

OBSERVER EFFECTS ON COMMON GOLDENEYE NEST DEFENSE¹MARK L. MALLORY² AND PATRICK J. WEATHERHEAD

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Key words: *Bucephala clangula*; *Common Goldeneye*; *observer effects*; *nest defense*.

Many factors are predicted to influence bird responses to nest predators (Montgomerie and Weatherhead 1988). The best studied of those factors is offspring age. From the time an egg is laid until the young fledges, the value of that offspring to the parent increases (Andersson et al. 1980). Studies have supported the prediction that parents should defend their offspring more vigorously as offspring get older (reviewed by Montgomerie and Weatherhead 1988, Redondo 1989). Thus, patterns of increasing defense through a nesting cycle might be considered the cornerstone of nest defense research. Knight and Temple (1986) challenged that cornerstone by demonstrating that the defensive behavior of parents appears to be positively reinforced as a result of repeated nest defense trials. In nest defense studies, each trial ends with the observer and/or model predator departing, leaving the nest unharmed. Thus, the defensive behavior of the parents was "successful" and is reinforced. Because many earlier studies of nest defense involved repeated visits to nests, Knight and Temple proposed that the increase in nest defense with offspring age may have been an artifact of repeated visits rather than confirmation of a prediction from parental investment theory. Many studies have now tested this alternative hypothesis (e.g., Breitwisch 1988, Weatherhead 1989, Westneat 1989) and collectively have found little evidence of positive reinforcement. Here we show that repeated visits to Common Goldeneye (*Bucephala clangula*) nests do appear to affect nest defense, albeit in a manner somewhat different from that demonstrated by Knight and Temple (1986).

METHODS

Common Goldeneyes are cavity-nesting ducks that breed primarily in the boreal forest (Bellrose 1980). Individuals typically have one annual nesting attempt (Zicus 1990). We studied a nest-box population of goldeneyes nesting on small (< 20 ha) lakes near Sudbury, Ontario (Mallory et al. 1993). Because of the isolation of our study lakes, nesting females probably experienced no human disturbance at the nest box during the breeding season other than our nest visits. Predation on goldeneyes was generally low (Mallory, unpubl.), so we suspect that disturbance from mammalian

predators was low. During 1989, 1990 and 1992, we observed the behavior of incubating goldeneyes as we approached the nest box. We recorded our distance from the nest when the female flushed, the estimated distance she flew before landing, any vocalizations given in flight, and whether the female subsequently performed any distraction displays. These behaviors covaried strongly (for example, all females that flushed when the observer was at the base of the tree vocalized, and almost every female exhibiting distraction displays did not flush until the observer was climbing the tree), so we grouped them into seven nest defense categories (Table 1). We include flushing distance in our index of nest defense because it involves the necessary trade-off (Montgomerie and Weatherhead 1988) between a risk to the female (i.e., flushing too late could endanger her life) and benefit to the young (i.e., delaying flushing reduces the chance of drawing attention to the nest if the predator has not detected it). Note that nest defense data were not collected on every visit, but we always knew the number of previous visits to the nest box. We determined the stage of incubation on each visit from known initiation dates or by backdating from hatch (Mallory et al. 1993). Natural variation in initiation dates and irregularities in our schedule of nest checks resulted in substantial variation among nests in the patterns of cumulative nest visits through incubation.

Nest checks involved a variety of activities, from simply counting and weighing the eggs, to banding females and installing automated incubation monitors (Mallory and Weatherhead 1992). We considered these latter two activities to constitute "major" disturbances, while all other visits to the nest box were considered "minor" disturbances. For consistency, in all subsequent analyses we consider only data collected from minor disturbances. Following many of these distur-

TABLE 1. Scoring procedure for nest defense behavior. Flushing distance refers to how far away the observer was from the female when she flushed.

| Score | Flushing distance (meters) | Landing distance (meters) | Other |
|-------|----------------------------|---------------------------|---------------------|
| 1 | >10 | out of sight | |
| 2 | >10 | 50-100 | |
| 3 | <10 | 50-100 | |
| 4 | >10 | 50-100 | Vocalization |
| 5 | <10 | 50-100 | Vocalization |
| 6 | Base of tree | <50 | Vocalization |
| 7 | On tree | <30 | Distraction display |

¹ Received 24 August 1992. Accepted 21 December 1992.

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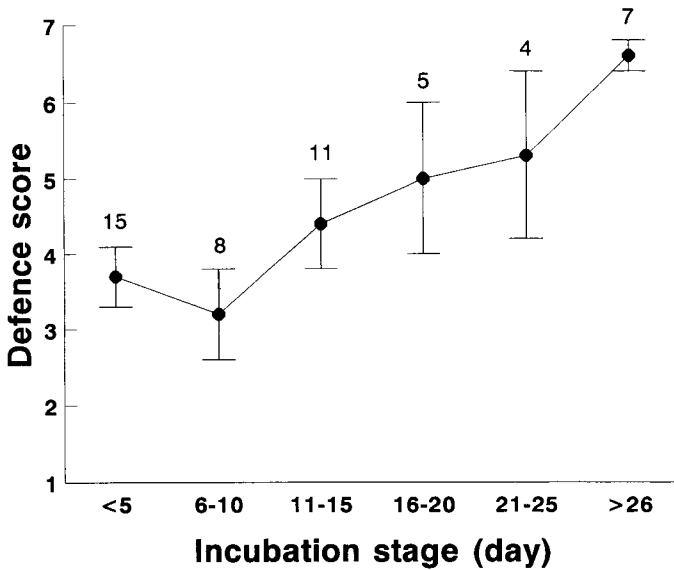


FIGURE 1. The pattern of nest defence (mean score \pm SE) by female goldeneyes during different stages of incubation. Numbers above error bars are the number of females sampled at each time period. No female was represented more than once at any stage.

bances, the elapsed time from flushing the female until she re-entered the box was recorded either electronically by the incubation monitors, or by a nearby, concealed observer. Because we obtained return times from several minor disturbances for many females, we were able to use these data as another index of nest defence and determine if the number of previous visits to the nest influenced return times.

All means are reported \pm SE, and all comparisons are made using nonparametric Wilcoxon tests unless otherwise noted.

RESULTS

We recorded nest defence scores for 29 female Common Goldeneyes. Nest defence increased during incubation (Fig. 1; Kruskal-Wallis, $\chi^2 = 18.9$, $n = 50$, $P = 0.002$), with females exhibiting distraction displays on the water only during the last six days of incubation. However, there was considerable variation in nest defence among females. On our initial nest visits, female defence scores ranged from one to six.

The observed pattern of nest defence (Fig. 1) could be attributable to three effects: (1) more vigorous defence as the value of young increases, (2) more vigorous defence in response to successful defense during previous observer visits, or (3) both of these factors. To determine if defense increased with incubation stage independently of the number of previous visits to the nest, we ideally would use defense scores on our initial visits to each nest. However, data from initial visits were collected early in incubation, and thus did not cover a broad enough range of incubation stages for a reliable test. Data from second and third visits occurred through much of incubation (day 7 to 30), and the incubation stage when second or third visits occurred did not differ ($P > 0.2$). Thus, we pooled data from

these nest visits. No female was represented more than once in these data. Consistent with the offspring-value hypothesis, nest defence tended to increase through the nesting cycle ($r_s = 0.47$, $n = 16$, $P = 0.06$).

To determine whether the number of previous visits affected the intensity of nest defence, we compared defence scores of females observed between day 10 and day 14 relative to the number of previous visits. We chose this time period because it provided the largest sample of nests within a short time interval that had variation in the number of previous visits. Females that had not been visited previously tended to respond less vigorously ($\bar{x} = 3.8 \pm 0.6$, $n = 9$) than females that had been visited previously ($\bar{x} = 5.4 \pm 0.4$, $n = 5$; $Z = 1.66$, $P = 0.097$). Although the sample sizes are small, this trend suggests that a previous visit to the nest by the observer may have influenced goldeneye defense behavior.

We recorded return times following minor disturbances of 12 females. Return times were unrelated to incubation stage for initial nest visits ($r_s = 0.36$, $n = 8$, $P = 0.39$) or for all nest visits ($r_s = 0.16$, $n = 28$, $P = 0.42$). However, return times of females that had not been visited previously tended to be shorter ($\bar{x} = 122 \pm 14$ min, $n = 8$) than those of females visited previously ($\bar{x} = 165 \pm 18$ min, $n = 20$; t -test, $P = 0.06$). After the initial nest visit, return times did not increase with increasing number of visits ($r_s = 0.14$, $n = 10$, $P = 0.6$).

DISCUSSION

As incubation proceeded, female Common Goldeneyes exhibited stronger nest defence behavior, supporting the prediction that nest defence should increase as young become more valuable. We also found that the intensity of nest defence behavior (particularly on

our initial visits) was highly variable among females, as has been found in many other birds (e.g., Montgomerie and Weatherhead 1988, Winkler 1992). The only stage during incubation where all females exhibited a similar intensity of defense (i.e., distraction displays) was the last six days of incubation. This stage corresponds approximately to the time when chicks are moving and making sounds inside the eggs (M. L. Mallory, pers. observ.). This cue may trigger the stronger defense behavior in all females because this is the first time during incubation that females can determine whether their efforts to date have been successful, and that further nest defense is for viable offspring.

The results from both the defense scores and return times suggested that the number of visits to the nest by the observer may have influenced Common Goldeneye nest defense behavior. Nevertheless, the two results appear contradictory. Defense scores of females that had been visited previously tended to be higher than for females visited for the first time, consistent with the positive reinforcement hypothesis of Knight and Temple (1986). However, if female goldeneyes respond to successfully repelling the observer by stronger nest defense on the next visit, then females should have returned more quickly to their nests after a disturbance if they had been visited previously. In fact, the opposite seemed to be true.

It is possible to reconcile these apparently contradictory results by reinterpreting the positive-reinforcement hypothesis. Although positive reinforcement is one reason that birds might defend their nests more vigorously as a result of previous visits to the nest, another reason is that the birds might learn to recognize humans as more serious potential threats to their clutch. Birds should defend their nest more vigorously against animals that are greater threats (Montgomerie and Weatherhead 1988). Female goldeneyes may learn to recognize humans as potentially more dangerous after seeing them climb the nest tree and open the box, even though the eggs were unharmed. Knight et al. (1987) offer a similar explanation for the difference in response to humans exhibited by rural and urban American Crows (*Corvus platyrhynchos*). Consistent with our interpretation, when we excluded data from first visits, we found no increase in return times following disturbance with increasing number of visits. Breitwisch (1988) also found that the only significant effect of prior visits to the nest in Northern Mockingbirds (*Mimus polyglottos*) resulted from the low response of males on the initial nest visit, although Weatherhead (1989) found no similar pattern in Song Sparrows (*Melospiza melodia*).

Our study was based on a relatively small sample of goldeneyes, and thus trends in nest defense may have been obscured somewhat by high variability in defense between females. Despite this limitation, our results suggesting an observer effect on nest defense behavior indicate two research needs. First, experiments are re-

quired to determine whether other instances of observer effects are best interpreted as positive reinforcement or as the parents learning to recognize the "threat" as something dangerous. Second, and perhaps related to the first need, is to determine why observer effects are documented in some studies and not in others.

We thank Jason Reaume, Don McNicol, Don Morgan, Mark Wayland, Bob Webster and especially Russ Walton for assistance with this project, and David Westneat for his review of the manuscript. Financial support was provided by the LRTAP Program of Environment Canada, the Wildlife Toxicology Fund (World Wildlife Fund Canada), Noranda Inc., a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to PJW, and a NSERC graduate scholarship to MLM.

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