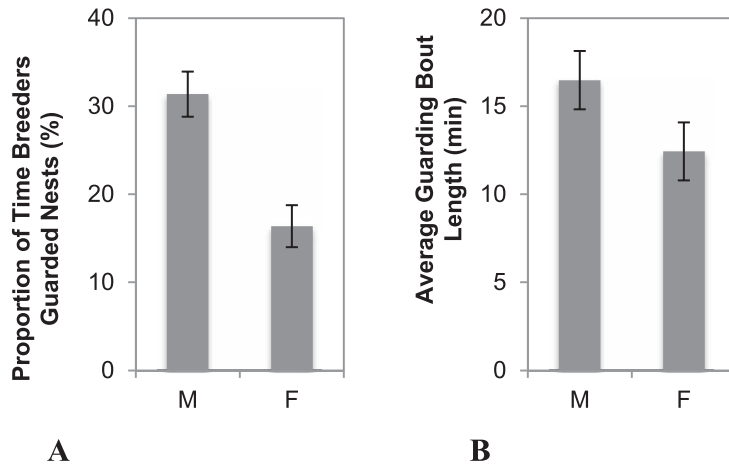


Figure 3. Total coverage (A) and average bout length (B) \pm SE of nest-guarding behavior exhibited by male (M) and female (F) Bald Eagles at 19 nests in the lower Chesapeake Bay during the first 3 wk post-hatch (2013). In this study, a breeding adult was considered to be nest guarding when it was within 500 m of the nest and not engaged in brooding, incubation, or feeding, and the mate was also present in the nest area, regardless of the mate’s activity.

nest site made up $16.3 \pm 2.5\%$ and $15.9 \pm 3.3\%$ of guarding events, respectively. Pairwise comparisons indicated significantly more guarding from perches in adjacent trees than all other locations (all $P < 0.011$). No other pairwise comparisons were significant (all $P > 0.530$). There was no correlation between observation time and total

guarding events observed per nest ($r_s = -0.070$, $n = 19$, $P = 0.776$).

DISCUSSION

Nest-guarding coverage changed over the nesting season, supporting our first hypothesis. In 2012, nests were guarded in the nestling period nearly

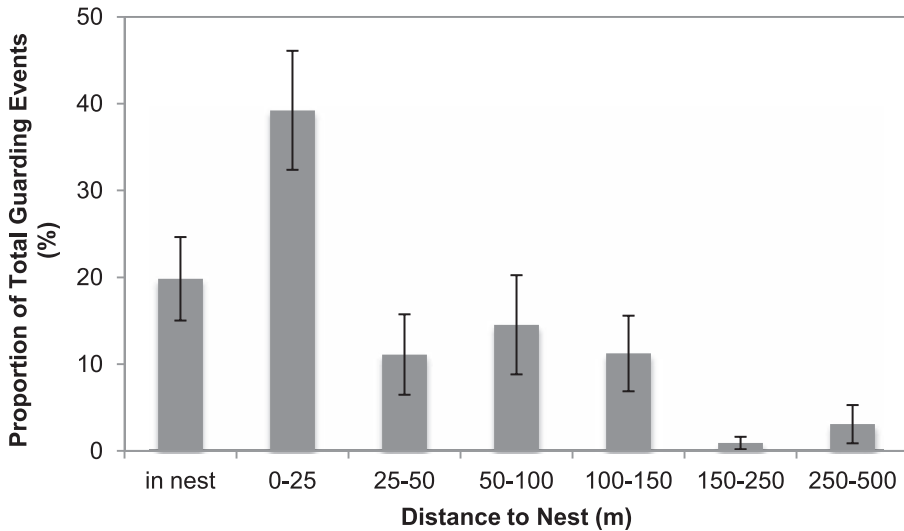


Figure 4. Distance to the nest during nest-guarding bouts of 19 Bald Eagle pairs nesting in the lower Chesapeake Bay (2013). Proportion of guarding events per breeding pair in each distance category was averaged (\pm SE) across study nests. A breeding adult was considered to be nest guarding when perched within 500 m of the nest and not engaged in brooding, incubation, or feeding, and the mate was also present in the nest area, regardless of the mate’s activity. Distances presented refer to the distance between the nest-guarding perch and the nest structure.

twice as often as in the pre-laying period and three times more often than during the incubation period. However, the difference between guarding coverage during the pre-laying and nestling stages was not significant. Our remaining hypotheses were supported in that there were sex biases in (2) nest attendance and (3) nest-guarding frequency, and (4) breeders used some nest-guarding locations more frequently than others. Although nest attendance was higher in female breeders, males guarded nests more often than females. Adults typically guarded 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.

Differences in observation effort among nests did not have significant effects on the results, with two possible exceptions. Female attendance coverage and nest-guarding bout length showed moderate positive correlations with observation effort ($r_s = 0.562$ and 0.568 , respectively). Despite the effect of observation time on female attendance coverage, our general finding that females attended nests more than males during the nestling period was consistent with observations of eagles within other populations. Bryan et al. (2005) observed a South Carolina Bald Eagle nest from hatching through fledging in 1997 and 1999, reporting attendance of 31.6–47.3% and 8.8–21.1% by females and males, respectively. Cain (1998) found attendance of approximately 60–70% and 20–30% by female and male breeders, respectively, during the first 3 wk of the nestling period at three nests in Alaska. A possible cause of the positive correlation between female guarding bout length and observation time is an observation boundary problem, as some birds were already guarding when a session began or were still guarding when the session ended. In this case, we expect that female bout length was underestimated at some nests. Interestingly, male behavioral bout lengths showed no effect of differences in observation time among nests. Taking into account the guarding bout lengths of males and females (16.5 ± 1.7 min and 12.4 ± 1.6 min, respectively) and the moderate positive correlation between female bout length and observation time, we expect that the average female bout length is greater than our reported estimate, but we still expect no difference between the averages for males and females. Because there was no effect of observation time on the number of guarding events observed per nest, we do not expect that analyses of nest-guarding locations were

affected by variation in observation time. No other study parameters were correlated with observation effort. We conclude that differences in observation time among nests did not influence the results concerning shifts in guarding effort during the nesting season, sex biases in total guarding effort, or variation in guarding distances and locations used.

We defined nest guarding as the presence of a member of the breeding pair within 500 m of the nest while its mate was also present, excluding individuals engaged in brooding, incubation, or feeding. Though this definition does not discriminate between guarding and loafing, the results support our assumption that the behaviors included under our definition were guarding and not incidental loafing near the nest. We would expect breeding pairs to loaf most often in the pre-laying and incubation periods, as there are relatively few demands on their time. In the pre-laying period, males may guard more intensively to prevent EPC, but females have more flexibility than they do in any other stage. In the incubation period, one member of the pair must be in attendance almost constantly to incubate the eggs, but the demands on the non-incubating adult are only to feed and possibly to guard the nest. During the nestling period, the need to guard the nest is still present, the consistent demand of incubating is replaced by that of brooding, and a new demand on the pair is introduced, as provisioning becomes essential to nestling-rearing. Despite the relatively higher demands on the pair during the nestling period, nest-guarding coverage was nearly double that of the pre-laying period and triple that of the incubation period, although only the latter comparison was statistically significantly different. This suggests that loafing did not constitute a large portion of the behaviors we defined as nest guarding. Furthermore, loafing need not occur within close proximity to the nest; thus, if adults are idling near the nest rather than near a food source or some other location, their choice of loafing site may indicate a motive of nest supervision. An individual loafing near the nest may switch to guarding upon the appearance of an intruder. For many reasons, nest guarding and loafing are difficult to distinguish, and thus our inclusive definition was used.

Because the motivation for nest guarding differs in each stage of the reproductive period, our results may 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 (EPC; Korpimäki et al.

1996, Mougeot et al. 2002) or to ward off potential attempts to usurp the territory (Nice 1941, Mougeot 2000). Bald Eagles form persistent pair bonds and are considered monogamous (Stalmaster 1987, Jenkins and Jackman 1993); however, in some species social monogamy masks relatively high rates of extra-pair fertilization. Mougeot (2004) examined copulation behavior in 19 socially monogamous raptor species and found that EPC occurred in 68% and that incidence of EPC increased with breeding density. Although there are no data on EPC prevalence in our study population, the prevalence of floaters suggests a high risk of both EPC and attempts to usurp the territory early in the breeding season when non-territory holders compete for breeding opportunities. Breeders guarded nests during $13.7 \pm 4.2\%$ of pre-laying observations. Studies in other raptor species indicate that males spend 40% of the pre-laying period mate guarding or attending the territory, presumably to guard mates from EPC attempts (Korpimäki et al. 1996, Mougeot et al. 2002). These studies defined mate guarding as the attendance of the male in the vicinity of the nest with his mate (Korpimäki et al. 1996) and territory attendance as the percentage of time spent within the breeding territory, either at the nest or perched within 300 m of the nest (Mougeot et al. 2002). The relatively low rate of guarding at our study nests suggests that guarding by Bald Eagles in the pre-laying period may not be motivated by EPC risk. However, there may be considerable variation in pre-laying guarding effort due to differences in local breeding density, site characteristics, location relative to flyways and roosts, breeder experience, and other factors. In addition, our definition of nest guarding was fairly conservative and may not be directly comparable to other studies.

Once eggs are laid, new risks are introduced and antipredator behaviors become more important in ensuring nest success. Though some passerine species nest guard for 60% of the incubation period to deter nest parasitism and predators (Slack 1976, Woodard and Murphy 1999), nest-guarding coverage by Bald Eagles during incubation was $6.8 \pm 2.2\%$. This low value may be an artifact of our relatively conservative definition of guarding; the aforementioned studies defined nest guarding to include male attendance in the nest area in the absence of the female (Slack 1976, Woodard and Murphy 1999), while our definition was restricted to guarding by an adult in the presence of the mate. It seems likely that an incubating female could simulta-

neously scan for predators or intruders and would be more able to do so than an adult engaged in feeding young, but her activity would not be considered guarding by our definition. During our observations, both adults were rarely in attendance at the same time during incubation. This is likely in part because eagles do not face the same nest parasitism threats as passerines. Furthermore, adult eagles have no true predators in this ecosystem. When the incubating adult is in attendance, their nests likely do not face the same magnitude of predation risk as passerine nests. In addition, adults are expected to invest time in guarding based on the potential for renesting if failure should occur and the probability of offspring survival (Montgomerie and Weatherhead 1988). Wood and Collopy (1993) found that 78% of pairs in northern Florida laid a second clutch within 29 d of experimental removal of the first clutch. The Chesapeake Bay population has a shorter potential breeding season than the Florida population as a result of the latitudinal gradient (Newton 1979). Reproductive surveys of the Chesapeake Bay population indicate that most pairs lay a replacement clutch when nests fail during incubation, but failures in the nestling stage generally occur too late in the season for pairs to attempt to renest (B.D. Watts and M.A. Byrd unpubl. data). Furthermore, the probability of offspring survival is higher for nestlings than for unhatched eggs, and nestlings are therefore a more valuable investment than eggs (Ricklefs 1973, Barash 1975). Guarding in the nestling period is critical to protecting altricial young from predators. In this population, nest cameras documented predation of nestlings up to 8 wk old (A.C. Markham and B.D. Watts unpubl. data). Finally, the observed peak in guarding may also relate to behavioral assessments of offspring and mates. Breeders may station themselves near the nest to gauge offspring feeding demands (e.g., Quillfeldt and Masello 2004, Hamer et al. 2006) or to indicate to the mate readiness to take over brooding (e.g., Debus et al. 2007). Though the relative importance of these motivators is unknown, nest guarding likely fulfills many roles simultaneously.

The timing of peak nest-guarding activity necessitates the presence of both breeders at the nest, with one adult brooding young 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 indicate that in eagles 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 young. This may suggest (1) that the female is vulnerable during brooding (Burton and Yasukawa 2001), (2) that both adults are essential for warding off intruders without leaving nestlings unprotected (Regelmann and Curio 1986), or (3) that both adults are at least twice as effective as one adult in deterring predators (Montgomerie and Weatherhead 1988). There is evidence supporting the second and third explanations. Simultaneous intrusions were observed during the study in multiple instances, with as many as four birds intruding at once (Turrin 2013). Breeders responded more often and more aggressively, usually with one breeder chasing or attacking the intruder, when both members of the breeding pair were present at the time of the intrusion event (Turrin and Watts 2014). The absence of the second adult at nests with older young suggests that reproductive tradeoffs shift for adults with older broods, possibly because older young are less vulnerable to potential predators.

As the Bald Eagle population in the Chesapeake Bay reaches saturation, breeders may reinforce nest-guarding efforts in response to the increasing risk of intraspecific intrusion. Time allocated to nest guarding during the nestling period may detract from the time available for other fundamental nestling-rearing behaviors. Males perform more provisioning than females, and our results indicate that they also nest guard more than females. If the quantity and quality of food provided to young is compromised by increased guarding effort, nestling rates of growth and mass gain may be negatively affected (Bortolotti 1989, Markham and Watts 2008). Alternatively, if adults do not adjust time budgets to increase nest-guarding coverage, pairs may face greater risk of nest failure resulting from an intrusion event. Infanticide and cannibalism by an intraspecific intruder has been documented in this population (Markham and Watts 2007).

Further research is needed before drawing any broad conclusions about the potential reproductive implications of increased guarding rates and the tradeoffs between different parental care strategies.

Future studies should investigate the relationships between nest-guarding effort and reproductive success as well as guarding effort and provisioning rate, as males seem to be principally responsible for both of these behaviors. In addition, further research into the causes of nest failure and the relative effect of factors that contribute to nest failure, though challenging, would be a valuable addition to our understanding of Bald Eagle breeding ecology.

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LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- BARASH, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the Alpine Accentor. *Wilson Bulletin* 87:367-373.
- BORTOLOTTI, G.R. 1989. Factors influencing the growth of Bald Eagles in north central Saskatchewan. *Canadian Journal of Zoology* 67:606-611.
- BRETAGNOLLE, V., F. MOUGEOT, AND J.C. THIBAUT. 2008. Density dependence in a recovering Osprey population: demographic and behavioural processes. *Journal of Animal Ecology* 77:998-1007.
- 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* 4:459-468.
- 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. Pages 73-94 in B.A. Wright and P.F. Schempf [Eds.], Bald Eagles in Alaska. Bald Eagle Research Institute, Juneau, AK U.S.A.
- DEBUS, S.J.S., T.S. HATFIELD, A.J. LEY, AND A.B. ROSE. 2007. Breeding biology and diet of the Little Eagle *Hieraetus morphnoides* in the New England region of New South Wales. *Australian Field Ornithology* 24:137-157.

- ELLIOTT, K.H., J.E. ELLIOTT, L.K. WILSON, I. JONES, AND K. STENERSON. 2011. Density-dependence in the survival and reproduction of Bald Eagles: linkages to chum salmon. *Journal of Wildlife Management* 75:1688–1699.
- GERRARD, J.M. AND G.R. BORTOLOTTI. 1988. The Bald Eagle. Smithsonian Institution, Washington, DC U.S.A.
- 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* 38:272–284.
- GREIG-SMITH, P.W. 1980. Parental investment in nest defence by Stonechats (*Saxicola torquata*). *Animal Behaviour* 28:604–619.
- 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.
- HAMER, K.C., P. QUILLFELDT, J.F. MASELLO, AND K.L. FLETCHER. 2006. Sex differences in provisioning rules: responses of Manx Shearwaters to supplementary chick feeding. *Behavioral Ecology* 17:132–137.
- 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.
- HUNT, W.G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos* 82:191–197.
- JENKINS, J.M. AND R.E. JACKMAN. 1993. Mate and nest site fidelity in a resident population of Bald Eagles. *Condor* 95:1053–1056.
- JONES, I.L. 2009. Associative nesting behaviour between Pacific Great Blue Herons and Bald Eagles in the Pacific Northwest: testing the predator protection hypothesis. M.S. thesis, Simon Fraser University, Burnaby, BC Canada.
- KAUFFMAN, M.J., J.F. POLLOCK, AND B. WALTON. 2004. Spatial structure, dispersal, and management of a recovering raptor population. *American Naturalist* 164:582–597.
- KOMDEUR, J. AND R.K.H. KATS. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles Warblers. *Behavioral Ecology* 10:648–658.
- 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* 51:945–955.
- LÓPEZ-SEPULCRE, A. AND H. KOKKO. 2005. Territorial defense, territory size, and population regulation. *American Naturalist* 166:317–329.
- MAHAFFY, M.S. AND L.D. FRENZEL. 1987. Elicited territorial responses of northern Bald Eagles near active nests. *Journal of Wildlife Management* 51:551–554.
- MARGALIDA, A. AND J. BERTRAN. 2005. Territorial defence and agonistic behavior of breeding vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. *Ethology Ecology and Evolution* 17:51–63.
- MARKHAM, A.C. AND B.D. WATTS. 2007. Documentation of infanticide and cannibalism in Bald Eagles. *Journal of Raptor Research* 41:41–44.
- AND ———. 2008. The influence of salinity on provisioning rates and nestling growth in Bald Eagles in the lower Chesapeake Bay. *Condor* 110:183–187.
- 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. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9:163–197.
- MCGOWAN, K.J. AND G.E. WOOLFENDEN. 1989. A sentinel system in the Florida Scrub Jay. *Animal Behaviour* 37:1000–1006.
- MØLLER, A.P. 1987. Intraspecific nest parasitism and anti-parasite behaviour in swallows, *Hirundo rustica*. *Animal Behaviour* 35:247–254.
- MONTGOMERIE, R.D. AND P.J. WEATHERHEAD. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology* 63:167–187.
- MOUGEOT, F. 2000. Territorial intrusions and copulation patterns in red kites, *Milvus milvus*, in relation to breeding density. *Animal Behaviour* 59:633–642.
- . 2004. Breeding density, cuckoldry risk and copulation behavior during the fertile period in raptors: a comparative analysis. *Animal Behaviour* 67:1067–1076.
- , S.M. REDPATH, F. LECKIE, AND P.J. HUDSON. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. *Nature* 421:737–739.
- , J.-C. THIBAUT, 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.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.
- . 1998. Population limitation in birds. Buteo Books, Vermillion, SD U.S.A.
- NICE, M.M. 1941. The role of territory in bird life. *American Midland Naturalist* 26:441–487.
- NORTON, M.E., P. ARCESE, AND P.W. EWALD. 1982. Effect of intrusion pressure on territory size in Black-chinned Hummingbirds (*Archilochus alexandri*). *Auk* 99:761–764.
- QUILLFELDT, P. AND J.F. MASELLO. 2004. Context-dependent honest begging in Cory's Shearwaters (*Calonectris diomedea*): influence of food availability. *Acta Ethologica* 7:73–80.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- REGELMANN, K. AND E. CURIO. 1986. How do Great Tit (*Parus major*) pair mates cooperate in brood defence? *Behaviour* 97:10–36.
- RICKLEFS, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.
- . 1973. Ecology. Chiron Press, New York, NY U.S.A.
- RIDLEY, J., J. KOMDEUR, AND W.J. SUTHERLAND. 2004. Incorporating territory compression into population models. *Oikos* 105:101–108.

- SKUTCH, A.F. 1935. Helpers at the nest. *Auk* 52:257–273.
- SLACK, R.D. 1976. Nest guarding behavior by male Gray Catbirds. *Auk* 93:292–300.
- STALMASTER, M. 1987. *The Bald Eagle*. Universe Books, NY U.S.A.
- SUNDE, P. AND M.S. BØLSTAD. 2004. A telemetry study of the social organization of a Tawny Owl (*Strix aluco*) population. *Journal of Zoology* 263:65–76.
- TURRIN, C. 2013. Rise of a floater class: behavioral adjustments by breeding Bald Eagles in a population approaching saturation. M.S. thesis, College of William and Mary, Williamsburg, VA U.S.A.
- AND B.D. WATTS. 2014. Intraspecific intrusion at Bald Eagle nests. *Ardea* 102:71–78.
- 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.
- WOOD, P.B. AND M.W. COLLOPY. 1993. Effects of egg removal on Bald Eagle productivity in northern Florida. *Journal of Wildlife Management* 57:1–9.
- WOODARD, J.D. AND M.T. MURPHY. 1999. Sex roles, parental experience and reproductive success of Eastern Kingbirds, *Tyrannus tyrannus*. *Animal Behaviour* 57:105–115.
- WRIGHT, J., E. BERG, S.R. DE KORT, V. KHAZIN, AND A.A. MAKLAKOV. 2001. Cooperative sentinel behavior in the Arabian Babbler. *Animal Behaviour* 62:973–979.

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