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Density-dependent nest predation in waterfowl: the relative importance of nest density versus nest dispersion

Kevin M. Ringelman · John M. Eadie · Joshua T. Ackerman

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Abstract When nest predation levels are very high or very low, the absolute range of observable nest success is constrained (a floor/ceiling effect), and it may be more difficult to detect density-dependent nest predation. Density-dependent nest predation may be more detectable in years with moderate predation rates, simply because there can be a greater absolute difference in nest success between sites. To test this, we replicated a predation experiment 10 years after the original study, using both natural and artificial nests, comparing a year when overall rates of nest predation were high (2000) to a year with moderate nest predation (2010). We found no evidence for density-dependent predation on artificial nests in either year, indicating that nest predation is not density-dependent at the spatial scale of our experimental replicates (1-ha patches). Using nearest-neighbor distances as a measure of nest dispersion, we also found little evidence for "dispersion-dependent" predation on artificial nests. However, when we tested for dispersion-dependent predation using natural nests, we found that nest survival increased with shorter nearest-neighbor distances, and that neighboring nests were more likely to share the same nest fate than non-adjacent nests. Thus, at small spatial scales, density-dependence appears to operate in the opposite direction as predicted: closer nearest neighbors are more likely to be successful. We suggest that local nest dispersion, rather than larger-scale measures of nest density per se, may play a more important role in density-dependent nest predation.

Keywords Artificial nest · Nearest-neighbor · Conspecific attraction · Waterfowl · Nest success

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K. M. Ringelman (✉) · J. M. Eadie
Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields Ave., Davis, CA 95616, USA
e-mail: kmringelman@ucdavis.edu

J. T. Ackerman
Western Ecological Research Center, U.S. Geological Survey, University of California, One Shields Ave., Davis, CA 95616, USA

Introduction

Understanding density-dependent processes is important for the conservation of exploited, endangered, or heavily-managed species (Hixon and Carr 1997; Ueno et al. 2010). In one such group, North American waterfowl, density dependence in population growth has been demonstrated consistently at large spatial and temporal scales (Vickery and Nudds 1984; Viljugrein et al. 2005; Saether et al. 2008; Murray et al. 2010), yet the underlying processes that produce these patterns remain elusive. Waterfowl populations are often limited by productivity on the breeding grounds (Hoekman et al. 2002), and nest predation is the primary cause of reproductive failure (Klett et al. 1988; Greenwood et al. 1995). Accordingly, predation has long been implicated as a potential driver of waterfowl populations. Indeed, in the most recent time series analysis of waterfowl populations, Murray et al. (2010) suggested that the long-term and continental-scale density dependence observed in waterfowl populations was caused by processes that operate at smaller temporal and spatial scales, such as nest predation.

Generalist mesopredators such as striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) have home ranges large enough to detect and respond to

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variation in prey density, and so are considered likely to exhibit density-dependent predation (Schmidt and Whelan 1999). Studies of predation risk and predator behavior using radio telemetry have reported that mesopredators, such as striped skunks, tend to forage within a specific area and may aggregate in areas of high nest density (Larivière and Messier 2000, 2001a; Phillips et al. 2003, 2004), possibly forming olfactory search images (Nams 1997). While it seems clear that mesopredators have the capacity to respond in a density-dependent manner to a patchily distributed resource (such as waterfowl nests), few studies have actually detected density-dependent nest predation.

The relationship between nest density and predation has been well studied in birds (reviewed in Major and Kendal 1996; Caro 2005), yet considerable uncertainty remains as to whether nest predation is density dependent (Major and Kendal 1996; Ackerman et al. 2004). Some artificial nest studies report strong patterns of density-dependent nest predation (e.g., Gunnarsson and Elmberg 2008), while others report weak (e.g., Clark and Wobeser 1997) or no (e.g., Padysakova et al. 2010) density-dependent effects on nest predation rates. The lack of consensus on the role of density-dependent predation may have arisen, in part, because of considerable variation in how researchers have studied nest predation. For example, studies have varied in the nest type (artificial vs. natural), methods for marking nests, nest density, overall sample size, visit frequency, predator community, predator densities, etc. (Major and Kendal 1996; Caro 2005). Furthermore, several of these parameters likely differ among geographic locations and over time, which generates considerable variation in nest success.

Indeed, it is possible that the wide range in nest success observed among locations, years and studies may be a principal reason why it has proven so difficult to detect evidence of density-dependent nest predation. For example, when predation levels are very high or very low, the absolute range of variation in nest success is necessarily constrained (a floor/ceiling effect). Although predation rates might still vary with nest density, at these extremes in nest survival, it could be difficult to detect density dependence without very large sample sizes. Researchers might be better able to detect density-dependent predation in years with moderate predation rates, simply because there can be greater variation in absolute levels of nest success and therefore a greater capacity to statistically detect density dependence even with moderate sample sizes. Because absolute levels of nest predation vary widely among small-scale studies, evidence for density dependence at this scale may be obscured or confounded. To evaluate this hypothesis, small-scale studies spanning a wide range of predation rates are needed, while controlling for extraneous variables. This is difficult logistically because it requires either directly manipulating predation levels, or conducting studies over long enough periods to observe sufficient variation in levels of nest predation (Lawton 1988).

Here, we test the hypothesis that density-dependent predation will be more likely to be detected in years with moderate levels of nest predation. To do so, we replicated an experimental study 10 years after the original study, comparing a year when nest predation was high (2000) with a year when it was moderate (2010). In the Suisun Marsh of California in 2000, Ackerman et al. (2004) found no evidence of density-dependent predation at any of three spatial scales, using both artificial and natural nests in a year with high nest predation rates. This may have been due to the fact that the majority of nests were depredated rapidly, regardless of density, potentially swamping any density-dependent signal that might have been present. Early in the 2010 nesting season at Suisun Marsh, we observed that predation levels were moderate, and we capitalized on this situation by repeating the study of Ackerman et al. (2004) using exactly the same experimental design, methodology, and geographical location. By simultaneously analyzing both datasets, we had a unique opportunity to examine how overall predation levels might influence the ability to detect density-dependent nest predation, while controlling for other confounding variables such as study site and experimental methods. Artificial nest experiments are often complemented by concurrent study of natural nests, which may be especially important if predation levels vary between the two types of nests (Major and Kendal 1996; Butler and Rotella 1998). Although several studies have considered nearest-neighbor effects on artificial nests (Sugden and Beyersbergen 1986; Clark and Wobeser 1997; Larivière and Messier 1998), surprisingly few have also examined nearest-neighbor effects on natural nests simultaneously (Andren 1991; Ackerman et al. 2004). In this study, we used artificial nests to explore whether absolute levels of predation can affect our ability to detect density-dependent predation at the field level, and also conducted a nearest-neighbor analysis using natural and artificial nests to study density-dependent predation at smaller spatial and temporal scales.

Materials and methods

We repeated the same experimental design and methods of Ackerman et al. (2004), so that our results would be directly comparable. Therefore, we only briefly describe our methods here with emphasis on the small differences between our two studies. See Ackerman et al. (2004) for complete details on study methods.

Study area

Our study took place on the Grizzly Island Wildlife Area, Suisun Marsh, CA, in the same block of upland nesting fields used by Ackerman et al. (2004). In general, the types of vegetation present in 2000 were still the predominant species during our study, though mustard (*Brassica* spp.) and thistle (family Asteraceae) have become increasingly common during the past 10 years. Over the past two decades, striped skunks (*Mephitis mephitis*) have been the major nest predator in this area (McLandress et al. 1996; Ackerman 2002), although the skunk population appears to have declined in recent years while predators such as raccoons (*Procyon lotor*) and common ravens (*Corvus corax*) have become more numerous (K.M. Ringelman, personal observation).

Natural nests

In 2010, we located and monitored natural waterfowl (mostly mallard *Anas platyrhynchos* and gadwall *Anas strepera*) nests in 16 upland fields (9 large fields 23.4 ± 3.1 ha, 7 small fields: 12.9 ± 1.6 ha; values are means ± SE) at Grizzly Island Wildlife Area. Fields that were part of the artificial nest experiment were searched and monitored, but were not included in natural nest analyses because artificial nests likely increased the nest densities perceived by predators and might have influenced predator behavior. Following the protocols of Ackerman et al. (2004), nest searches were conducted from April 1 through early July, and each field was searched at 3-week intervals following standard protocols (Klett et al. 1986; Gloutney et al. 1993; McLandress et al. 1996). The incubation stage of the nest was determined by candling (Weller 1956), and the nest initiation date was calculated by adding the clutch size and incubation stage, and subtracting that value from the date the nest was found. Nests were revisited every 7 days until nest termination, and we considered a natural nest to be depredated as soon as the predator found the nest; that is, when one or more eggs were destroyed or missing. For nests that were partially depredated and then abandoned, we were able to determine the date of depredation by candling the remaining eggs. For all other depredated nests, the date of depredation was estimated to be 3 days after the previous nest check. For successful nests, we extrapolated the incubation stage at the previous nest check to determine the estimated hatching date. Nests that were partially depredated when found or that were abandoned due to investigator disturbance were not included in analyses.

Nearest-neighbor distances provide a measure of nest dispersion (i.e. local nest clustering) within a field (Clark and Evans 1954), and may provide deeper insight into processes that operate at very local spatial and temporal scales, such as conspecific attraction in nesting waterfowl and area-restricted search by predators (Benhamou 1992). However, even with such analyses, the methods used in previous studies may have obscured evidence of nearest-neighbor effects. Typically, most nearest-neighbor analyses (Andren 1991; Ackerman et al. 2004) identify nearest-neighboring nests using all nests in a season, regardless of whether the neighboring nests were active simultaneously. However, another way to assess nearest-neighbor effects would be to restrict the pool of "neighbors" to only those nests active at the same time as the focal nest, which more accurately reflects what a predator could encounter in a given foraging bout. Thus, we calculated two nearest-neighbor distances for each natural duck nest:

1. For all nests, the nearest neighbor at any point during the entire nesting season, even if the two nests were not active at the same time.
2. Our second method used only simultaneously active nests to identify the nearest neighbor. For depredated nests, we assumed that risk to neighbors was greatest during the focal nest's depredation event; hence, we identified the nearest neighbor as the closest active nest on the date when the focal nest was depredated. For successful nests, we determined the nearest active neighbor on the midpoint date between nest initiation and hatching.

Artificial nests

Following the methods of Ackerman et al. (2004), we deployed artificial nests in a complete randomized block design within 8 blocks, each of which consisted of an upland nesting field (4 large and 4 small fields). Fields were not selected randomly due to logistical constraints; however, fields were geographically dispersed and each contained a similar (heterogeneous) mix of habitat types. Four of the eight fields used in 2010 were also used in the 2000 study, and the other fields were chosen to be similar in size, location, and habitat to those fields studied in 2000. Within each field (block), three 1-ha treatment plots were selected systematically using methods established by Ackerman et al. (2004). In each replicate, we randomly assigned each treatment plot as low (5 nests/ha), medium (10 nests/ha), or high (20 nests/ha) nest density. These density treatments are identical to the study conducted in 2000 and are also similar to those used in other artificial nest predation experiments (Larivière and Messier 1998; Gunnarsson and Elmberg 2008) to facilitate comparisons among studies. Our artificial nest densities were not influenced so much by natural nests as to effectively change overall nest density; the average number of natural nests in each treatment (over

all exposure intervals) was 0.59, 0.84, and 0.84 nests for the low, medium, and high density plots, respectively.

We attempted to reduce the potential of predators to respond to nest flags (Hein and Hein 1996) by randomly positioning 20 nest markers within each treatment plot (regardless of the artificial nest density it was assigned) at least 4 days before the beginning of the experiment (following the methods of Ackerman et al. 2004). In the low density treatment plots, only five of the nest markers were associated with an artificial nest, whereas in the high density treatments, all markers were associated with a nest. Each actual or potential nest site (a site flagged to control for predator attraction) was marked with a 2-m bamboo stake placed 4 m north of the nest bowl, and a smaller stake was placed at the nest bowl level with the vegetation height. Each actual or potential nest site was similarly visited and disturbed during each visit.

Artificial nests of nine dyed chicken eggs were created following the methods of Ackerman et al. (2004). The only difference in protocol was that Ackerman et al. (2004) used down collected from hunter-harvested birds to cover artificial nests after observer visits, whereas we used down collected earlier in the 2010 nesting season from hatched and abandoned nests. To distribute scent evenly, down from different nests was mixed together and stored in paper bags before use. In addition, 3–5 drops of commercial duck scent (Cabela's, Sidney, NE, USA) were deposited on the nest at each visit to simulate the presence of an incubating hen as other studies have done (e.g., Clark and Wobeser 1997; Larivière and Messier 1998). We visited artificial nests every 8 days over a 32-day exposure period. This is a representative exposure period for many dabbling ducks, whose nests hatch at an average age (nest age = laying + incubation) of 32–35 days (Klett et al. 1986). A nest was considered depredated if one or more eggs were missing or destroyed (Larivière and Messier 1998; Ackerman et al. 2004).

Statistics

Following Ackerman et al. (2004), we analyzed artificial and natural nest data from 2010 and 2000 together using a repeated-measures ANOVA. Our response variable was the proportion of nests surviving to each exposure window (8, 16, 24, and 32 days), arcsine-square root-transformed to improve normality. Nest locations were recorded with a Garmin GPSMAP 76 GPS receiver (Garmin International, Olathe, KS, USA). Nest GPS locations were used to calculate nearest-neighbor distances in ArcMap 10 (ESRI, 2010), and analyses were conducted using logistic regression in JMP 8.0 (SAS Institute, 2008).

Table 1 Global repeated measures ANOVA model, with the proportion of nests surviving at each interval as the dependent variable

Variable	Exact *F*	*df*	*P* value
All between	8.3	9	<0.0001
Intercept	15.9	1	0.0003
Year	15.0	1	**0.0004**
Density	0.4	2	0.67
Date	5.4	1	**0.0257**
Year × date	34.9	1	**<0.0001**
Year × density	0.4	2	0.68
Density × date	0.5	2	0.63

Year refers to either 2000 or 2010, *Density* to the different treatment groups, and *Date* to the calendar date on which the treatments were initiated

Significant *P* values (defined as $p < 0.05$) are shown in bold

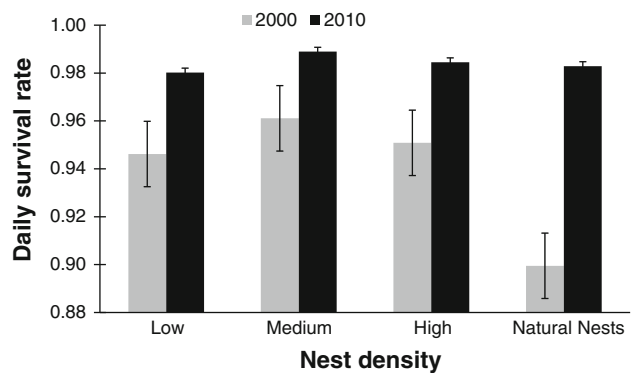

Fig. 1 A comparison of daily survival rates (with standard errors) between 2000 and 2010 among artificial nest density treatments

Results

Predation at the field scale

When overall predation levels were high in 2000, only 28 out of 280 artificial nests (10%) survived the 32-day exposure period. In contrast, overall predation levels in 2010 were lower, and 182 of 280 artificial nests (65%) survived to the end of the exposure period. The proportion of artificial nests surviving in 2010 was significantly higher than in 2000 (Table 1; Fig. 1). The proportion of nests surviving also differed among fields in 2010 (repeated measures ANOVA: $F_{7,14} = 22.1$, $p < 0.0001$) as they did in 2000. Survival was highest in field six where 34 out of 35 (97%) nests survived and lowest in field five where only 1 out of 35 (3%) nests survived. In most of the eight fields, predation levels were low, with >85% nest survival in five of the eight fields.

Table 2 nearest-neighbor distances and neighbor fate for 2010 natural and artificial nests

	Average nearest-neighbor distance	Successful nearest neighbors	Depredated nearest neighbors
Artificial nests			
Successful nests = 182	15.9 m	**88% (*n* = 161)**	12% (*n* = 21)
Depredated nests = 98	17.5 m	28% (*n* = 27)	**72% (*n* = 71)**
Natural nests (entire nesting season)			
Successful nests = 384	36.9 m	**65% (*n* = 250)**	35% (*n* = 134)
Depredated nests = 275	34.9 m	48% (*n* = 133)	**52% (*n* = 142)**
Natural nests (simultaneously active)			
Successful nests = 384	64.6 m[a]	**72% (*n* = 277)**	28% (*n* = 107)
Depredated nests = 275	79.4 m[a]	44% (*n* = 121)	**56% (*n* = 154)**

Neighbor pairs sharing the same fate are shown in bold; the tendency for neighbors to share the same fate was significant in all analyses

[a] Nearest-neighbor distance was only a significant determinant of nest fate in simultaneously active natural nests

The percentages of artificial nests surviving to 32 days of exposure in 2010 for the low, intermediate, and high nest density plots were 55 ± 14, 71 ± 12, and 64 ± 15%, respectively. In 2000, artificial nest survival was much lower with 15 ± 12, 15 ± 11, and 6 ± 4%, respectively, surviving after 32 days at the same densities. There was no significant effect of density treatment in either year on nest predation levels (Table 1; Fig. 2). In both years, nest survival was lower for nests exposed later in the season (effect of Date), and there was an interaction between the exposure interval and study year (Year × Date; Table 1), reflecting the fact that predation increased more dramatically over the course of the season in 2000 than in 2010. Ackerman et al. (2004) initiated their experimental fields between April 12 and May 24, and our experimental fields were initiated between May 6 and May 28. The central spans (10th to 90th percentile) of natural nests in 2000 and 2010 were very similar (2000: April 6–May 24; 2010: April 5–May 31). Therefore, artificial nests deployed in 2010 spanned a slightly later portion of the waterfowl breeding season; however, this is a conservative bias in our low-predation results in 2010, as predation tends to increase over the course of the breeding season in our study area for artificial (Ackerman et al. 2004) and natural nests.

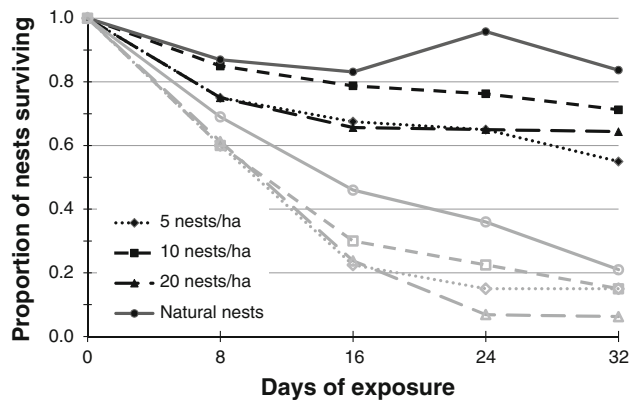

Fig. 2 A comparison of survivorship curves for artificial nests deployed at three different densities in 2010 (*closed symbols*, *darker lines*) and 2000 (*open symbols*, *lighter lines*). Natural nests are also shown for comparison

Nearest-neighbor distance and fate: artificial nests

In 2010, distances between nearest-neighboring artificial nests in the low, intermediate, and high nest densities averaged 28.3 ± 1.3, 17.9 ± 1.2, and 12.8 ± 0.5 m, respectively. Similar to Ackerman et al. (2004), we found no effect of nearest-neighbor distance on focal nest success ($\chi^2 = 2.2$, $df = 1$, $p = 0.14$). However, in 2010, nearest-neighboring nests shared the same fate significantly more often than expected by chance, while controlling for block (field-level) effects ($\chi^2 = 3.9$, $df = 1$, $p = 0.05$; Table 2). Ackerman et al. (2004) found a similar result, although the effect became non-significant after they removed one field with unusually high nest survival. In 2010, nearest neighbors were more often both successful, while in 2000, nearest neighbors were more often both depredated.

Nearest-neighbor distance and fate: natural nests

The distance between nearest neighbors, measured using the entire distribution of nests for the nesting season ($n = 659$), averaged 36.1 ± 1.0 m, commensurate with the distances reported by Ackerman et al. (2004) for natural nests in 2000. Similar to Ackerman et al. (2004), we found that nearest-neighbor distance had no effect on nest fate ($\chi^2 = 1.0$, $df = 1$, $p = 0.32$). We also found that neighboring nests were more likely to share the same fate ($\chi^2 = 18.2$, $df = 1$, $p < 0.001$).

The first step in our analysis calculated nearest-neighbor distances using all nests observed over the entire nesting season (3 months), yet many of these nests were not active at the same time. Therefore, we repeated our analysis selecting only those nests that were active simultaneously as potential nearest neighbors, and we recalculated the

Table 3 Summary of nearest-neighbor analyses

Nearest-neighbor summary
Artificial nests
Nest fate was not affected by nearest-neighbor distance
Neighbors shared the same fate
Natural nests (all nests)
Nest fate was not affected by nearest-neighbor distance
Neighbors shared the same fate
Natural nests (simultaneously active)
Nests with *closer* neighbors were more successful
Neighbors shared the same fate

distance to the nearest-neighboring nest. Using this refined temporal method, nearest-neighbor distances were much larger, and averaged 70.8 ± 2.5 m. Interestingly, we found that nests were more likely to survive when neighboring nests were closer ($\chi^2 = 5.9$, $df = 1$, $p = 0.015$; Table 2). We also found that neighboring nests, (similar to the longer temporal analysis above) were more likely to share the same fate ($\chi^2 = 19.1$, $df = 1$, $p < 0.0001$), regardless of distance. Nearest-neighbor-analyses are summarized in Tables 2 and 3.

Discussion

Field-level nest density

During a year of high nest predation and low nest success, Ackerman et al. (2004) found little evidence of density-dependent predation at any of three spatial scales. However, density dependence may have been difficult to detect because nest predation was high in 2000, regardless of experimental density. We hypothesized that a density-dependent signal might be evident in a year with intermediate predation levels, such as in 2010. However, we did not find any evidence of density-dependent nest predation among 1-ha patches. In fact, nest predation levels in density treatments did not even fall out in the expected rank-order—medium density fields had the highest nest success and, interestingly, this was also true in 2000 at much higher nest predation levels (Fig. 2). Failure to find evidence of density-dependent nest predation in two different years with two very different predation levels indicates that variation in predation levels among years is unlikely to obscure patterns of density-dependent predation, contrary to our initial hypothesis. It is possible that predation may yet be density-dependent on very short time scales (e.g., during the first few days after incubation) and our nest-check interval of 8 days may have failed to detect this. However, these effects, if they exist, would have been slight as we failed to find any evidence of density-density dependent nest failure in any of our exposure periods. Accordingly, our results, in combination with those of Ackerman et al. (2004), support the conclusion that predation is not density dependent in our population at an intermediate spatial scale (field and patch scales).

Dispersion of nests within a field

The results of the nearest-neighbor analyses suggests that nest dispersion within a field (as measured by nearest-neighbor distances), rather than nest density per se, may yet be an important predictor of nest success. When we tested for "dispersion-dependent" nest predation on artificial nests at the scale of nearest neighbors, we found no effect of nearest-neighbor distance on nest fate, similar to Ackerman et al. (2004). However, nearest-neighboring nests tended to share the same fate, suggesting that clusters of artificial nests survived, or were depredated as a group. In 2010, nearest neighbors were more often both successful, whereas in 2000, nearest neighbors were more often both depredated.

In our first set of nearest-neighbor analyses on natural nests, we calculated nearest-neighbor distances using all natural nests in 2010, regardless of whether those nests overlapped temporally. Here, our results paralleled what we found for artificial nests: there was no effect of nearest-neighbor distance on nest fate, although nest fate was still influenced by the fate of its nearest neighbor, suggesting that there are clusters of successful nests and clusters of depredated nests. Similar results have been found for cavity-nesting (Pöysä 1999) and ground-nesting (Larivière and Messier 1998; Ackerman et al. 2004) waterfowl, though Andren (1991) failed to detect shared-fate effects at very close fixed distances. Analyzing nearest-neighbor affects using all nests in season addresses the question of whether predators respond slowly to nest density over the course of a nesting season, which may be the case (Larivière and Messier 1998). This type of analysis is also useful in identifying relatively static spatial factors that might influence nest predation, such as underlying habitat characteristics or predator den locations.

Is this patchiness in predation generated on long (seasonal) or short time scales? Is a cluster of depredated nests just a case of being in "the wrong place," or is it more aptly described as being in "the wrong place at the wrong time?" In our second set of nearest-neighbor analyses, we identified neighbors using only simultaneously active nests to better understand the temporal scale at which clusters of depredated and successful nests are generated. Using this method, we found that natural nests' fate was directly related to the fate of their nearest neighbor, similar to our artificial and natural nest results at a larger scale. Moreover,

at this refined temporal scale, we also found that nearest-neighbor distance strongly influenced nest fate: natural nests were more likely to be successful when neighboring nests were *closer*.

Thus, it appears that nest success was higher when natural nests were more densely clustered. To the best of our knowledge, this is a unique finding in studies of waterfowl nest predation. Whereas it is believed that waterfowl nest predators should respond positively to nest density (thereby decreasing nest success in high density patches) (Larivière and Messier 2001b; Gunnarsson and Elmberg 2008), our results show the opposite pattern, that nest success is higher when neighbors are closer. How do dense clusters of nests form? The grouping of nests on the landscape is caused by (presumably adaptive) hen nest-site selection behavior, which may include philopatry, shared habitat preferences, conspecific attraction, and female copying of habitat selection decisions. For example, dense clusters may form because a group of successful nests will produce more offspring that may return to breed in the same location in later years (natal philopatry) (Anderson et al. 1992). Furthermore, successful mallards tend to return to the same nesting location (Majewski and Beszterda 1990). Many birds use conspecific cues and public information to make breeding decisions (e.g., Danchin et al. 1998, 2004; Pöysä 1999; Doligez et al. 2004), so it seems plausible that inexperienced conspecifics might follow experienced hens to low-predation areas. In many cases, this strategy works if hens copy the habitat selection decision of a bird that makes a "good" choice (e.g., selects an area with good nesting cover or historically low predator densities); this group of nests may be more likely to avoid detection by predators, and all nests in the group will survive. Nevertheless, some hens will copy a bird making a "bad" (or unlucky) habitat selection decision; this group of nests may be more likely to be located by a predator, in which case all nests in the group will be destroyed. Thus, a predator may often find none of the nests in a group, especially if predation levels are relatively low (i.e. having close neighbors is generally good, nest fate is strongly correlated with neighbor fate), but occasionally predators will find all the nests in a group (nest fates are correlated). This situation has been dubbed "cryptic density dependence" (Shima and Osenberg 2003), where the pure effects of density dependence are masked by habitat quality. In our system, this effect may be exacerbated by females copying other's habitat selection decisions. Under cryptic density dependence, some high density clusters will survive (because they are in good habitat), while others will be depredated (because they are in poor habitat), so parsing out pure density-dependent effects is difficult. This variability may cause the effects of density-dependent predation to wash out at larger spatial scales (Rastetter et al. 1992), which could explain the results of Ackerman et al. (2004) as well as this study.

In the past, researchers often have studied density-dependent predation by dividing up the landscape and calculating the "nest density" in each section. However, studying density-dependent nest predation at these somewhat arbitrary scales has yielded mixed results. We suggest that the spatial configuration of nests might yet influence predation levels, but at a much smaller spatial and temporal scale. The small-scale clustering of nests in space and time may represent a more biologically relevant "density," and this nest clustering/dispersion is likely determined in large part by hen habitat selection behavior. If our interpretation is correct, these results may have important conservation implications. The way nests are clustered at small scales on the landscape can play a critical, yet currently unknown, role in determining the location and extent of nest predation. The process by which these clusters form is also largely unknown. The inherent spatial clustering of vegetation types may affect the propensity for waterfowl to nest in clusters, and the vegetation selected may in turn affect predation risk (Crabtree et al. 1989; Clark and Shutler 1999). However, we suspect that waterfowl conspecific attraction may play a larger role than previously appreciated. Conspecific attraction has long been recognized as an important factor in avian habitat selection (Hilden 1965), and recent observational and experimental work has shown that conspecific attraction can convey useful information about habitat quality and breeding success (Danchin et al. 2004; Doligez et al. 2004; Ward and Schlossberg 2004). Few waterfowl studies have explicitly studied conspecific attraction, but each has found that conspecific attraction can be a more important cue than habitat in nest site selection (Pöysä et al. 1998; Coulton et al. 2011).

There is strong evidence that density dependence is an important regulator of waterfowl populations at the continental scale across years, and nest predation has long been implicated as a likely source of this pattern. Our results are difficult to interpret within this framework: predators seem to respond to nest density, although in the opposite direction as predicted, and at a smaller spatial and temporal scale than we had previously suspected. More research is needed to study the behavioral *processes* of density-dependent nest predation—how clusters of nests form and why they are depredated.

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