

# RISK-TAKING BY INCUBATING COMMON GOLDENEYES AND HOODED MERGANSERS<sup>1</sup>

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**Abstract.** We studied nest defense by Common Goldeneyes (*Bucephala clangula*) and Hooded Mergansers (*Lophodytes cucullatus*) nesting near Sudbury, Canada between 1989–1995. As incubation proceeded, female Common Goldeneyes took greater risks by allowing the observer to approach the nest more closely before flushing, landing closer to the nest after flushing, vocalizing more commonly when flushed, and giving more broken wing or distraction displays. Hooded Merganser females exhibited relatively strong defense at all stages, including giving distraction displays much earlier in incubation. An index of all four behaviors increased for each species as incubation proceeded. Nest defense by these cavity-nesting ducks differed from patterns known for ground-nesting waterfowl, perhaps due to effects of nest location, predation type and intensity, and nest parasitism. Future nest defense studies should consider the overall suite of behaviors that comprise parental strategies for defending their nests and/or offspring.

**Key words:** *Bucephala clangula*, cavity-nesting, Common Goldeneye, Hooded Merganser, *Lophodytes cucullatus*, nest defense.

## INTRODUCTION

Egg-laying and incubation expose female birds to a variety of risks, perhaps the greatest being predation on the female or her clutch (Montgomerie and Weatherhead 1988). When females defend their nests against predators, they face a tradeoff: decreased risk of clutch predation (Andersson et al. 1980) vs. increased risk of injury or death which affects future prospects for breeding (Curio and Regelman 1985). The costs and benefits associated with this tradeoff will be determined in part by the current value of the clutch, which generally increases with clutch size and as incubation proceeds (Montgomerie and Weatherhead 1988). Females are therefore expected to defend larger clutches more rigorously and to increase their efforts as incubation proceeds (Montgomerie and Weatherhead 1988).

One group of precocial birds that has received little attention in nest defense research is waterfowl, particularly cavity-nesting ducks. They lack adequate physical features that could serve

as “weapons” (Montgomerie and Weatherhead 1988) in active defense against most predators, so their nest defense behaviors may rely on other tactics. One tactic is to remain on the nest in the presence of a predator. This protects the clutch by not drawing attention to it, but puts the female at greater risk because it reduces her time to escape if the predator gets too close (Forbes et al. 1994). A second defense tactic is to perform a distraction display. A series of behaviors can be grouped under this tactic, ranging from vocalizations when flushed, to landing nearby on the water, to the familiar “broken wing” displays exhibited by many species (Montgomerie and Weatherhead 1988). The common element to all of these behaviors is that the female risks being captured by the predator. Nest defense theory predicts that she gauges the level of acceptable risk by the current value of her clutch.

In this paper, we quantify such risk-taking by incubating Common Goldeneyes (*Bucephala clangula*) and Hooded Mergansers (*Lophodytes cucullatus*), both cavity-nesting waterfowl. We monitored female behaviors during nest visits which simulated approaches by predators. In preliminary studies (Mallory et al. 1993a, Mallory and Weatherhead 1993), both species exhibited the risk-taking behaviors described

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above (remaining on the nest, vocalizing, landing nearby, and broken wing displays) during incubation. Our objectives in this study were to refine earlier analyses by examining each behavior independently in relation to incubation stage and clutch size, and to test several specific predictions regarding nest defense and nesting habits of these species. First, because female goldeneyes and mergansers could use any combination of the above four behaviors to defend their nest, we predicted that individual nest defense behaviors would exhibit similar changes in intensity through incubation, and thus that overall nest defense intensity would increase as incubation proceeded. Second, we examined whether nesting females appeared to alter their behavior in response to repeated visits to the nest by observers, because patterns of defense related to incubation stage might instead be explained by effects of previous visits on female behavior (Knight and Temple 1986). Finally, because nest parasitism is known to influence nest defense in some altricial species (Weatherhead et al. 1994), we analyzed whether nest defense was related to interspecific nest parasitism.

## METHODS

We collected data between 1989 and 1995 on risk-taking by female Common Goldeneyes and Hooded Mergansers nesting in nest boxes erected on small study lakes (generally < 20 ha) northeast of Sudbury, Ontario, Canada (46°54'N, 80°41'W). Characteristics of the study site and nest boxes are described in McNicol et al. (1987, 1997). Physical dimensions and position of the nest box site on the lake were similar among boxes. One box was erected per lake, and in almost all cases there was only one nesting female per lake (Mallory et al. 1993b; known exceptions occurred on two lakes with occupied natural cavities). Both species have one annual breeding attempt and incubation periods of about 30 days, and typically lay 8–10 eggs (Dugger et al. 1994, Eadie et al. 1995). The study site is at the southern boundary of the Common Goldeneye's breeding range but is in the northern third of the Hooded Merganser's breeding range (McNicol et al. 1995).

Females were studied intensively in 1989 and 1990 (Mallory et al. 1994, Wayland and McNicol 1994), with nest visits occurring as often as every 5 days during May and June. Nest boxes were not checked in 1991, but were checked

at least once during incubation (late May) each year between 1992 and 1995. Because of their isolation and the lack of sportfish in the majority of our study lakes, nesting females probably experienced no other human disturbance at the nest box during incubation. We did not measure disturbance by predators at the nest site, but successful predation was generally low (McNicol et al. 1997). Also, female age (i.e., residual reproductive value and breeding experience, which can influence nest defense) was not known for most females in this study, and thus its potential effects were not examined.

When we visited a nest, we observed the behavior of incubating females on our approach. We recorded the distance of the observer from the nest when the female flushed (estimated to 1 m), the estimated distance she flew before landing (estimated to 10 m, to 100 m if she landed > 100 m away), any vocalizations given in flight, and whether she performed any distraction displays. Because the nests of these species are located above the ground, we had to treat flushing distances somewhat differently than for ground-nesters (Forbes et al. 1994). When a female flushed from a nest box, we used the actual distance of the observer from the nesting tree as the score. However, if a female flushed when the observer was at the base of the tree or on the tree, we assigned scores to represent this "finer scale" behavior: "0.5 m" if the observer was at the base of the tree, "0.25 m" when the observer was climbing the tree, and "0.1 m" if the observer was opening the nest box.

To assess total nest defense, we ranked each of the four measured variables (flushing distance (range 1.5–71.5), landing distance (16–77), with closer distances ranked higher; vocalizations (24.5–67), with higher rank given to birds that gave calls; broken wing displays (39.5–82), with higher rank to birds that gave displays) for all first visit data among all females from both species within each behavior. We then divided ranks for each variable by the maximum rank for each variable, and added the resultant indices for each variable together for each female. These cumulative indices were then divided by the maximum cumulative index to generate a total composite nest defense index for each female, with a maximum value of 1.0. Note that this approach assumes equal weighting for each behavior; we considered this the most conservative approach

because there are no data on the relative value of each behavior to these species.

Nest defense data were not collected on every visit, but we always knew the number of previous visits to the nest. Variation in nest initiation dates and our schedule of nest visits resulted in nest defense data across the range of incubation stages. To determine the stage of incubation at the time of the nest visit, we used egg flotation (Alberico 1995) to estimate days to hatch (error in estimates for 61 eggs:  $-0.2 \pm 0.3$  days in first 20 days of incubation; unpubl. data). We determined hatching success (percent of eggs within each nest that hatched) on visits to the nest after incubation was complete.

#### STATISTICAL ANALYSES

Because some behaviors were not distributed normally (flushing distance, landing distance) and others were not continuous (vocalizations, distraction displays), we used nonparametric statistics for most analyses. To test for patterns in flushing distance, we used Kendall's Tau ( $\tau$ ) partial correlation to control for the weak but significant effects of Julian date (all  $P$ s  $< 0.05$ ), because observed patterns could have resulted from season (time of year) rather than incubation stage (Forbes et al. 1994). Kruskal-Wallis or Wilcoxon tests were applied for categorical variable comparisons. To examine composite nest defense indices, we used an ANCOVA (incubation stage as covariate). All means are reported  $\pm$  SE unless otherwise noted.

#### RESULTS

##### FIRST AND REPEAT VISITS

We were unable to detect any difference in defense data among years (Kruskal-Wallis tests on residuals of first visit flushing distance, landing distance, and vocalizations after controlling for incubation stage by regression, all  $P$ s  $\geq 0.2$ ), so all data were pooled. Using data from first visits to the nest only, female Common Goldeneyes tended to allow observers to approach closer to the nest before flushing as incubation proceeded ( $\tau = -0.149$ ,  $n = 49$ ,  $P < 0.1$ ), consistent with our predictions. However, using only data from the same year with repeat visits to nests, this pattern was reversed ( $\tau = 0.45$ ,  $n = 26$ ,  $P < 0.05$ ; data were insufficient for a similar comparison for Hooded Mergansers). This suggests that females that had been visited at least once earlier in incubation modified their natural re-

sponse and flushed while the observer was farther away on subsequent visits. Hereafter, all comparisons for both species use only data from first visits to the nest.

##### FLUSHING AND LANDING DISTANCE

Whereas female Common Goldeneyes flushed at closer distances as incubation proceeded (above), female Hooded Mergansers did not exhibit any significant difference in flushing distance through incubation ( $\tau = 0.11$ ,  $n = 27$ ,  $P > 0.1$ ). Lack of a significant trend was attributable to the fact that many female Hooded Mergansers (63% of first visits) did not flush until the observer was on the tree even though it may have been early in incubation (Fig. 1). For both species, females landed closer to the nest when they were flushed later in incubation (Fig. 1; Kruskal-Wallis tests: goldeneyes,  $H = 14.2$ ,  $P < 0.001$ ; mergansers,  $H = 7.3$ ,  $P = 0.03$ ). For goldeneyes, females that allowed the observer to approach closer before flushing also landed closer to the nest ( $H = 10.4$ ,  $n = 49$ ,  $P = 0.006$ ), although this was not true for Hooded Mergansers ( $H = 1.9$ ,  $n = 27$ ,  $P = 0.38$ ). Similar proportions of merganser (61%, 17 of 28) and goldeneye (43%, 21 of 49) females waited until the observer was on the tree before flushing (Fisher Exact test,  $P = 0.16$ ).

##### VOCALIZATIONS AND DISTRACTION DISPLAYS

For both species, females flushed from the nest vocalized more commonly later in incubation and when they landed closer to the nest (Table 1), consistent with distraction display behavior. Common Goldeneye females performed broken wing displays later in incubation (earliest display on day 23 of incubation), and these displays were associated with remaining on the nest longer before flushing and landing on the water closer to the nest (Table 1). Hooded Merganser females performed these displays much earlier in incubation (earliest display on day 12), and displays were not associated with closer flushing distances (because mergansers tended to remain on the nest at all stages of incubation), but females performing broken wing displays did land on the water close to the nest (Table 1). Note that these results are based upon small sample sizes (due to limited numbers of first visits late in incubation), so our results should be interpreted cautiously.

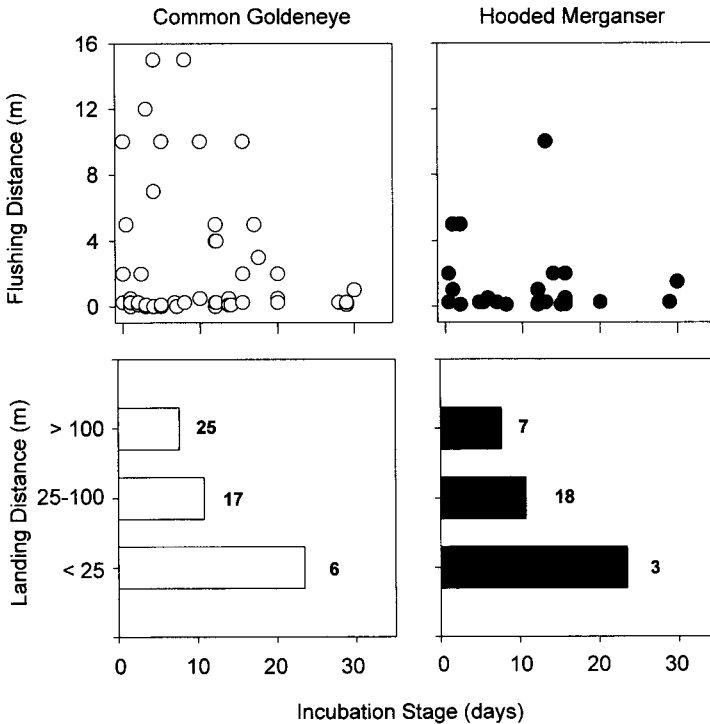


FIGURE 1. First visit flushing distance (m) and landing distance (m) for incubating female Common Goldeneyes and Hooded Mergansers in relation to incubation stage (days since the start of incubation). Numbers on bar charts are sample sizes.

#### COMPOSITE NEST DEFENSE

Although the above analyses described patterns in particular behaviors, we also were interested in the whole pattern of nest defense of each species (i.e., the combined effects of each of the four measured behaviors), and thus we generated a composite nest defense index. In a preliminary analysis, we included incubation stage and Julian date as independent variables in stepwise multiple regressions, but Julian date was not included as a significant predictor of the defense index. Composite nest defense increased as incubation proceeded for both Common Goldeneyes ( $r = 0.50$ ,  $n = 49$ ,  $P = 0.002$ ) and Hooded Mergansers ( $r = 0.49$ ,  $n = 27$ ,  $P = 0.006$ ), although there was clearly considerable variation among females, especially goldeneyes (Fig. 2). After controlling for the significant effect of incubation stage ( $F_{1,69} = 7.1$ ,  $P = 0.01$ ), mergansers tended to have higher composite nest defense scores than goldeneyes (Fig. 2; ANCOVA;  $F_{1,69} = 4.4$ ,  $P = 0.04$ ) in the first 20 days of

incubation (where data were well-represented for both species).

To test whether larger clutches were defended more vigorously and whether interspecifically parasitized clutches were defended less vigorously, we used the residual composite nest defense index (from above, after controlling for incubation stage) as our estimate of defense intensity, because this incorporated possible combinations of behaviors for each female. For goldeneyes and mergansers, there was no difference in defense intensity between nests with high or low clutch size or hatching success (Table 2, Wilcoxon tests,  $P_s > 0.1$ ). Furthermore, mean residual composite nest defense of parasitized goldeneyes ( $-7.0 \pm 7.7$ ,  $n = 19$ ) and mergansers ( $-0.5 \pm 4.5$ ,  $n = 16$ ) did not differ significantly from mean residual composite nest defense for unparasitized goldeneyes ( $5.2 \pm 6.7$ ,  $n = 34$ ) and mergansers ( $-1.4 \pm 5.4$ ,  $n = 11$ ), respectively (Wilcoxon tests, both  $P > 0.4$ ).

TABLE 1. A comparison of  $\bar{x} \pm SE$  ( $n$ ) incubation stage and nest defense behaviors among female Common Goldeneyes and Hooded Mergansers that did or did not give broken wing displays or did or did not vocalize when flushed from the nest box on first visits (Wilcoxon tests). Within each species, significant differences ( $P < 0.05$ ) between those that did and did not display are separated by an asterisk (\*).

Displays	Common Goldeneye			Hooded Merganser		
	Incubation stage (days)	Flushing distance (m)	Landing distance (m)	Incubation stage (days)	Flushing distance (m)	Landing distance (m)
No broken wing	8.7 $\pm$ 0.9 (53) *	3.2 $\pm$ 0.6 (53)	600 $\pm$ 70 (53) *	9.0 $\pm$ 1.2 (25)	1.3 $\pm$ 0.4 (25)	300 $\pm$ 80 (25) *
Broken wing	25.2 $\pm$ 3.8 (4)	0.4 $\pm$ 0.2 (4)	12.5 $\pm$ 3.2 (4)	18.3 $\pm$ 5.8 (3)	0.6 $\pm$ 0.4 (3)	16 $\pm$ 0.4 (3)
No vocalization	7.6 $\pm$ 1.1 (33) *	3.2 $\pm$ 0.9 (33)	700 $\pm$ 85 (33) *	7.6 $\pm$ 1.6 (15)	1.5 $\pm$ 0.7 (15)	400 $\pm$ 120 (15) *
Vocalization	13.0 $\pm$ 1.8 (25)	2.8 $\pm$ 0.8 (25)	300 $\pm$ 90 (25)	12.8 $\pm$ 2.0 (13)	1.4 $\pm$ 0.4 (13)	67 $\pm$ 10.5 (13)

## DISCUSSION

Both Common Goldeneyes and Hooded Mergansers exhibited increased intensity of some nest defense behaviors as incubation proceeded, and composite nest defense increased for both species. Furthermore, the four types of "risky" behavior tended to be well-correlated with each other; that is, females that allowed observers to approach closer to the nest before flushing were more likely to vocalize when flushed, land closer to the nest, and in some instances were more likely to perform distraction displays. Collectively, these results are consistent with predictions of nest defense theory (Montgomerie and Weatherhead 1988) and agree with results from other waterfowl species (Forbes et al. 1994).

It is important to note that our results are not simply an artifact of repeated visits to the nest, because we restricted analyses to data collected from first visits to each nest. In this study, female goldeneyes tended to flush when the observer was closer to the nest as incubation proceeded, but this relationship was opposite when data from repeat visits were used. Forbes et al. (1994) found similar responses to repeated observer visits in three of six ground-nesting waterfowl species. These patterns support the hypothesis that repeated visits to the nest can influence female bird behavior (Knight et al. 1987, Montgomerie and Weatherhead 1988). However, the results suggest that females do not habituate to visitors, nor do the behavioral responses follow the predictions of the positive reinforcement hypothesis, which is that females will respond with more vigorous defense with repeated visits (Knight and Temple 1986).

Despite the general agreement between our results and predictions from nest defense theory, we found considerable variation in defense behaviors among females and between species, particularly for flushing distances. High variability among females has been observed in many studies (Montgomerie and Weatherhead 1988). Forbes et al. (1994) also found that flushing distance and incubation stage were significantly correlated in only two of six ground-nesting waterfowl, although correlations were all in the expected direction. Clearly, many female Common Goldeneyes and especially Hooded Mergansers exhibited relatively strong defense early in incubation (e.g., remained on the nest until the observer was very close; Fig. 1),

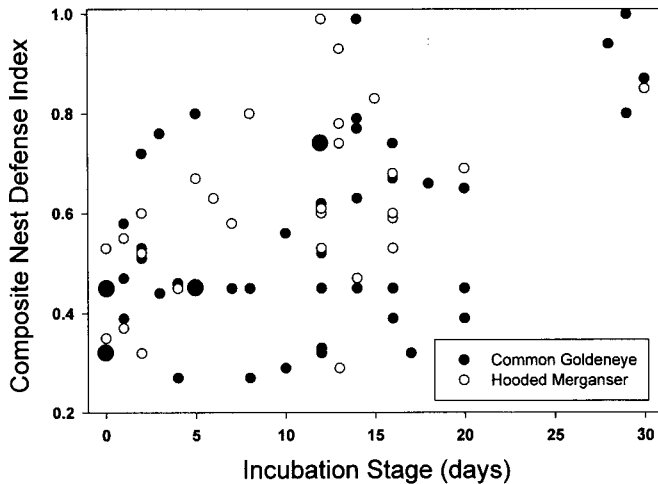


FIGURE 2. Composite index of total nest defense for Common Goldeneyes and Hooded Mergansers plotted against incubation stage (larger dots represent two identical scores). The index was derived from cumulative ranks of flushing distance, landing distance, vocalizations, and broken wing displays, and then converted to an index when divided by the maximum cumulative rank. For both species, composite nest defense increased through incubation (both  $r \geq 0.49$ ,  $P < 0.01$  for first 20 days where data are well represented).

whereas others flushed while the observer was at some distance.

We do not know why flushing distance varied among females so much through incubation, but we acknowledge two potential confounds that we could not assess. First, because we did not have a marked population for most of the study, it is possible that some of the females exhibiting high defense early in incubation had experience with observers from a previous year that affected their response in a subsequent year. Less than half of the females, however, appeared to survive and return each year based on observations in 1989 and 1990 (Mallory et al. 1994), so the majority of females were naive in this respect. Moreover, after 1990 most females would have been visited only once during incubation in a year. Second, some females may rely more on other behaviors or a combination of behaviors than relying primarily on flushing for nest de-

fense, as suggested by Forbes et al. (1994). Our study supports the hypothesis that females use a combination of behaviors, given that nest defense behaviors were positively correlated with each other, but an experimental study would be required to evaluate the role of each tactic in overall defense.

We found some interesting differences in nest defense between these two species. Whereas Common Goldeneye females generally behaved in agreement with predictions of nest defense theory, Hooded Merganser females did not exhibit the expected relationship between incubation stage and flushing distance. Although they took greater risks with some behaviors as incubation proceeded, compared to goldeneyes, mergansers exhibited relatively low variation and high defense at all stages (Fig. 2), including giving distraction displays on the water before incubation was half-complete. Life history pat-

TABLE 2. Mean  $\pm$  SE ( $n$ ) clutch size and hatching success of female Common Goldeneyes and Hooded Mergansers that exhibited varying degrees of nest defense intensity (measured by residual composite nest defense index – high is positive and low is negative residual) on their initial flush from the nest box (after controlling for incubation stage). There were no differences within species.

	Common Goldeneye		Hooded Merganser	
	Clutch size	Hatching success (%)	Clutch size	Hatching success (%)
High	8.2 $\pm$ 0.4 (24)	77.8 $\pm$ 8.4 (24)	9.4 $\pm$ 0.5 (13)	87.1 $\pm$ 7.8 (13)
Low	9.3 $\pm$ 0.4 (25)	75.8 $\pm$ 7.4 (25)	10.8 $\pm$ 1.0 (14)	87.0 $\pm$ 7.1 (14)

terns apparently do not explain this difference as they may for other waterfowl (Forbes et al. 1994), because both species typically have one annual nesting attempt, similar sized clutches, similar survival rates, and similar longevity records (Dugger et al. 1994, Eadie et al. 1995). In the absence of additional, comprehensive life history information, relatively strong nest defense by Hooded Mergansers appears to be another curious aspect of this species' unusual breeding biology (Mallory et al. 1993a, Dugger et al. 1994).

We detected no significant relationship between nest defense intensity by either species and nest parasitism, clutch size, or hatching success. According to parental investment theory, larger clutches should generally be more valuable because they represent a greater return for the current reproductive attempt (Montgomerie and Weatherhead 1988). Consistent with theoretical predictions, Forbes et al. (1994) found that three of six prairie duck species decreased flushing distance with increased clutch size. We have two possible explanations why we failed to detect a relationship between clutch size and nest defense. First, in goldeneyes and mergansers, intra- and interspecific nest parasitism and thus variable clutch sizes are regular features of their breeding strategies (Dugger et al. 1994, Eadie et al. 1995), unlike the ground-nesting species studied by Forbes et al. (1994). Because much intraspecific nest parasitism is undetected (Eadie et al. 1995), the clutch sizes we observed may not reflect the real reproductive effort of the female. Related to this point, nest and hatching success are generally unaffected in goldeneyes for clutches of 16 or fewer eggs (Eadie et al. 1995; > 90% of clutches at our site are < 16 eggs, McNicol et al. 1997), and thus females might defend their nest with similar intensity despite having one or four additional, parasitic eggs. Second, for species that only have one annual nesting attempt and for which suitable nest sites are usually limited (Eadie et al. 1995; although they were clearly not limited in this study, McNicol et al. 1997), the relative influence of clutch size or nest parasitism on nest defense may be small in comparison to the importance of finding a site, and defending and incubating the clutch successfully. This small influence may not be detectable with the sample sizes available to us, and the effects of relatively

high breeding densities and nest parasitism rates found in this unique site (McNicol et al. 1997).

This study and that of Forbes et al. (1994) point to some interesting differences in nest defense within ducks (subfamily Anatinae). Although Forbes et al. (1994) found generally good support for a direct relationship between flushing distance and various measures of clutch value among ground-nesting waterfowl species, we found little support in Hooded Mergansers and weak but positive support in Common Goldeneyes. The difference between studies may be attributable to differences in nest location and main predators. Rates of predation are high on ground-nesting birds, including prairie waterfowl (Sargeant et al. 1984), whereas cavity-nesting birds generally experience lower predation rates (Martin and Li 1992). Thus, for ground-nesting ducks, assessing the risk from an approaching predator and flushing may be a key strategy in surviving to renest or breed another year. In contrast, flushing from a cavity while a predator is still on the ground may draw attention to the nest more often than it serves to save the female, because it is less probable that the predator will notice the cavity, and the female can probably escape once the predator begins to climb the tree. Revealing the nest location is clearly very costly for cavity-nesting species that cannot renest. Hence, flushing distance may not be as reliable a measure of nest defense in cavity-nesters as it is for ground-nesters.

This study supports the hypothesis that female cavity-nesting waterfowl would take greater risks to defend their clutch as clutch value increases, but we did find some differences between Common Goldeneyes and Hooded Mergansers among nest defense measures and through incubation. Our data also suggest that patterns of nest defense differ from ground-nesting waterfowl, and thus nest location may be an important factor influencing nest defense. Further studies on waterfowl should focus on the role of nest location, predatory species, predation intensity, and the role of alternative defense behaviors in overall defense strategies.

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