Visual and olfactory concealment of duck nests: influence on nest site selection and success

Jennifer S. Borgo, Department of Science & Mathematics, Coker College, 300 E. College Ave., Hartsville, SC 29550, USA jborgo@coker.edu

Michael R. Conover, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

Abstract: Selecting a nest site is an important decision for waterfowl. Because most nest failure is due to depredation, the primary selective pressure in choosing a nest site should be to reduce depredation risk. This task is difficult, however, because predators use differing tactics to locate nests, such as olfactory or visual cues. The purpose of this research was to evaluate both the olfactory and visual components of waterfowl nest site selection and nest depredation in North Dakota. We located waterfowl nests, monitored them until termination (hatched or depredated), and collected both visual and olfactory concealment characteristics of nest sites and paired random sites in 2006 and 2007. Waterfowl nest sites and random sites did not differ in their olfactory concealment characteristics. However, waterfowl did select nesting sites with greater lateral concealment than random sites, a visual characteristic. The only difference found between successful and depredated nests consisted of lateral dispersion, an olfactory concealment characteristic. These results indicate that while waterfowl may select nest sites based on visual concealment characteristics, those characteristics were not predictive of nest success. Olfactory concealment characteristics may be more important for nest success in our study area because the dominant nest predators, including raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), primarily utilize olfactory cues to locate nest sites.

Key words: nest depredation, nest site selection, North Dakota, Prairie Pothole Region, waterfowl

For birds, the selection of nest sites is an important decision. Birds should primarily select nest sites to reduce depredation risk given that the highest cause of nest failure in most species is nest depredation (Klett et al. 1988, Howlett and Stutchbury 1996, Walker et al. 2005, Pitman et al. 2006, Franzreb 2007, Perkins and Vickery 2007). But what constitutes a safe nest site? Overall, bird species with high rates of nest depredation should attempt to conceal their nest from predators, but predators can use various means to locate nests. The 2 main types of cues predators use to detect nests are visual and olfactory. Predators may use both types of cues while foraging, but different predators rely more heavily on 1 sense or the other (Wells and Lehner 1978). To determine the characteristics of safe nest sites, we must be cognizant of how the different predator guilds (visual and olfactory) forage.

Visual cues to nest location include parental behavior (e.g., incubation constancy and recess patterns), conspicuousness of the nest itself, or site characteristics that indicate a likely nest site (With 1994, Guyn and Clark 1997, Eggers et al. 2005). Eggers et al. (2005) found a positive relationship between depredation rates on Siberian jay (*Perisoreus infaustus)* nests and the frequency of visitation trips by the adults. Selection of certain nest site characteristics can also reduce visual cues. Vegetative cover increases nest success by reducing the likelihood of visual predators locating the nest. Several waterfowl species prefer to nest in tall, dense cover that provides concealment (Page and Cassel 1971, Kirsch et al. 1978, Duebbert et al. 1983, Lokemoen et al. 1984, Kruse and Bowen 1996). Duck nest success can be higher in these areas (Kirsch et al. 1978). In many studies, depredation rates of artificial and natural nests were lower if vegetative cover was present over the nest (Schranck 1972, Sugden and Beyersbergen 1987, Guyn and Clark 1997, Jobin and Picman 1997).

Important sources of olfactory cues from the nest include feces, eggs, and incubating birds (Stoddart 1980, Burtt and Ichida 2004). Olfactory predators forage by traveling the landscape

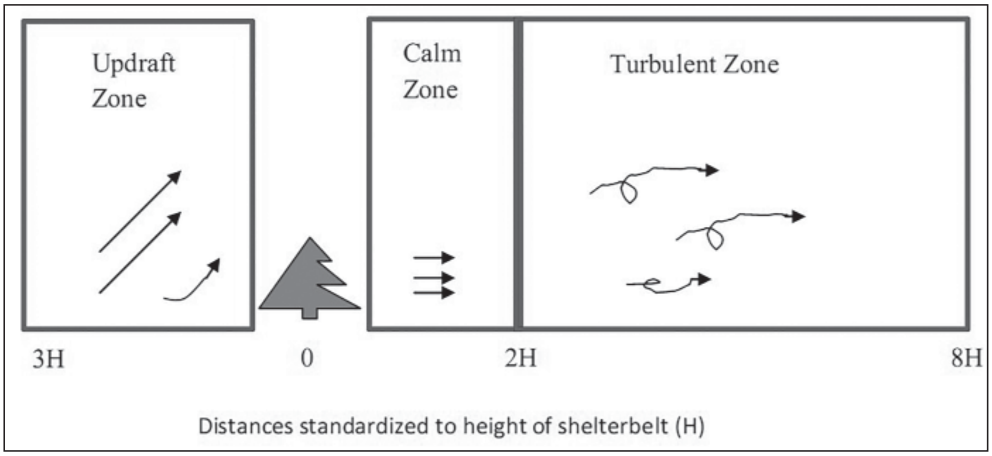

Figure 1. Diagram of the effect of shelterbelts on wind flow patterns around them (length of arrows reflecting relative wind velocity and distance from the shelterbelt is relative to the shelterbelt's height).

until they recognize an odor cue from a food source. Once recognized, predators find the source by following the odor's concentration gradient or traveling upwind (Stoddart 1980, Jolly and Jolly 1992). Birds can reduce the risk posed from olfactory predators by lowering the predators' likelihood of detecting and tracking odors (Conover 2007). By decreasing odorant release, a bird would reduce cues to olfactory predators. Fecal matter present near artificial nests increases depredation rates (Petit et al. 1989, Clark and Wobeser 1997, Olson and Rohwer 1998). Therefore, birds may reduce odors associated with the nest by removing or ingesting the fecal sacs of their nestlings. These behaviors are found in many species, such as Eastern bluebirds (*Sialia sialius*), American crows *(Corvus brachyrhynchos*), and Florida scrub jays (*Aphelocoma coerulescens*; McGowan 1995, Lang et al. 2002). Birds could also place nests above the detection zone of predators, thereby decreasing the ability of a predator to access an odor. The inability of predators to access odor cues may be one reason mammalian depredation rates are higher on ground nests than elevated nests (Piper and Catterall 2004).

Changes in wind patterns caused by surface features should influence an olfactory predator's ability to locate nests (Conover 2007). Ground-nesting birds can use these surface features to select nest sites that are safer from olfactory predators. Olfactory cues are harder to track in areas with updrafts, as the odor plume generated by the nest is carried above the predator's detection zone (Conover 2007). Turbulence (variability in wind direction and speed) causes an odor plume to change course frequently and to expand its shape (Finelli et al. 1999, Moore and Crimaldi 2004, Conover 2007). This unpredictability should make foraging more difficult for olfactory predators because odorant distributions are more variable across space and reach undetectable levels at relatively short distances from the nest (Vickers 2000, Shivik 2002, Moore and Crimaldi 2004, Conover 2007). Alternatively, nests are easier to find when the plumes resulting from them are straight and remain at detectable levels for a longer period. This type of plume occurs in areas where surface features have not altered wind flow patterns or induced turbulence, such as in open fields with no trees (Çengel and Cimbala 2006).

A ground-nesting bird selecting a nest site in the Great Plains faces many nest predators, including both visual predators, like American crows or black-billed magpies (*Pica hudsonia),* and olfactory predators, like raccoons *(Procyon lotor)* or striped skunks *(Mephitis mephitis).* While the importance of a particular predator guild may vary spatially, both types occur throughout the Great Plains.

The purpose of this study was to determine if upland-nesting waterfowl selected nest sites that offered concealment from visual and/or olfactory predators and to determine if these concealment characteristics influenced nest success. We surveyed for nests in areas around

Figure 2. Chain-dragging an open-field area.

shelterbelts (planted tree rows) because the shelterbelts provided a range of olfactory concealment characteristics through altering wind flow (Figure 1; Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). We predicted that waterfowl would select nesting sites that provided concealment from both visual and olfactory predators (i.e., they would select sites with greater visual concealment and faster dispersion of odorants than random sites), and that these characteristics would also differ between successful and unsuccessful nests.

Methods

Study area

We conducted this study within the Prairie Pothole Region of North Dakota, which is characterized by numerous shallow wetlands (Stewart and Kantrud 1974). Detailed information on the physiography of the area can be found in Stewart and Kantrud (1972). Sites were located on Waterfowl Production Areas (WPA) managed by the United States Fish and Wildlife Service in the counties of Barnes, Cass, Cavalier, Griggs, Ramsey, Steele, and Stutsman. The WPAs used were Alice, Avocet Island, Becker, Billings Lake, Edwards, Erickson, Evers, Fingal, Gaier, Gunder, Jamestown College, Lost Island, Major, Miller, Ohnstad, Pintail, Shaw, Stinkeoway, Storhoff, Tolstad, Tompkins, Wengeler, and Zimmerman. Within these WPAs, we observed several duck nest predators, including American crows, coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), raccoons, striped skunks, and ground squirrels (*Spermophilus* spp.). These WPAs ranged from 33 to 948 ha, and they were usually embedded in an agricultural matrix of cereal, oilseed, and hay production. We selected WPAs that contained shelterbelts and only searched 1 shelterbelt per WPA. For those WPAs with >1 shelterbelt, we randomly selected which shelterbelt to search. Shelterbelt height ranged from 6.3 to 26.6 m ($\bar{x}$ = 12.6). Shelterbelt areas were separated from each other by ≥3 km ($\bar{x}$ = 14.5 km to the nearest shelterbelt area). We searched for nests along the length of the shelterbelt and out to a distance of >3 times the height of the shelterbelt on the windward side of the belt (north or west side) and 8 times the height of the shelterbelt on the leeward side (south or east side;). We selected these distances because they were within the area where wind flow was altered by the presence of the shelterbelt (Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). Search areas for shelterbelts ranged from 2–14 ha. Each shelterbelt area was paired with a random area of similar size that was devoid of trees (open-field area [OF area]). The OF area had to be >100 m from shelterbelts and was visually estimated from the field to be the approximate size of the shelterbelt search area. Search areas for OF areas ranged from 2–11 ha. If possible, each OF area was located within the same WPA as its paired shelterbelt. In 5 cases, no OF area of the approximate size of the shelterbelt search area and >100 m from a shelterbelt were present, and the OF area was placed on the nearest suitable WPA. These OF areas were 5–17 km from their corresponding shelterbelt area.

Nest searching

We searched all shelterbelt areas and OF areas for nests of upland-nesting waterfowl (Anatidae) every 3–5 weeks from May to July of each year. Each field was searched twice in 2006 and 3 times in 2007. Each shelterbelt area and its paired OF area were searched within 1 day of each other. We systematically searched the shelterbelt areas and OF areas by dragging a 30-m chain between 2 all-terrain vehicles (ATVs) using the method of Higgins et al. (1969; Figure 2). When a bird was flushed, we stopped the ATVs, walked over to where the bird flushed, and searched for a nest. When we found a nest, we recorded its GPS location. We used the Weller method to candle eggs to determine their stage of development and expected hatch date (Klett et al. 1986). We determined nesting species from the appearance of the flushed hen, feathers, and egg characteristics. We placed a 1-m-tall stake 10 m directly north of the nest to aid in relocation of the nest. The stakes were visually inconspicuous (green bamboo) to minimize the possibility of nest predators using them to locate nests. We also took precautions to avoid scent deposition in the nesting areas (rubber boots and nitrile gloves).

We inspected nests every 7–10 days to determine nest fate. We differentiated between a successful nest (≥1 egg hatched) and a depredated nest by looking at the membranes and egg shell remnants (Klett et al. 1986; Figure 3). If the egg's membrane was in one piece and not connected to the shell, we considered the nest hatched. If the membrane was ripped into many pieces and still connected to shell remnants, we considered the nest depredated.

Figure 3. Northern pintail ducklings found during a nest inspection.

Visual concealment characteristics of nest sites

We collected visual concealment characteristics of nest sites and their paired random sites after a nest was terminated (no longer being incubated) to reduce the risk of observer-induced mortality. The paired random sites of OF nests were also in the OF areas. For nests on shelterbelt areas, the paired random sites were on the same shelterbelt area and within the same distance class from the shelterbelt as their nest site (Figure 1). The specific location of each paired random site was generated by dividing the search area into a grid and using a random number table to select a grid cell. Once within the cell, we randomized a distance (number of steps) and direction for the paired random site. Maximum vegetation height was measured as the tallest vegetation within 0.5 m of the nest or random site (Esler and Grand 1993). For an obstruction rating, we averaged Robel pole readings (minimum height that the pole was visible when placed in the nest bowl) when an observer looked back at the pole from a height of 1 m and a distance of 4 m away from the nest or random site in the 4 cardinal directions (Esler and Grand 1993). We used a cover board to determine overhead concealment by laying the board on the nest or random site, standing over it, and subtracting the number of cells visible from 100. The board was 10 x 10 cm, on which 100 1-cm^2 squares were marked in a checkerboard pattern. We determined lateral concealment of the nest by placing the cover board vertically on the nest or random site and observing the percentage of cells on the cover board that were obscured by vegetation from 4 m away and at a height of 1 m (Jones 1968).

Olfactory concealment characteristics of nest sites

The olfactory concealment characteristics of each nest site were determined using 2 sonic anemometers (Campbell Scientific, Logan, Utah) that measured wind speed in 3 dimensions. We concurrently measured wind speed at a nest and its paired random site at a height of 0.25 m. For olfactory concealment characteristics, the paired random site was always located on the nest's corresponding OF area. The measurements were made instantaneously 10 times per second for 30 minutes. These measurements occurred at randomly determined daytime periods. The purpose of these measurements was to determine how localized surface features affected wind flow patterns. These surface features (slope, aspect, isolated trees, or shelterbelts) should not change over time. As such, it was justifiable to measure wind flow characteristics after the nest was terminated to minimize disturbance to the hen.

Data output was given as wind speed on an x,y,z coordinate system with the x-axis running north to south, y-axis running east to west, and z-axis running vertically. These axes were rotated to the u,v,w coordinate system commonly used in micrometeorology with u pointing in the wind direction, the w-axis running vertically, and the v-axis running perpendicular to both u and w. The mean of all u coordinates (*U*) indicated the mean wind speed over the recording period in the streamwise direction. Mean of all w coordinates (*W*) indicated the vertical windspeed over the recording period, with positive values for updrafts and negative values for downdrafts. We calculated both the standard deviation for *U* and *W* (σ_u, σ_w, respectively) over the recording period to provide measures of both the lateral and vertical spread of a hypothetical odor plume. Turbulence (T) was calculated as the sum of the standard deviations along all 3 axes ($\sigma_x + \sigma_y + \sigma_z$). We calculated the friction velocity (U^*; square root of the covariance between the instantaneous u [u′] and instantaneous w [w′] over the recording period) to provide a parameter for the characteristic velocity scale of turbulence (i.e., the average rotational speed of a hypothetical eddy given current conditions).

To determine whether waterfowl were selecting for olfactory concealment characteristics, we only used nests in OF areas. Olfactory concealment characteristics of nest sites within shelterbelt areas were dominated by the alteration of wind flow patterns created by the trees themselves (Figure 1) and would not necessarily reflect waterfowl nest selection. We compared the characteristics of each OF nest site to the characteristics at its paired random site in the same OF.

In 2006, we randomly selected 1 nest from each of 3 distance classes at 6 shelterbelt areas (Figure 1). We collected olfactory and visual concealment characteristics on a total of 13 nests because some shelterbelt areas did not have nests in each distance class. Equipment malfunction reduced the olfactory concealment characteristics to 12 nests for 2006. In 2007, we randomly selected 1 successful and 1 depredated nest at each of 3 distance classes at 12 shelterbelt areas and from their respective OF areas. Mowing occurred prior to collection of olfactory characteristics at 7 nest sites. Therefore, we censored those 7 nests from our data and have olfactory concealment characteristics of 39 nest sites in 2007, of which 17 were located in OF areas. Blue-winged teal (*Anas discors*) constituted the major nesting species in the area, followed by mallard (*A. platyrhynchos*), gadwall (*A. strepera*), Northern pintail (*A. acuta*), Northern shoveler (*A. clypeata*), lesser scaup (*Aythya affinis*), and American widgeon (*Anas americana*).

Statistical analyses

Due to small sample sizes, species were pooled for analyses unless otherwise specified. We used paired *t*-tests to determine whether nest sites in shelterbelt and OF areas (pooled) differed from their paired random sites in overhead concealment, Robel reading, and maximum vegetation height (Zar 1999). Lateral concealment data were not normally distributed, so we used a Wilcoxon signed rank test to compare nest sites to paired random sites (Zar 1999). We had a sufficient number of blue-winged teal nests to analyze their selection of visual concealment characteristics separately. To determine whether nest sites differed from their paired random sites in olfactory concealment characteristics, we compared characteristics solely between nests located within the OF area and their paired random site (also in the OF area) using a paired *t*-test. Mean stream-wise wind speed data were not normally distributed, so again we used a Wilcoxon signed rank test.

There was no difference in nest success among species ($X^2_5 = 9.47$, exact $P = 0.09$), so species were pooled for comparisons between successful and unsuccessful nests. We used *t*-tests to determine whether successful nests differed from depredated nests in visual concealment characteristics across all areas (shelterbelt and OF areas; pooled method; Zar 1999). We used a Mann-Whitney test for lateral concealment because the data were not normally distributed (Zar 1999). We compared the means of the differences between a nest site and its paired random site in olfactory concealment characteristics for successful and depredated nests across all areas using *t*-tests (pooled method). In the case of non-normal data (*U*), we used a Mann-Whitney test. We used the difference between a nest and its paired random site instead of olfactory concealment characteristics of the nest itself to diminish the influence of variability in meteorological conditions among recording periods. All analyses were 2-tailed, and we considered results significant if $P < 0.05$.

Results

Nest site selection

Nests within shelterbelt and OF areas had higher lateral concealment (mean ± SE; 81.3 ± 2.7) than random sites within the same shelterbelt or OF area (74.7 ± 2.9; $P = 0.05$; Table 1). There was no difference ($P > 0.05$) for any other visual concealment characteristic (i.e., overhead concealment, Robel reading, or maximum vegetation height; Table 1). Blue-winged teal nest sites had shorter maximum vegetation height (0.83 m ± 0.04) than random sites (0.92 m ± 0.03; $P = 0.04$; Table 2). There was no difference for any other visual concealment characteristic of blue-winged teal nests (Table 2). Olfactory concealment characteristics between OF area nests and their paired random sites did not differ ($P > 0.05$; Table 3).

Nest site success

Of the 59 nests where we measured visual concealment characteristics across all areas (shelterbelt and OF areas), 25 were successful and 34 were depredated. Visual concealment characteristics were not different between successful and depredated nests (Table 4). Of the 51 nests where we measured olfactory concealment characteristics across all areas (shelterbelt and OF areas), 22 were successful and 29 were depredated. Lateral dispersion (σ_u) differed between successful and depredated nests ($t_{49} = 2.12$, $P = 0.04$; Table 5). Successful nests had less of a difference in lateral dispersion between themselves and their paired random sites (0.003 ± 0.017) than depredated nests (0.056 ± 0.018; Table 5).

Discussion

Nest site selection

While waterfowl did not select nest sites that offered more concealment from olfactory predators than random sites, they do appear to be selecting for particular visual concealment characteristics in their nest sites. Waterfowl selected nest sites with greater levels of lateral concealment than random sites. Increased lateral concealment would make it difficult for a predator on the ground to locate nests using visual cues. Our results are consistent with previous studies that also found waterfowl selecting nesting sites with higher levels of concealment or cover than random sites (Kruse and Bowen 1996, Guyn and Clark 1997).

Nest site selection in waterfowl may be species-specific (Livezey 1981, Kruse and Bowen 1996, Gloutney and Clark 1997). We found that blue-winged teal selected for shorter vegetation height than random sites and showed no selection for lateral concealment. These results are consistent with previous findings that teal select for microhabitat characteristics at nest sites, particularly short-grass cover (Livezey 1981). Blue-winged teal may nest in shorter vegetation due to an increased ability to detect approaching predators (Götmark et al. 1995).

Table 1. Visual concealment characteristics of waterfowl nest sites and paired random sites in North Dakota during the 2006 and 2007 nesting seasons and the results of paired *t*-tests or a Wilcoxon signed rank test between nests and random sites.

Characteristic	Nest $\bar{x}$ ± SE	Random location $\bar{x}$ ± SE	Test statistic	*P*-value
Overhead concealment (%)	50.5 ± 3.6	41.5 ± 4.4	$t_{57} = 1.18$	0.08
Lateral concealment (%)	81.3 ± 2.7	74.7 ± 2.9	$S_{57} = 244$	0.05
Robel reading (m)	0.33 ± 0.02	0.31 ± 0.01	$t_{57} = 1.35$	0.18
Tallest vegetation (m)	0.89 ± 0.03	0.94 ± 0.02	$S_{57} = -174.5$	0.13

Table 2. Visual concealment characteristics of blue-winged teal nest sites and paired random sites in North Dakota during the 2006 and 2007 nesting seasons and the results of paired *t*-tests comparing values between nests and random sites.

Characteristic	Nest $\bar{x}$ ± SE	Random site $\bar{x}$ ± SE	Test statistic	*P*-value
Overhead concealment (%)	46.3 ± 4.2	36.3 ± 5.9	$t_{30} = 1.62$	0.12
Lateral concealment (%)	77.5 ± 3.9	73.4 ± 4.0	$t_{30} = 0.69$	0.50
Robel reading (m)	0.31 ± 0.02	0.30 ± 0.02	$t_{30} = 0.46$	0.65
Tallest vegetation (m)	0.83 ± 0.04	0.92 ± 0.03	$t_{30} = -2.19$	0.04

Table 3. Olfactory characteristics of open-field waterfowl nest sites and their paired random sites in North Dakota during the 2006 and 2007 nesting seasons and the results of paired *t*-tests or a Wilcoxon signed rank test comparing the open-field nests with their paired random sites.

	Open-field nests $\bar{x}$ ± SE	Paired site $\bar{x}$ ± SE	Test statistic	*P*-value
U	0.425 ± 0.035	0.402 ± 0.041	$S_{15} = 16.50$	0.46
W	−0.021 ± 0.005	−0.002 ± 0.007	$t_{15} = -1.87$	0.08
σ_u	0.266 ± 0.022	0.244 ± 0.025	$t_{15} = 1.61$	0.13
σ_w	0.175 ± 0.013	0.176 ± 0.018	$t_{15} = 1.27$	0.22
T	0.748 ± 0.054	0.715 ± 0.680	$t_{15} = 1.60$	0.13
U^*	0.263 ± 0.015	0.245 ± 0.025	$t_{15} = 1.02$	0.32

Nest site success

Fate of nests was not related to the degree of visual concealment in any characteristic measured in this study. The relationship between visual concealment and success in natural nests is unclear in the literature. Some studies have found a relationship between visual concealment and nest success (Guyn and Clark 1997, Albrecht and Klvaňa 2004), while others investigating the same characteristics have found no effect (Schieck and Hannon 1993, Howlett and Stutchbury 1996, Brua 1999, Burhans and Thompson 2001). The impact of visual concealment on nest success may be related to the predator assemblage of an area (Rangen et al. 1999). In areas where visual predators dominate, visual concealment should be related to nest success (Sugden and Beyersbergen 1987). One would expect that visual concealment would not be strongly related to nest success in areas where the primary nest predators are mammals that rely on olfactory cues to locate nests, such as our study area. This is consistent with both our results and other studies where the predators responsible for nest depredations were determined (Rangen et al. 1999).

Table 4. Visual concealment characteristics of successful and depredated waterfowl nest sites in North Dakota during the 2006 and 2007 nesting seasons and the results of *t*-tests and a Mann-Whitney test comparing values of successful and depredated nests.

	Successful $\bar{x}$ ± SE	Depredated $\bar{x}$ ± SE	Test statistic	*P*-value
Overhead concealment (%)	53.2 ± 5.4	48.5 ± 4.8	$t_{57} = -0.65$	0.52
Lateral concealment (%)	83.0 ± 4.2	80.0 ± 3.5	$Z_{57} = 0.88$	0.38
Robel reading (m)	0.32 ± 0.02	0.34 ± 0.02	$t_{57} = 0.64$	0.52
Tallest vegetation (m)	0.84 ± 0.05	0.92 ± 0.03	$t_{57} = 1.58$	0.12

Table 5. Differences between olfactory characteristics of successful and depredated waterfowl nest sites and their paired random sites in North Dakota during the 2006 and 2007 nesting seasons and the results of *t*-tests and a Mann-Whitney test comparing those differences between successful and depredated nests.

	Successful $\bar{x}$ ± SE	Depredated $\bar{x}$ ± SE	Test statistic	*P*-value
U	−0.002 ± 0.026	0.069 ± 0.034	$Z_{49} = -1.19$	0.23
W	−0.017 ± 0.009	−0.019 ± 0.007	$t_{49} = -0.15$	0.88
σ_u	0.002 ± 0.017	0.056 ± 0.018	$t_{49} = 2.12$	0.04
σ_w	0.007 ± 0.012	0.016 ± 0.010	$t_{49} = 0.55$	0.59
T	0.012 ± 0.040	0.116 ± 0.039	$t_{49} = 1.82$	0.07
U^*	0.032 ± 0.026	−0.004 ± 0.027	$t_{49} = -0.96$	0.34

Olfactory concealment of nests within shelterbelt and OF areas was related to depredation risk. In this study, successful nests in shelterbelt and OF areas had a similar lateral dispersion to random sites, while depredated nests had higher levels of lateral dispersion than the random sites. Lateral dispersion is the variability in both wind speed and direction and can be generated by wind flowing past shelterbelts, local vegetation near the nest, and rough surfaces (Conover 2007). It remains unclear whether depredation on nests with higher lateral dispersion is due either to predators locating nests based on the surface features that increase lateral dispersion or if a wider odor plume aids predators in locating nests.

These results indicate that waterfowl are selecting nest sites that differ from random sites in only 1 of the variables measured (lateral concealment). However, this characteristic was not predictive of nest success. Predator searching efficiency increases with both search image formation and the number of sensory cues that predict the presence of nests (Bowman and Harris 1980, Bell 1990). Therefore, consistently selecting nest sites with similar visual or olfactory concealment characteristics should result in reduced nest success. This could be one reason for the lack of predictive correlations between characteristics of nest selection and success in either our study or others.

The low overall nest success in the Prairie Pothole Region may be due to the large number of different predator species throughout the landscape (Cowardin and Johnson 1979, Klett et al. 1988, Sargeant et al. 1993). Previous work in our study area documented several predator species foraging within a patch over the course of a single night (Jiménez et al. 2007). Random nest site selection makes nest locations less predictable to predators and reduces the ability of predators to develop search images of likely nest locations in landscapes with a diverse predator assemblage using multiple foraging techniques (Martin 1988, Bell 1990, Filliater et al. 1994, Clark et al. 1999, Jiménez et al. 2007). This can be seen in the inconsistent effect of visual concealment on waterfowl nest site selection and depredation among studies, areas, and years. Factors such as overhead concealment, vegetation density, and vegetation height impacted waterfowl nest success or simulated nest success in some studies (Schranck 1972, Mankin and Warner 1992, Brua 1999) but had no effect on success in other studies (Dwernychuk and Boag 1972, Guyn and Clark 1997, Yerkes 2000). Even when particular nest site characteristics were preferentially selected by nesting birds, those choices did not necessarily translate into higher nest success (this study, Willms and Crawford 1989, Guyn and Clark 1997, Clark et al. 1999, Clark and Shutler 1999). Additionally, associations between patch or nest site characteristics and nest success can change from year to year (Clark and Shutler 1999, Jiménez et al. 2007). By placing nests randomly throughout appropriate habitat, nesting success could be improved because search image formation by nest predators would be more difficult (Martin 1988, Bell 1990).

Our study has a low sample size, which may have obscured differences between species in selection characteristics, especially olfactory concealment characteristics. However, our study remains useful because it is among the first to investigate olfactory concealment of waterfowl nests. We found that lateral dispersion, an olfactory concealment characteristic, impacted the fate of waterfowl nests, while visual characteristics did not. More attention to the olfactory concealment of nests is clearly warranted, given that the primary nest predators in many locations are mammals that rely heavily on olfactory cues to locate nests (Bowman and Harris 1980, Johnson et al. 1989, Sovada et al. 2000).

Management implications

Managers try to increase recruitment in waterfowl, and much of their effort is focused on improving nest success (West and Messmer 2004). This effort has been confounded by the lack of consistent vegetation characteristics that improve nest success. How should managers improve habitat if the best nest choice in this landscape is random? The number of potential nest sites may be increased by increasing heterogeneity in nesting areas (Bowman and Harris 1980, Martin 1988, Bell 1990). If waterfowl select nesting sites within that habitat randomly, the predators would have a more difficult time forming search images (Martin 1988, Bell 1990). Given that predators use different modalities to locate nests, managers should consider heterogeneity on ≥2 levels: visual and olfactory.

Dense nesting cover (DNC) can increase heterogeneity by providing areas with different visual concealment characteristics in the same patch (Lapointe et al. 2000, Conover 2007). DNC may also increase heterogeneity in olfactory concealment characteristics if it provides differing levels of surface roughness across the planted area. It is therefore not surprising that areas with DNC have lower nest depredation rates than the surrounding habitat (Pasitschniak-Arts and Messier 1995, McKinnon and Duncan 1999). This result has generally been attributed to physical obstruction and visual concealment characteristics. However, Jimenez et al. (2007) did not find a relationship between physical or visual obstruction and nest success in DNC. The benefit of DNC may be more related to olfactory concealment characteristics than visual concealment characteristics. This study indicates the importance of considering both types of modalities when in a landscape with a diverse predator assemblage.

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JENNIFER BORGO is an associate professor of biology and director of the honors program at Coker College. She obtained her B.S. degree in zoology from Auburn University, and her M.S. and Ph.D. degrees in wildlife biology at Utah State University.

MICHAEL CONOVER is a professor of wildland resources at Utah State University. He obtained his B.S. degree in biology from Eckerd College, M.S. degrees in both psychology and zoology from Washington State University, and his Ph.D. degree in zoology from Washington State University.