

Variation in nest defense in ducks: methodological and biological insights

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Studies of avian nest defense generally explain only a small proportion of the total variation in defense behavior. We explored two potential methodological sources of variation in nest defense in three species of ducks. One common method of quantifying nest defense rests on the assumption that different components of nest defense (e.g. flushing distance, distraction displays) are highly positively correlated. Defense behaviors we observed in this study were weakly related or unrelated to each other. Thus, the assumption of strong positive covariance between components of nest defense was not supported. We also considered the effect of repeated visits to the same nests on nest defense. Females of all three species took less risk defending their nests with repeated visits, and the effect of visit number on nest defense was greater than the effect of increasing value of nests associated with advancing incubation. Ducks appear to be different from other birds in the consistency with which they alter their nest defense in response to repeated nest visits. We propose that this could be a consequence of having nest predators that return to the vicinity of a nest if they were previously unsuccessful finding the nest, thus making repeated nest visits more dangerous to the ducks. By testing this or other hypotheses it should be possible to go beyond understanding the methodological implications of the effect of repeated visits on nest defense, and use this phenomenon to gain insight into the predator-prey interactions that underlie nest defense.

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When breeding birds are confronted with a potential predator near their nest, they generally respond by behaving in ways that reduce the probability of predation. Such nest defense behavior has been the subject of substantial research, testing both general aspects of life-history theory (Montgomerie and Weatherhead 1988, Redondo 1989), and specific issues such as whether parents value their offspring differently under different circumstances (e.g. when the probability of paternity varies (Weatherhead et al. 1994), or when the threat to the nest is from a brood parasite vs a predator (Sealy et al. 1998)). Although the extensive research on nest defense attests to the general success that has been realized in the applications mentioned, at least one important issue has not been resolved. A consistent feature of nest defense studies is that much of the

variation in the behavior remains unexplained, even when many independent variables are considered (Regelmann and Curio 1983, Montgomerie and Weatherhead 1988). Our goal in this study is to investigate two potential methodological sources of variation in nest defense, using prairie-nesting ducks as our study system. While meeting this goal should provide useful methodological guidance for future research, we expect that a more important achievement will be gaining insights into the biology of nest defense.

The first methodological issue we consider involves the way that researchers quantify nest defense. One common approach is to use a single behavior to quantify defense (e.g. Westneat 1989, Wiklund 1990, Forbes et al. 1994, Viñuela et al. 1995), even though nest defense usually involves several different behaviors. The

assumption here is that by scoring one component of nest defense (e.g. frequency of alarm calls), one has essentially scored all components of nest defense. However, if other components of defense do not covary with the behavior that is quantified, then substantial variation in that behavior is unlikely to be explained by factors that affect all aspects of nest defense.

Some indirect evidence suggests that it may be correct to assume there is strong covariation among different components of nest defense. For example, both alarm calls and approach distance by savannah sparrows *Passerculus sandwichensis* and song sparrows *Melospiza melodia* change in a similar fashion with increasing brood age (Weatherhead 1979, 1989). However, other indirect evidence suggests that the assumption may not always be valid. For example, Mallory and Weatherhead (1993) found that the time it took female common goldeneyes *Bucephala clangula* to return to their nest after a disturbance followed a different pattern from other aspects of nest defense over the incubation period. Some studies have examined covariation between nest defense components directly. Regelman and Curio (1983) found that three of four measures of nest defense were significantly correlated in the great tit *Parus major*, although these responses were still differentially sensitive to the influences of independent variables. Redondo and Carranza (1989) found that some components of magpie *Pica pica* nest defense were strongly correlated, while others were not. Our first objective in this study is to assess how components of nest defense are correlated, and whether the factors that influence nest defense affect all components of defense similarly.

The second methodological issue we consider was first raised by Knight and Temple (1986a), and involves how birds respond to repeated encounters with the same potential predator. Many early studies confirmed the prediction that nest defense should increase with nesting stage (i.e. offspring age) because as offspring get older, they become more valuable to their parents (Montgomerie and Weatherhead 1988). However, Knight and Temple (1986a) proposed that these results may be an artifact of repeated testing of the same individuals, so that nests that were tested later in the nesting cycle had also been visited more often. The increase in response through the nesting cycle may simply have been a consequence of researchers always leaving nests unharmed. Thus, defending parents may have perceived their defense to have been successful, and defended even more vigorously at the next encounter due to positive reinforcement. Most studies that have tested whether repeated trials at the same nest explain the increase in nest defense have failed to confirm Knight and Temple's (1986a, b) results. After controlling for repeat visits, nest defense has still been shown to increase with offspring age (e.g. Breitwisch 1988, Redondo and Carranza 1989, Weatherhead 1989, 1990, Westneat 1989).

Despite the general lack of support for Knight and Temple's (1986a) hypothesis, some studies of waterfowl have found an effect of repeated visits on nest defense, independent of nesting stage. Mallory and Weatherhead (1993) found that common goldeneye increased some forms of defense with more visits, but decreased other forms of defense. Forbes et al. (1994) found that where visit number influenced nest defense of some dabbling ducks, the direction of the relationship was opposite to that predicted by Knight and Temple (1986a). In Canada geese *Branta canadensis*, however, Sjöberg (1994) found no effect of repeated visits on nest defense. These waterfowl studies differed in the type of nesting habitat and in the variables used to score nest defense. Nonetheless, it appears that repeatedly visiting waterfowl nests can sometimes affect subsequent nest defense. It is easy to avoid the problem of repeated visits affecting nest defense either methodologically or statistically. However, this overlooks the interesting biological question of why waterfowl sometimes behave differently when their nests are visited more than once. Thus, our second objective was to determine whether repeated visits affected nest defense in three species of dabbling ducks, whether any effect was consistent among species, and to consider why some waterfowl should respond differently from other birds to repeated nest visits.

We investigated nest defense in three species of dabbling ducks: blue-winged teal *Anas discors*, gadwall *A. strepera* and mallard *A. platyrhynchos*. We selected ducks for this study for several reasons. First, as discussed above, repeated nest visits have been reported to affect nest defense by ducks. Second, the great majority of past research on nest defense has focused on passerine birds, so broadening the scope to include other taxa seems likely to be informative. Finally, ducks are well suited to research on nest defense. Predation is responsible for the failure of a large proportion of dabbling duck nests (Sargeant and Raveling 1992) and is also a significant source of mortality of adult female ducks during the nesting season (Sargeant 1972, Greenwood et al. 1995). Thus, nest defense by ducks appears to satisfy the prerequisites of involving both potential benefits to the parents (i.e. protecting their nests) and significant risks (i.e. their own mortality).

Methods

Study area and general methods

We conducted this study in 1997 in Sheridan and Wells counties of central North Dakota. Much of this work was done within Lonetree Wildlife Management Area in a study area of 100 km². Other state-managed lands and private or federal lands that were within 35 km of the main site and which included similar habitat were

also used. All the sites we used in the study were grasslands, with wetlands of various sizes interspersed throughout.

Our study was conducted in conjunction with a larger study investigating the effects of mammalian predation on duck nesting success, which allowed us to use nests found as part of that project in our study. The same protocols were followed for all nests up to the point that our data collection was complete. Sites were searched for nests between 0800 hours and 1400 hours beginning in early May and continuing until late June. Nests were found by driving two all terrain vehicles with a 30 m length of chain suspended between them through fields with appropriate nesting habitat. This caused ducks to flush but did not harm nests. Nests were found by searching the area from which ducks flushed as the chain passed over them.

Nests of mallard, gadwall and blue-winged teal found on a given day were alternately assigned to one of two groups to be visited either every fifth day or every tenth day. Eggs were candled to estimate the current stage of incubation (Weller 1956). Because nest desertion is more likely when nests are disturbed during laying or early incubation (Gloutney et al. 1993), nests found during laying were not checked again until the predicted fifth day of incubation. We recorded wind speed, air temperature, and time of day at each nest visit.

Scoring nest defense

Excluding the visit when a nest was discovered, we scored nest defense in response to a human observer approaching the nest. This takes advantage of the fact that ducks respond to humans at their nest as predicted by life-history theory (Forbes et al. 1994). We considered nest defense to be any behavior in the presence of a predator (real or simulated) that may be a risk to a female, while potentially improving the chances her offspring will escape predation. Female ducks perform active defense, such as injury-feigning displays that can draw a predator's attention away from the nest (e.g. Brunton 1990). Another form of nest defense by incubating ducks is to remain on the nest despite the approach of a predator. By remaining on the nest, the cryptically colored hen decreases the likelihood that the nest will be detected. However, the risk to the female of being captured increases as the predator gets closer. Predation of nesting female ducks is common (Johnson and Sargeant 1977, Sargeant et al. 1984). Thus, the distance at which a female flushes from the nest as an observer approaches is a useful measure of nest defense (Forbes et al. 1994, Guinness et al. 2001).

On each visit to a nest, a lone observer slowly approached the nest on foot. The observer always approached from downwind to avoid the formation of trails to nests visited multiple times, and because we

assumed this method approximated the direction of approach of real mammalian predators. When incubating birds were on the nest, the observer measured the distance from the nest when the female responded (hereafter called the flushing distance) and estimated the nearest landing distance after the female flushed from the nest (if she landed within sight of the observer). When an incubating female was not present we assumed she was on an incubation break and repeated the trial later that day or the next day. When the female was present the observer also recorded whether the bird was aggressive to the observer (the few instances of aggression involved pecking at the observer before leaving the nest), whether the bird vocalized as she left the nest, whether she flew overhead while the observer was at the nest, and whether she performed distraction displays upon landing. Recording these defense behaviors as binary responses (present or absent) seemed appropriate because the behaviors were not performed in many trials (see below). This approach also standardized data recording among the several observers who performed trials. Reducing these behaviors to binary variables potentially overlooks meaningful variation in the behaviors when they were performed. However, our primary goal was simply to determine whether the performance of one behavior was independent of the other behaviors.

Data analysis

We transformed flushing distance to achieve normality for analysis with parametric statistics ($\ln[\text{flushing distance} + 1]$; Zar 1984). Landing distance created a problem because females often flew out of sight immediately after flushing. We arbitrarily assigned a landing distance of > 150 m in these trials because it was beyond any distance at which a female might be able to affect activity at the nest. Because this arbitrary score made the distribution of landing distances highly skewed, we converted landing distance to an ordinal variable (1 = landed < 25 m from observer, 2 = landed 26–75 m from observer, 3 = 76–150 m from observer, 4 = > 150 m or out of sight of observer).

All statistical analyses were performed using the statistical software JMP (SAS Institute 1994). Statistical significance was accepted at $\alpha \leq 0.05$. Unless otherwise stated, we performed each analysis for each of the three species.

Results

We collected data from 97 mallard nests, 82 gadwall nests and 174 blue-winged teal nests. Numbers of observations per nest averaged 1.94 ± 1.07 (range = 1–6, total = 216) for mallard, 1.54 ± 0.74 (range = 1–3, to-

tal = 138) for gadwall and 1.84 ± 1.05 (range = 1–6, total = 348) for teal. Only blue-winged teal were ever aggressive toward an observer, and teal also performed distraction displays more than the other species (Table 1). Overhead flights and vocalizations were performed infrequently by all three species.

Covariation among behaviors

The general prediction we test is that as one component of nest defense becomes riskier, other components should also become riskier. Thus, flushing and landing distances should be positively correlated with each other, but negatively correlated with distraction displays. We restricted analysis to flushing distance, landing distance and distraction displays because the other behaviors were performed so infrequently (Table 1). To assess the relationship between flushing and landing distance we used Spearman correlation. To determine whether distraction displays were performed independently of flushing or landing distance we compared distances in trials with and without distraction displays using Mann-Whitney U-tests. To ensure independence of the data we restricted these analyses to observations from second visits to nests.

For blue-winged teal and mallards, the distance that a hen flushed from her nest was unrelated to how far from the nest she landed ($r_s = 0.09$ and -0.03 , $P = 0.27$ and 0.81 , respectively). However, gadwall hens landed further from the nest when they flushed further from the observer ($r_s = 0.28$, $N = 79$, $P = 0.01$). Flushing distance varied independently of whether or not a duck performed a distraction display in teal and mallards ($z = -0.84$ and -0.02 , $P = 0.40$ and 0.98 , respectively). However, both teal and mallards landed closer to the nest when they performed distraction displays ($z = -2.20$ and -3.82 , $P = 0.03$ and 0.0001 , respectively). Gadwall performed distraction displays too infrequently (Table 1) to warrant analysis.

Effect of multiple nest visits

To assess how multiple visits affected nest defense we analyzed each of the three principal variables (flushing distance, nearest landing distance, distraction displays)

separately. It was necessary to control for incubation stage because it obviously also varies with the number of visits to a nest, and is also expected to affect nest defense (Montgomerie and Weatherhead 1988). Preliminary investigation of the potential influences of wind, temperature and time of day on nest defense indicated that these factors did not significantly influence any nest defense behavior.

Flushing distance

To test the effects of incubation stage and number of previous visits on flushing distance, we extracted subsets of the data such that one variable was constant within each subset. For example, all second visits were extracted so that there was only one observation per female and thus no variation in visits. We then used simple linear regression to examine the relationship between incubation stage and flushing distance. We repeated this approach with three unique subsets of data with number of visits held constant and three unique subsets of data with incubation stage held constant. These analyses showed that flushing distance increased with increasing number of visits to blue-winged teal nests (Table 2). For both mallard or gadwall, however, only one of the three tests indicated that the ducks flushed significantly further from the observer with increasing number of visits, although the trend was in this direction for all tests. These analyses also indicated that flushing distance decreased with advancing incubation in blue-winged teal, but failed to show an effect of incubation on flushing distance for mallard or gadwall (Table 2).

The preceding analyses show that female ducks generally responded to repeated nest visits by flushing further from the observer, and in some cases flushed closer to the observer as incubation progressed. To determine which of these two factors influenced flushing distance the most we used a binomial test to compare the number of birds whose response increased over time with the number of birds whose response decreased over time, for females visited at least twice. If incubation stage had the greater effect, more birds would show a decrease in flushing distance. If the number of visits had the greater effect, more birds would show an increase in flushing distance. These binomial tests indicated that significantly more females

Table 1. Frequencies and means of behavioral observations. The modal measurement is presented for nearest landing distance because it is a categorical variable. Binomial variables are presented as frequencies (percentage of total observations). All calculations are based on second visits only, so each female is included only once.

Species	N	Mean flushing distance (m)	Modal landing distance	Frequency of distraction displays	Frequency of overhead flights	Frequency of vocalizations
Blue-winged teal	170	1.41	1	35.3%	3.5%	5.3%
Gadwall	81	3.08	4	2.5%	6.2%	2.5%
Mallard	96	3.46	4	18.7%	9.4%	7.3%

Table 2. Simple linear regression models of the effect of incubation on flushing distance with visit number held constant and of the effect of visit number on flushing distance with incubation stage held constant. Only one observation per nest is included in each of these analyses.

Species	Test	Constant	N	r	F	P
Blue-winged teal	Incubation ^a	Second visits	169	-0.12	2.45	0.12
		Third visits	105	-0.35	14.07	0.0003
		Fourth visits	44	-0.46	11.12	0.002
	Visit ^b	7-9 days inc.	56	0.51	18.53	0.000
		14-16 days inc.	53	0.67	40.46	0.000
		18-21 days inc.	69	0.55	29.60	0.000
Gadwall	Incubation ^a	Second visits	81	-0.22	4.07	0.05
		Third visits	34	-0.07	0.15	0.70
		Fourth visits	15	-0.32	1.53	0.24
	Visit ^b	7-10 days inc.	29	0.26	2.03	0.17
		16-19 days inc.	16	0.43	3.14	0.10
		20-22 days inc.	20	0.56	8.03	0.01
Mallard	Incubation ^a	Second visits	96	0.01	0.01	0.91
		Third visits	62	-0.042	0.11	0.74
		Fourth visits	37	-0.15	0.85	0.37
	Visit ^b	12-14 days inc.	31	0.31	3.01	0.09
		18-19 days inc.	23	0.27	1.61	0.22
		22-23 days inc.	34	0.42	6.88	0.01

^a Visit number held constant.

^b Incubation stage held constant.

Table 3. Logistic regressions of the effect of incubation on probability of distraction display (DD = 1) with visit number held constant, and of the effects of visit number on probability of distraction display with incubation stage held constant. Only one observation per nest is included in each analysis.

Species	Test	Constant	N	R ²	Parameter	Wald χ^2	P
Blue-winged teal	Incubation ^a	Second visits	170	0.001	0.01	0.12	0.73
		Third visits	105	0.06	0.10	6.34	0.02
		Fourth visits	44	0.04	0.10	1.95	0.16
	Visit ^b	7-9 days inc.	56	0.03	-0.95	1.29	0.26
		14-16 days inc.	53	0.001	0.08	0.05	0.82
		18-21 days inc.	70	0.10	0.58	6.58	0.01
Mallard	Incubation ^a	Second visits	96	0.07	0.11	6.10	0.01
		Third visits	62	0.08	0.18	4.13	0.04
		Fourth visits	38	0.12	0.24	3.59	0.06
	Visit ^b	12-14 days inc.	31	0.12	-11.60	0.003	0.95
		18-19 days inc.	23	0.04	0.99	0.74	0.39
		22-23 days inc.	34	0.09	-0.71	2.73	0.10

^a Visit number held constant.

^b Incubation stage held constant.

of each of the three species increased rather than decreased flushing distance over time (blue-winged teal, 58 of 94 birds, $P = 0.01$; gadwall, 24 of 34, $P = 0.01$; mallard, 44 of 62, $P = 0.001$). This indicates that, for the sampling regime we used, the effect of visit number was more important than the effect of incubation stage in all three species. With a different sampling regime (e.g., more time between visits and thus a greater change in incubation stage), the relative effects of the two variables could change.

Landing distance

We repeated the procedure used above in the analysis of flushing distance to eliminate the problem of non-independence. Thus, we extracted subsets of the data such that either incubation stage or visit number was

constant within each subset, and then determined the effect of the other variable, in this case using Spearman correlation. All of these analyses failed to indicate any significant effect of incubation stage (mallard: all $P > 0.29$; teal: all $P > 0.14$; gadwall: all $P > 0.40$) or number of visits (mallard: all $P > 0.09$; teal: all $P > 0.28$; gadwall: all $P > 0.28$) on the distance that females landed after flushing.

Distraction displays

Logistic regression suggested that blue-winged teal and mallard hens were more likely to perform distraction displays later in incubation. The sign of the relationship was positive in all instances, although not all analyses were significant (Table 3). The analyses assessing the effect of visit number were less consistent, and only one

was significant (Table 3), indicating that the likelihood of a female performing distraction displays was generally unaffected by how often her nest had been visited. Note that gadwall were excluded from these analyses because they seldom performed distraction displays.

Discussion

Covariation among behaviors

Our first goal in this study was to determine the extent to which different components of nest defense covaried, and the consequent implications for quantifying nest defense. Of the three principal nest defense behaviors we recorded, flushing distance varied independently of landing distance and distraction displays in blue-winged teal and mallards, but was positively correlated with landing distance in gadwall. Performance of distraction displays by mallard and teal was unrelated to how far hens flushed from the observer, but when hens performed distraction displays they landed closer to the observer. The latter result makes sense, because a distraction display should be more likely to lead the predator away from the nest if the displaying duck is closer to the predator. However, the general conclusion from these results is that different nest defense behaviors performed by the same individual were often not highly correlated. Furthermore, analyses assessing how incubation stage and number of nest visits affected nest defense produced quite different results for flushing distance, landing distance and the occurrence of distraction displays. This lack of consistency in how each of these behaviors was affected by incubation stage and visit number confirms the weakness of correlations among them.

Theory predicts that parents should risk more for their nests as the value of the nests increases (Montgomerie and Weatherhead 1988). Although our results were inconsistent, some ducks tended to wait longer to flush and were more likely to perform distraction displays as incubation progressed, as predicted by theory. Previous research on ducks has shown that flushing distance varies with incubation stage as expected (Mallory and Weatherhead 1993, Forbes et al. 1994). If both flushing distance and distraction displays vary with brood value, it is unclear why they were unrelated to each other. One reason these behaviors were not highly correlated is that females flushed in every trial we scored, but performed distraction displays in only a fraction of trials. However, a positive relation was still possible under these circumstances.

Landing distance is problematic because on the one hand it was correlated with the performance of dis-

traction displays, while on the other hand it showed little relationship with either incubation stage or the number of previous visits. As we suggested above, the association between landing distance and distraction displays may be a consequence of distraction displays being a form of active defense that was made more effective if the female landed closer to the threat. When females did not exhibit active defense, they may have simply flown a safe distance from the observer and landed, with variation in what each individual perceived to be a safe distance being unrelated to the value of the nest. Because the ducks we studied did not actively defend their nests on most occasions they were flushed, variation in the distance they landed from the observer would not be a meaningful index of nest defense on most occasions. If this interpretation is correct, then we would recommend that landing distance not be used to quantify nest defense. Note, however, that other distance measures, such as how close a bird approaches the observer during some defined period, have been used successfully as measures of nest defense in other species (e.g., Weatherhead 1979), presumably because approaching an observer is an active defense.

One implication of these results is that using a single behavior to quantify nest defense will leave substantial variation in overall nest defense unexplained, regardless of which behavior is used. An alternative approach would be to combine all defense behaviors into an index of nest defense, as has been done by many researchers (e.g., Blancher and Robertson 1982, Hudson and Newborn 1990). However, were we to use this approach with our data, and use landing distance in the index, we would probably be able to explain less variation in nest defense with our independent variables than were landing distance excluded. Thus, the most appropriate approach might be first to perform preliminary studies/analyses to identify the behaviors that vary with a factor of general importance to nest defense such as nesting stage (Montgomerie and Weatherhead 1988). Second, only those behaviors should be used to develop a general index to explore how other factors affect nest defense.

Effects of repeated nest visits

Female dabbling ducks altered their nest defense in response to repeated visits, and over the incubation period that we sampled, nest defense was affected more by repeated visits than by incubation stage. This change in response was not due to positive reinforcement of apparently effective behavior, however, as suggested by Knight and Temple (1986a). Rather, for all three species, nest defense (measured by flushing distance) decreased as nests were visited more often. In a previous study, Forbes et al. (1994) also

found that female ducks increased flushing distance in response to an increasing number of visits.

The clear effect of repeated visits on flushing distance raises the question of why the ducks reduced the risks they took when visited more often. Several authors have suggested that the appropriate approach to this question is to consider how experience with a potential predator alters a parent bird's perception of the costs and benefits of nest defense (Coleman 1987, Montgomerie and Weatherhead 1988, Mallory and Weatherhead 1993). If the perceived costs and benefits are affected asymmetrically by repeated nest visits, the bird's behavior should change. We consider two hypotheses based on this cost-benefit approach. First, because the nest is left unharmed on each visit, the bird may learn that the observer is not as serious a threat to the nest as first perceived. However, the bird's perception of its own risk from the observer remains unchanged with repeated visits. Thus, the benefits of nest defense are reduced, while the costs remain the same, so with successive visits nest defense declines. A bird nesting for the first time must learn to differentiate animals that pose serious threats to its nest from other animals that just happen to live in the vicinity of the nest.

In the second hypothesis, the risks to the parent change with repeated exposure to the predator. A predator that flushes a duck from its nest and is successfully distracted away from the nest by the duck may be likely to return to the vicinity of the nest in the near future. When the predator does return, it may pose more of a risk to the duck because the predator will be better prepared for the duck to flush from its nest and because it will have some knowledge of the location of the nest. In either case, the risks to the duck are higher on the return visit and would warrant an earlier departure from the nest.

If experience with a predator changes the perceived costs and benefits of nest defense as hypothesized above, why is that effect different among different species of birds? The answer seems likely to involve both the behavior of the birds' natural predators (e.g., do they return to search for nests they failed to find on a previous visit?), and how the birds perceive the threat used by the researcher (e.g., a person standing near the nest). The use of humans and model predators has been very successful in the study of avian nest defense. Ironically, however, it may ultimately be necessary to study the interactions between nesting birds and real predators if we are to understand all facets of how the birds react to simulated predators.

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