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Intraspecific intrusion at Bald Eagle nests

Courtney Turrin* **& Bryan D. Watts**

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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 behaviours at active Bald Eagle *Haliaeetus leucocephalus* nests in the lower Chesapeake Bay in 2012 and 2013. The average intrusion rate experienced at study nests during the reproductive period was 0.28 ± 0.32 intrusions/h. 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, and 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 significantly more often and more aggressively when in the presence of their mate. Further research is necessary to broadly describe the relationship between intrusion frequency and the frequency of nest failure.

Key words: intrusion, territorial interaction, intraspecific interaction, floater, nest defence, Bald Eagle, *Haliaeetus leucocephalus*

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Factors that contribute to population regulation have been the focus of ecological study for decades (Murdoch 1994). One prominent type of population regulator is density dependence (Newton 1998). Population size is limited by density-dependent competition for critical resources, including food (e.g. Martin 1987, Newton 1998) and breeding sites (Newton 1998). For territorial species like the Bald Eagle *Haliaeetus leucocephalus*, competition for breeding sites often provides the ultimate limit to population size (Newton 1979; Hunt 1998). As populations approach saturation, space needed to establish new territories becomes limiting and increasing numbers of floaters result (Newton 1979, Hunt 1998). Contests for breeding space may act as a density-dependent regulator of population growth by increasing adult mortality (Newton 1979, 1998) and reduce 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. Bald Eagles reach sexual maturity in their fifth calendar year (Grier *et al.* 1983). 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 1990s. By 2013, that percentage had fallen to 17%, indicating that 4 out of every 5 birds of recruitment age are floaters (Turrin 2013). Data from tracked birds in the Chesapeake Bay population (Watts & Mojica 2012) indicate that these individuals have not established nesting territories at the expected breeding age (Watts & Mojica, unpubl. data). An increase in age-to-first-reproduction provides further evidence of floaters.

Little is known about the nature of interactions between 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 & Frenzel 1987), or anecdotes (Gerrard *et al.* 1980, Gerrard & 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 behaviours 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 behavioural 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 breeding opportunities, either by extra pair copulation (e.g. Mougeot 2004) or mate replacement (e.g. Jenkins & Jackman 1993). Thus, we expect that the rate of intrusion by adult-plumaged birds may vary throughout the reproductive period to reflect times of greatest vulnerability. If intruders are motivated to acquire extra pair copulations, intruders would be expected to target the pre-laying period. If intruders are motivated to acquire a territory, intruders may target the period when nest failure is most common, as nest failures may result in mate replacement (Jenkins & Jackman 1993). 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 proximity of the intruder to the nest and when the mate is present to assist in the defensive effort.

METHODS

Study sites

We observed a total of 31 Bald Eagle nests (Figure 1) located 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). In order to best represent the variation in the population, study nests were located along the nesting density gradient, with nearest neighbour distances ranging from 14 to 7063 m (mean ± SD: 981 ± 1328 m). In 2012, we monitored 12 nest sites throughout the reproductive period from pre-laying through the fifth week of the post-hatching period. An assessment of the 2012 data indicated that intrusion frequency was not higher in the pre-laying period, when extra pair copulations would be expected. In 2013, we selected 19 nests for observation, and we refined our time frame to focus on the period when nests are most vulnerable to failure, which has been identified as the first 3 weeks following hatching (Turrin 2013). This time period is when intruders have the greatest potential to break up a nesting attempt, possibly creating a breeding opportunity. In this paper, we will refer to this period as 'the sensitive window'.

Direct observations

We conducted three-hour focal 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 2 nests that were not observed prior to egg laying. In 2012, nests were observed during 3 to 5 sessions in the post-hatching period, with 2 to 4 sessions in the first 3 weeks after hatching and 0 to 2 sessions in weeks 4 and 5. In 2013, all observations were focused on the first 3 weeks after hatching, during which nests were observed for 4 or 5 sessions. Observation sessions in 2012 and 2013 were distributed as evenly across the aforementioned time periods as time and other factors allowed. Nests were observed during morning (06:00 to 10:00 h) and early afternoon (11:00 to 15:00 h) 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.

Intrusion

An intrusion was defined as a Bald Eagle that is not a member of the breeding pair approaching within 500 m of the nest. Mahaffy & 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 500 m 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

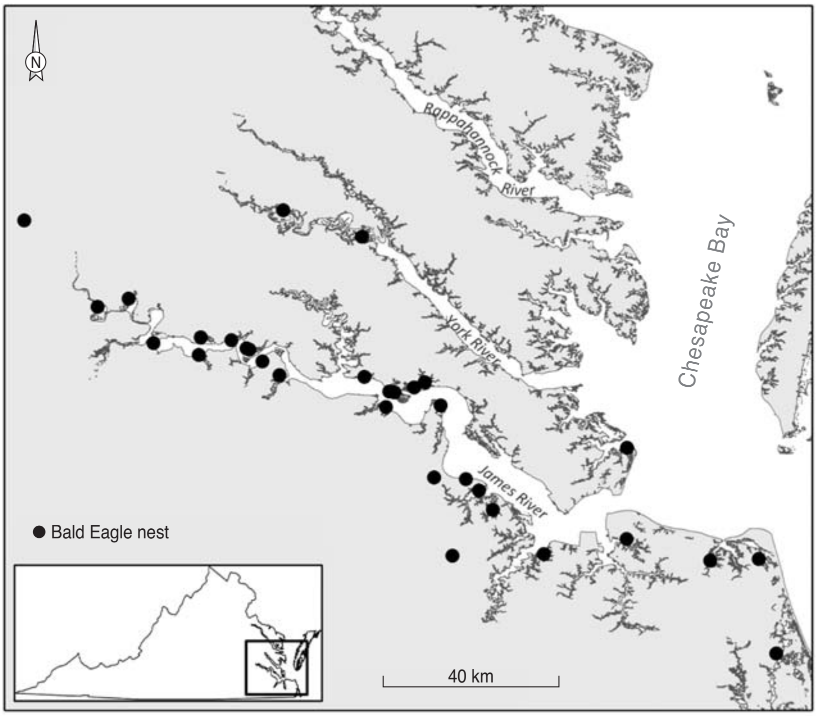

Figure 1. Locations of nests in the lower Chesapeake Bay used in observational monitoring study (2012–2013).

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 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.

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 behaviours 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 from out of view to perch by the nest or circling the nest area. We defined a non-response as a breeder present at the time of intrusion showing no behavioural 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 breeder response framework, though these events were included in all other analyses.

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 tests. 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. To calculate the expected frequency of adult intrusions in each distance category, we assumed that the proportion of adult intrusions falling in each category were the same as the proportion of juvenile intrusions at that same distance. Thus, we multiplied the total number of adult intrusions by the proportion of juvenile intrusions in each distance category to calculate the expected adult intrusion frequency 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). Significance of all test results was assessed at a probability level of 0.05.

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 any 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 540 hours of nest observation, 163 intraspecific intrusion events were observed, translating into an average intrusion rate of 0.28 ± 0.32 intrusions/h (mean ± SD). The intrusion rate of adult-plumaged birds was 0.12 ± 0.12 intrusions/h and the intrusion rate of juvenile-plumaged birds was 0.17 ± 0.26 intrusions/h. There was considerable variation in intrusion rates among nests, ranging from 0 to 20 intrusion events in 12 hours of observation.

Intrusion patterns in the period of highest nest failure were similar to those observed outside of this time 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 this time period. The average intrusion rate in the period of highest nest failure was 0.30 ± 0.37 intrusions/h, compared to 0.38 ± 0.22 intrusions/h outside of the sensitive window. Adult intruders did not target the period of highest nest failure, as intrusions by adults occurred at a rate of 0.12 ± 0.14 intrusions/h during this period and 0.15 ± 0.15 intrusions/h during the other study time. Intrusions by juveniles during the sensitive window occurred at a rate of 0.18 ± 0.30 intrusions/h, compared to 0.23 ± 0.18 intrusions/h outside of the sensitive window. Furthermore, intruders did not seem to target the pre-laying period, when extra pair copulations would be expected. Intrusion rates remained fairly consistent across all reproductive periods assessed in 2012, with an average intrusion rate of 0.34 ± 0.15 intrusions/h during the pre-laying period, 0.42 ± 0.07 intrusions/h during the incubation period and 0.36 ± 0.06 intrusions/h during the post-hatching period.

Intrusions were not the result of random movement over the landscape. Intruders were attracted to the nest structures during both the entire reproductive period ($\chi^2_5 = 2384$, $P < 0.0001$; Figure 2) and during the sensitive window ($\chi^2_5 = 1645$, $P < 0.0001$). Juveniles approached closer to nests compared to adult-plumaged intruders during the entire observation

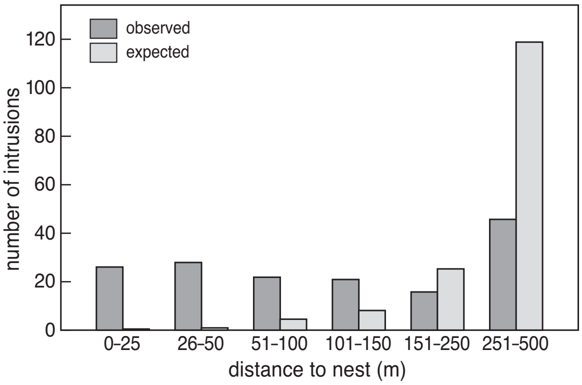

Figure 2. Approach distances of intraspecific intruders to nest sites of breeding Bald Eagles in the lower Chesapeake Bay (2012 and 2013). Expected frequencies were calculated based on relative area within each distance category to represent a random distribution of intrusions.

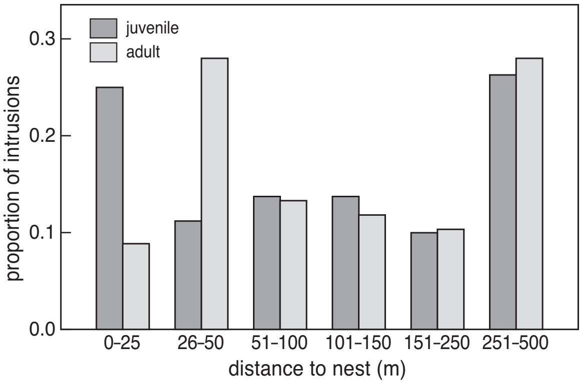

Figure 3. Approach distances of juvenile and adult intruders around nests of breeding Bald Eagles in the lower Chesapeake Bay (2012 and 2013) as proportions of the total intrusions by each age class.

period (χ^2_5 = 24.245, $P < 0.001$; Figure 3) and sensitive window (χ^2_5 = 23.682, $P < 0.001$). Unknown-aged intruders had no significant influence on frequency comparisons for either approach distance or intruder age (all $\chi^2_5 > 22.5$, $P < 0.001$).

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_5 = 6.004, P = 0.31). 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, *df* = 1, P = 0.002).

Though there were relatively few intruders of unknown age, 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. 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, *df* = 1, P = 0.072). If all unknowns were juveniles, there would be no effect on significance (*G*-statistic = 11.06, *df* = 1, $P < 0.001$). Likewise, if all unknowns were adults, the difference in breeder response to juvenile and adult intruders would remain significant (*G*-statistic = 6.062, *df* = 1, P = 0.014).

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 = 12.69, df = 1, $P < 0.001$). Of the 37 intrusions that occurred in the presence of both adults, a single adult responded more often than both adults responded together (83.8% and 16.2% of responses, resp.; χ^2_1 = 16.89, $P < 0.0001$). There was no significant difference in the probability of response by male (0.605) and female (0.395) breeders when both were present (χ^2_1 = 1.884, P = 0.170).

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, *df* = 1, P = 0.002; Figure 4).

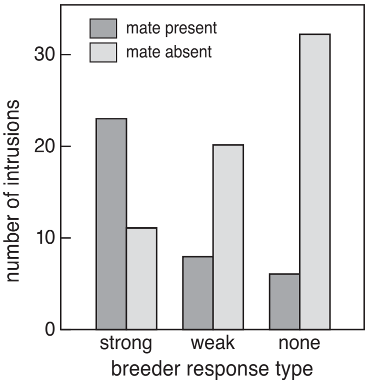

Figure 4. Response type (strong, weak or no response) by breeding Bald Eagles in the lower Chesapeake Bay (2012 and 2013) given mate presence. Strong responses involved chasing or attacking intruders, while weak responses involved calling, watching the intruder or exhibiting a defensive posture.

There was a significant relationship between breeder sex and the probability that a breeder would call 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_1 = 5.158, P = 0.023). The single instance of a breeder of unknown sex calling during an intrusion had no effect on the result (all $\chi^2_1 > 4.333$, $P < 0.037$). 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 = 1.653, P = 0.20).

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 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 present at the nest site, the adult must remain on the nest to protect the offspring or leave the nest temporarily vulnerable 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 & Anthony (2000) in an Alaskan sub-population along the Gulkana River Basin (59% and 59.2%, resp.). 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 & Anthony 2000). The reason for this discrepancy is unclear, but one possible explanation is that pairs nesting in the lower Chesapeake Bay may adjust attendance behaviour 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 & 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 behaviour of intruders may affect breeder response behaviour. Breeding pairs may also habituate to consistent activity near the nest (Watson *et al.* 1999, Steidl & Anthony 2000). In territorial species, breeders may become accustomed to neighbouring pairs (Galeotti & Pavan 1993, Hardouin *et al.* 2006) and perceive these familiar individuals as less threatening than strangers once territorial boundaries are established (Temeles 1994). If breeding pairs respond less frequently or less aggressively toward neighbours than toward unknown birds, then our estimates of the frequency and strength of response by breeders toward adult intruders are likely conservative.

Though some of the observed intrusions may have been accidental effects of movement through areas of high nest density, our results indicate that intruders tend to approach the nest more closely than we would expect if intrusions were a result of random movements. This suggests that many intrusions are intentional, but the motivation for these interactions 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. Though it has not been observed in Bald Eagles, helping behaviour may arise in populations as a result of ecological constraints (Emlen 1982). In a population at saturation, breeding adults may increase fitness by allowing offspring to assist with chick rearing, and juveniles benefit via inclusive fitness and from the skills learned while helping (Emlen 1982). It is possible that breeding Bald Eagles tolerate juvenile intruders when they are offspring from previous years. More likely, the differential response toward juvenile and adult intruders relates to the motive of the latter age group. Intrusion has been linked to mate death and mate replacement in Bald Eagles (Grubb *et al.* 1988, Jenkins & Jackman 1993). If a conflict between an adult intruder and a breeding adult results in the breeder's death, the intruder may replace that individual, thereby gaining a territory, a mate and a breeding opportunity. It is less likely that juvenile intruders are motivated by the possibility of acquiring a territory, as they will not have use for a breeding territory until they reach reproductive maturity. Further research on the frequency of intrusion-related breeder deaths and the aftermath of such events is necessary to examine mate replacement and territory takeover as a potential motivator of adult intruders.

In this population the probability of nest failure is highest in the first two to three weeks after hatching (Turrin 2013), therefore we would expect intrusions during this period to pose the greatest threat to nest success. If an intruder breaks up a breeding attempt, there may be a future breeding opportunity via extra pair copulation or mate replacement. Interestingly, there was no apparent difference in intrusion rates of juvenile and adult-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 do not target the period of highest nest failure. Furthermore, despite the observed intrusions none of the study nests failed, though our sample size was insufficient to draw any conclusions about population-level effects of intrusion. Though documented cases are rare, there is anecdotal evidence from multiple Bald Eagle populations that intraspecific intruders kill nestlings. In the Chesapeake Bay, infanticide has been recorded by nest cameras at sites on the James River in 2002 (Markham & Watts 2007), at Aberdeen Proving Ground in 2009 (unpubl.), and at Blackwater National Wildlife Refuge in Maryland in 2012 (unpubl.). Collectively, these anecdotes indicate that conspecific intrusion can result in infanticide and brood loss, though the lack of supporting evidence from our observational study suggests that these events may be rare in the population. Given the episodic and unpredictable nature of intrusion, we are not currently able to broadly measure the relationship between intrusion frequency and the frequency of nest failure.

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SAMENVATTING

De groei van populaties wordt door tal van mechanismes gereguleerd, waaronder dichtheidsafhankelijke concurrentie om voedsel en nestplaatsen. Dat laatste is vooral voor territoriale soorten, waaronder de Amerikaanse Zeearend *Haliaeetus leucocephalus*, de uiteindelijke begrenzer van de groei. Naarmate er meer arenden bijkomen, terwijl het aantal nestplaatsen beperkt is, neemt de kans op sterfte onder volwassen vogels toe, of anders neemt de reproductie wel af doordat de oudervogels moeite hebben hun jongen te voeden en te beschermen. De populatie Amerikaanse Zeearenden in de Chesapeake Bay in de oostelijke Verenigde Staten groeit al minstens 30 jaar. In de vroege jaren negentig wisten nog bijna alle arenden die de reproductieve leeftijd bereikten direct een territorium te verwerven. In 2013 was dat nog maar 17%. Tegenwoordig kunnen gemiddeld vier van de vijf vogels tot de niet-broedende populatie worden gerekend, de zogenaamde *floaters*. In dit onderzoek wordt gekeken naar de invloed van *floaters* binnen de lokale populatie, bezien vanuit het perspectief van de broedvogels. Welke vogels dringen hoe vaak en wanneer het nestgebied van een paar binnen en hoe reageren de broedvogels op die inbreuk? Gebaseerd op eerdere waarnemingen werd de aandacht vooral gericht op de eerste drie weken na het uitkomen van de eieren, omdat broedpogingen het vaakst in die periode mislukten. Daarbij wordt ervan uitgegaan dat een binnendringer gebaat is bij het mislukken van een broedpoging. Dat vergroot immers de kans op overname van het territorium, zeker als één van de broedvogels de dood heeft gevonden. Door telkens drie uur achtereen de nesten te observeren, gespreid over het broedseizoen (voorafgaande aan de eileg, tijdens de incubatieperiode en in de jongenfase) en over de dag, werd een indruk verkregen van het aantal niet-broeders dat op minder dan 500 m van het nest passeerde (hier gelijkgesteld met een binnendringing van de nestomgeving). Op 540 waarnemingsuren kwam dat 163 keer voor, maar er werden grote verschillen per nest gevonden en de incidentie van binnendringing was erratisch. Gemiddeld vond eens per 3.5 uur een grensoverschrijding plaats. Voor volwassen *floaters* lag dat op eens per 8.3 uur. Juveniele arenden kwamen gemiddeld dichter in de buurt van nesten dan niet-broedende volwassen arenden. Die laatste konden bovendien vaker op een reactie van de broedvogels rekenen (78% tegen 47% van de juveniele vogels). De reactie op een binnendringer was minder uitgesproken als slechts één oudervogel op of bij het nest zat. Bij aanwezigheid van beide oudervogels kon de *floater* die te dicht in de buurt van het nest kwam een fellere reactie tegemoet zien (meestal van het mannetje). Hoewel de verliezen op het nest het grootst waren in de drie weken na het uitkomen van de eieren, werd voor die periode geen verschil in de frequentie van binnendringing van het nestgebied gevonden voor adulte en juveniele niet-broeders. Dat lijkt er niet op te wijzen dat volwassen *floaters* specifiek de gevoelige fase binnen de broedcyclus uitkiezen om zich in de broedpopulatie binnen te knokken. Daar komt bij dat dit onderzoek geen nestverliezen constateerde tijdens de periode van observatie, hoewel er anekdotische informatie bestaat die bewijst dat nestjongen door vreemde soortgenoten kunnen worden gedood. Misschien dat infanticide weinig voorkomt bij Amerikaanse Zeearenden, al kan de steekproefgrootte ook een rol spelen bij het al dan niet constateren van infanticide. (RGB)

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