Effects of Olfactory and Visual Predators on Nest Success and Nest-Site Selection of Waterfowl in North Dakota

Jennifer Borgo

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Effects of Olfactory and Visual Predators on Nest Success and Nest-Site Selection of Waterfowl in North Dakota.

Jennifer Borgo
Utah State University

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EFFECTS OF OLFATORY AND VISUAL PREDATORS ON NEST SUCCESS
AND NEST-SITE SELECTION OF WATERFOWL
IN NORTH DAKOTA

by

Jennifer S. Borgo

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Wildlife Biology

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2008
ABSTRACT

Effects of Olfactory and Visual Predators on Nest Success and Nest Site Selection of Waterfowl in North Dakota

by

Jennifer S. Borgo, Doctor of Philosophy

Utah State University, 2008

Major Professor: Dr. Michael R. Conover
Department: Wildland Resources

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 because predators use differing tactics to locate nests, such as olfactory or visual cues. I investigated several components of waterfowl nest-site selection and success on sites with shelterbelts (planted tree-rows) in North Dakota, during the 2006 and 2007 nesting seasons.

I found that meteorological conditions impacted nest depredation; artificial nests were more likely to be depredated when either temperature or dew point was high. These meteorological conditions should improve foraging efficiency for olfactory predators by increasing odor concentration.

Waterfowl selected nesting sites with greater visual concealment than random locations (lateral concealment). However, the only difference found between successful and depredated nests was lateral dispersion, an olfactory concealment characteristic.
Nest density was higher in areas without shelterbelts than in areas near shelterbelts. Nest success for waterfowl decreased as shelterbelt height increased. Other shelterbelt characteristics, like porosity and orientation, did not affect nest success or nest density.

Given that nest predators differ in foraging habitat, temporal patterns of activity, and searching modalities, nest site characteristics that conceal the nest from 1 predator species may increase its vulnerability to another predator. For instance, risk due to olfactory predators should be reduced near shelterbelts because locating nests would be more difficult as turbulence is generated by the shelterbelts. Concomitantly, shelterbelts could also increase the presence of visual predators, by providing nesting sites and vantage points. In my study, any benefits shelterbelts provide in reducing nest depredation by olfactory predators may have been offset by increasing nest depredation from visual predators. Hence nesting near shelterbelts was neither a liability nor a benefit to ducks.

(162 pages)
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Jennifer S. Borgo
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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

For birds, selection of nest sites is an important decision. Given that the highest cause of nest failure in most species is nest depredation, evolutionary and ecological principles suggest that birds should primarily select nest sites to reduce depredation risk (Duebbert and Lokemoen 1976, Greenwood 1986, Losito et al. 1995, Cowardin et al. 1998, Pietz et al. 2003, Emery et al. 2005, Drever and Clark 2007). The characteristics a bird associates with safety from predators depend on genetics and past experience. The genetic component to site selection is based on the fitness of previous generations (Cink 1976). These preferences can be modified by a bird’s own experience, including natal experiences (Dow and Fredga 1985, Sonerud 1985, Johnson and Grier 1988).

What constitutes a safe nest site? Overall, birds should conceal their nests from predators, but different predators use differing means to locate nests. The 2 main methods that predators use to find nests utilize olfactory and visual cues. Predators may use both types of cues while foraging, but they usually rely most heavily on one or the other. Coyotes (Canis latrans), for example, appear to be primarily visual predators, but still use olfactory cues (Wells and Lehner 1978). The removal of either type of stimuli resulted in increased time to find a prey item (rabbit) in a laboratory, with visual cue removal having the greatest effect (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 predators generally utilize visual cues for locating food sources. This method is easier for humans to understand because we also rely heavily on visual cues. Visual cues to nest location include parental behavior (such as flushing), conspicuousness of the nest itself, or site characteristics that indicate a likely nest site (visual search image). Visual predators can search for nest cues from an elevated stationary site. For some species, such as American crows (Corvus brachyrhynchos) and black-billed magpies (Pica hudsonia), trees fill this role by providing a perch from which to scan the surrounding area (Preston 1957, Gazda et al. 2002). Another visual foraging method is to search for cues while in motion, but this is not ideal because it consumes energy. Peregrine falcons (Falco peregrinus) scan for ducks from trees when available, but in areas where trees are scarce, they search while in flight (Dekker 1987).

Either way, to protect against visual predators, visual cues should be minimized. Nesting birds can modify their behavior to help conceal their nests. 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. Visual predators could also use cues from birds that flush from the nest to determine nest site location. Therefore, if an incubating bird leaves the nest area before flying or only flushes after it is detected by a predator, the ability of predators to locate the nest should be reduced. Burhans and Thompson (2001) found that the birds with more visible nests flushed when the researcher was farther away than those with greater amounts of nest concealment, indicating that those nests with increased concealment allow birds to minimize flushing.
Nest site characteristics may be used to reduce visual cues. Birds can select for sites with greater spatial heterogeneity or in areas away from perching sites. Spatial heterogeneity leads to more potential nest sites for predators to search and can decrease the foraging efficiency of predators (Bowman and Harris 1980). Therefore, it is not surprising that several studies have found reduced nest depredation rates on both artificial and natural nests located in sites that are more heterogeneous (Crabtree et al. 1989, Mankin and Warner 1992, Bayne et al. 1997, Fleming and Guiliano 2001). Additionally, nesting far from the trees that may serve as vantage points for predators, could reduce depredation risk (Preston 1957, Gazda et al. 2002).

Unlike visual predators, olfactory predators rely mainly on olfactory cues for locating food sources. For nests, important sources of odor cues include feces, chemicals secreted from the uropygial gland, and microorganisms living on feathers (Stoddart 1980, Burtt and Ichida 2004). Olfactory predators forage by traveling the landscape until they recognize an odor cue. Once they recognize an odor cue, they can find the source by following the odor’s concentration gradient or by traveling upwind (Stoddart 1980, Jolly and Jolly 1992). The odor cue becomes harder to follow when wind direction varies widely, resulting in longer search times before a predator is able to locate the odor source (Shivik 2002). The development of olfactory search images further aids in locating prey items. Search images allow striped skunks (*Mephitis mephitis*) to recognize prey odors from greater distances (Nams 1997). In explosive-detection dogs, the development of search images for a particular explosive results in higher detection rates for that explosive (Gazit et al. 2005).
Risk from olfactory predators can be reduced by lowering the ability of predators to detect and track odors or by selecting sites under-utilized by predators. By decreasing odorant release, a bird would reduce cues to olfactory predators. Fecal matter present near nests increases depredation rates in artificial nests (Petit et al. 1989, Clark and Wobeser 1997, Olson and Rohwer 1998). Therefore, birds could reduce odors associated with the nest by removing or ingesting nestling fecal sacs. These behaviors are found in many species. For example, eastern bluebirds (*Sialia sialis*) remove fecal sacs an average of 91 m from the nest (Lang et al. 2002). Eastern bluebirds, American crows, and Florida scrub jays (*Aphelocoma coerulescens*) often place fecal sacs from nests on elevated sites, such as trees, fence posts, or electric wires (McGowan 1995, Lang et al. 2002). This activity may provide added benefit by keeping the fecal sac’s odor plume above the predator’s detection zone. Birds could also place nests above the detection zone of predators, thereby decreasing the ability of a predator to access an odor. Predators’ inability to access odor cues may explain why mammalian depredation rates are lower on elevated nests than on nests that are at ground level (Piper and Catterall 2004).

Birds could also reduce the risk from predators depredating their nests by placing nests where predators rarely travel. For example, islands are known to have higher nest density and success for ducks than the adjacent mainland because the access of many mammalian predators is restricted by water (Duebbert et al. 1983, Lokemoen et al. 1984, Jobin and Picman 1997). Additionally, dense nesting cover (DNC) is often used as a
management tool to increase duck nest success because predators are believed to have difficulty travelling through thick vegetation (McKinnon and Duncan 1999).

In selecting a safe nest site, birds should attempt to reduce their conspicuousness to all predators in the area, especially the predominant nest predator. However, sites that reduce conspicuousness to 1 predator guild may increase the depredation risk from predators using another modality to locate nests. Nest height is an example of this phenomenon. As nests increase in height, the amount of depredation due to olfactory predators may decrease, while that of visual predators might increase. Piper and Catterall (2004) found evidence of this relationship using both ground and elevated artificial nests in Australia’s eucalypt forests. Ground nests were 4 times more likely to be depredated by mammalian and reptilian predators than elevated nests. Conversely, the percentage of ground nests depredated by avian predators was half that of elevated nests. Ideally, birds should select nesting sites with a low depredation risk to both predator types. However, when these sites cannot be found, site selection could be based on the main predator type or on the entire predator assemblage.

THE GREAT PLAINS, WIND, AND SHELTERBELTS

The Great Plains extends across the mid-continental United States and through the Canadian provinces of Alberta, Saskatchewan, and Manitoba (Steinauer and Collins 1996, Cunfer 2005). Prairies are usually described in terms of the primary grass species present. Moving east to west, the 3 main prairie types are tall-grass prairie, mixed-grass prairie, and short-grass prairie. Agricultural practices have resulted in habitat loss throughout the prairies. The tall-grass prairie, for example, is 1 of the most endangered
ecosystems in the world, with an estimated loss of up to 99% of the original range (Flores 1996). Even with high levels of habitat loss, the prairies remain very important in terms of waterfowl production (Batt et al. 1989).

The weather of the Great Plains can be highly variable. Year-round, there is a huge range between the daily high and low temperatures (Nuttonson 1965). Additionally, strong winds and variable precipitation amounts are characteristic of the area (Nuttonson 1965). Cunfer (2005) found that wind speeds are at the highest in the spring and lowest in summer and winter. Between 1932 and 1940, high winds combined with drought conditions, high temperatures, and land mismanagement, resulted in the Dust Bowl (Hurt 1981, Cunfer 2005). Although the Dust Bowl led to many problems, it also resulted in a greater understanding of the need to protect the top-soil from high winds and increased interest in shelterbelt development around homes and crops (Hurt 1981, Cunfer 2005).

A shelterbelt is a row of trees or shrubs planted as a windbreak. Shelterbelts are used to protect structures/crops from damaging winds, drifting snow, and erosion (George 1943, George et al. 1963). They moderate the effects of wind; reducing both soil erosion and heat loss for humans, domestic animals, and farm buildings (George et al. 1963). Shelterbelts are designed to alter wind flow. There is an updraft zone immediately windward of the shelterbelt (upwind of it). A noticeable reduction in wind speed occurs at distances several times the height of the shelterbelt on the windward side (Nord 1991). This is caused by the obstruction of the trees/shrubs deflecting air upward and over the shelterbelt and by drag associated with the shelterbelt (Sturrock 1972, McNaughton 1988, Nord 1991).
Unless the shelterbelt is completely solid, some air will still travel through it but at a reduced speed due to drag from the vegetation (McNaughton 1988, Nord 1991). This causes a calm zone of decreased wind speed and smaller eddy (swirling currents of air indicative of turbulence) sizes immediately on the leeward side of the shelterbelt (downwind) compared to open-field flow and the updraft zone (Heisler and DeWalle 1988, McNaughton 1988). Within this zone, the greatest reduction in wind speed occurs at a range of distances of 2-5 times the height of the shelterbelt downwind, depending on its porosity (Bean et al. 1975, Miller et al. 1975).

Beyond the calm zone, a turbulent zone occurs where the fast winds that flowed over the shelterbelt mix with the slower winds that passed through the shelterbelt (McNaughton 1988). This region has increased turbulence and large eddies (Heisler and DeWalle 1988, McNaughton 1988). Eventually, the differences in velocity that generate this disturbance even out and wind flow returns to its original form (McNaughton 1988).

Factors that influence the strength of the shelterbelt effects include the porosity of the belt, the initial wind speed, and atmospheric stability (Heisler and DeWalle 1988). Porosity affects wind flow through shelterbelts. The relationship between the area of reduced wind speed and porosity is typically evaluated experimentally. Plate (1971) found that an intermediate porosity produced the greatest reduction in wind speed over the largest area. Very porous shelterbelts have fewer, smaller eddies in the turbulent zone than non-porous belts, but overall wind reduction is less than with intermediate belts (Plate 1971, Heisler and DeWalle 1988, McNaughton 1988). Dense belts cause a large
reduction in wind speed, but the sheltered area is shorter than with intermediate belts (Nord 1991).

The wind patterns in different shelterbelt zones should influence an olfactory predator’s ability to find nests. Mammalian predators should have a harder time tracking olfactory cues in the updraft zone, as updrafts carry the odor plume above the ground where the predator forages (Conover 2007). In turbulent air, the resultant odor plume may meander and change direction rapidly (Finelli et al. 1999, Moore and Crimaldi 2004). This unpredictability should make foraging in the turbulent zone more difficult for olfactory predators because scent is more patchily distributed (Vickers 2000, Moore and Crimaldi 2004, Conover 2007). Olfactory predators should have an easier time foraging in the calm zone, attributable to a decrease in the occurrence and size of eddies (McNaughton 1988), making the odor plume more predictable and easier to track (Conover 2007). Open fields have relatively even flow, allowing for easier tracking of olfactory cues than any of the shelterbelt zones due to reduced turbulence compared to areas around the shelterbelt.

Predators that primarily use visual cues to detect nest location should not be impacted by changing airflow patterns around shelterbelts. Instead, visual predators could take advantage of the trees in windbreaks as perching sites to aid in locating nests (Preston 1957, Gazda et al. 2002). For this reason, I would expect more visual depredation of nests located in the areas immediately adjacent to the windbreaks than in the open fields.
UPLAND–NESTING WATERFOWL

Many waterfowl breed in North Dakota. I focused this study on upland-nesting species such as northern pintail (*Anas acuta*), northern shoveler (*A. clypeata*), blue-winged teal (*A. discors*), mallard (*A. platyrhynchos*), and gadwall (*A. strepera*; Stewart 1975). Most of these ducks nest from May through July, although some start nesting in April (Stewart 1975).

Depredation of nests, ducklings, and incubating females are the primary factors limiting the population growth rate of mallards in the Prairie Pothole, with nest success explaining the largest amount of variability (43%; Hoekman et al. 2002). Nest success has declined since the 1930s and changes in predator communities are thought to be partially responsible (Sargeant et al. 1993, Beauchamp et al. 1996a, Drever et al. 2004). There have been 3 general approaches to predator management in waterfowl nesting areas: the physical separation of predators from nesting areas, the direct removal of predators, and the creation of dense nesting cover (Sovada et al. 2001).

Physical separation of predators from nesting areas can be accomplished through the creation of predator exclosures or islands within water bodies. Predator exclosures have been found effective in the Prairie Potholes, with higher waterfowl nest success inside exclosures than in the surrounding areas (Greenwood et al. 1990, Beauchamp et al. 1996b, Cowardin et al. 1998). Nest success is also higher on islands (Duebbert 1982, Lokemoen et al. 1984, Beauchamp et al. 1996b). Therefore, small artificial islands have been used to improve waterfowl nesting in some areas (Giroux 1981, Higgins 1986, Willms and Crawford 1989).
Predator removal has also been used to increase duck nest success, but results have been mixed. Predator removal in localized areas has not led to higher levels of nest success (Sargeant et al. 1995), and the targeted removal of particular species has not increased nest success (Greenwood 1986, Clark et al. 1995). However, larger scale efforts (both spatially and across predator species) have increased nest success in some areas (Duebbert and Kantrud 1974, Duebbert and Lokemoen 1980, Garrettson and Rohwer 2001).

Finally, the management of dense nesting cover (DNC) has been used to increase nest success in waterfowl. DNC has increased nest success in many areas (Duebbert and Kantrud 1974, Livezey 1981, McKinnon and Duncan 1990). Residual cover from past years is especially important for early nesting species, like mallards (Kadlec and Smith 1992). In addition, Schrank (1972) found nest success rates 1.5 times higher in heavy cover as compared to sparse cover. Managing habitat patches to increase spatial heterogeneity may also increase nest success by decreasing predator foraging efficiency (Bowman and Harris 1980). My research focused on the habitat component of nest predation.

**RESEARCH OBJECTIVES**

An upland-nesting duck in the Great Plains should select a site that will conceal its nest from a variety of predators, including both visually oriented species, like crows or black-billed magpies, and olfactory oriented species, like raccoons (*Procyon lotor*) or striped skunks. While the importance of a particular predator guild may vary spatially, both types occur throughout the Great Plains. Shelterbelts in the Great Plains offer a
unique opportunity to study nest site selection and depredation. Their alteration of wind flow makes it harder for olfactory predators to forage, while the vantage points provided by trees make foraging easier for visual predators.

The purpose of this research was to determine the relationship between depredation rates, waterfowl nest-site selection, and hypothesized odor plume characteristics. In chapter 2, I tested a timer-device that allows researchers to determine the exact time a nest is depredated. Chapter 3 investigates the spatio-temporal patterns of nest-site selection and depredation. Chapter 4 examines whether particular nest-site characteristics were selected for by waterfowl and if those characteristics affected nest depredation by olfactory and visual predators. Finally, chapter 5 evaluates the relationship between shelterbelt characteristics and waterfowl nest density and nest depredation. This research will provide land managers with additional insight into the dynamics of waterfowl nest depredation and how factors not previously focused on, like meteorological conditions or the differences between visual and olfactory predators, impact it. The following chapters are in stand-alone form and are formatted to the Journal of Wildlife Management guidelines.

LITERATURE CITED


Stewart, R. E. 1975. Breeding birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, North Dakota, USA.


CHAPTER 2
A DEVICE TO RECORD THE SPECIFIC TIME AN ARTIFICIAL NEST IS DEPREDATED

ABSTRACT I designed a timing device that records the calendar date and time of a depredation event on an artificial nest. This clock was simple to construct and successful in field trials with only 6% failing (3 of 48 clocks). The average difference between actual and estimated depredation time was 4.6 minutes. Use of this clock improves the estimates of daily survival, provides insight into predator activity patterns, and allows the evaluation of investigator-induced depredation.

INTRODUCTION
High levels of nest depredation reduce the nesting success of many bird species (Klett et al. 1988, Howlett and Stutchbury 1996, Pitman et al. 2006, Franzreb 2007, Perkins and Vickery 2007). For this reason, many studies have investigated nest depredation patterns. Artificial nests are frequently used in these studies because they allow for a more rigorous experimental design than observational studies on natural nests. Argument continues over the utility of artificial nests given that predation rates between natural and artificial nests often differ (see Faaborg 2004, Moore and Robinson 2004). Nonetheless, artificial nests remain widely used to evaluate the effect of several factors on nest depredation including nest density, egg color, vegetation structure, odor, nest concealment, clutch size, seasonal and landscape characteristics (Sugden and Beyersbergen 1986, Major and Kendal 1996, Jobin and Picman 2002, Conner and Perkins 2003, Ackerman et al. 2004).
Estimating nest survival rates can be problematic in both natural and artificial nesting studies. Although frequent visitation of nests by investigators can increase depredation rates (Major 1990, Esler and Grand 1993), longer periods between nest visits reduce accuracy in determining when these events occur. If an investigator knew the exact time and date of depredation events without frequent visits, more could be learned about predator activity patterns and the factors that influence predator foraging behavior. I modified a nest timer design by Ball et al. (1994) to create a device that told both the calendar date and time of a depredation event on an artificial nest. Additionally, my timer was easier to construct because it only involved altering the wiring to the battery and, unlike Ball et al.’s design (1994), did not necessitate locating the clock’s oscillating crystal. I also provided a method to stabilize the trigger, minimizing conspicuousness of the device at the nest site. The purpose of this paper was to describe how to make the device and evaluate its effectiveness.

METHODS

Construction of Clocks

I purchased digital alarm clocks (Travel Alarm Clock®, $8.24 each) that displayed both time and calendar date. The wire connecting the clock body to the positive battery terminal was disconnected using a soldering iron. New wires (20–22 gauge hook-up wire, 1 to 1.5 m long) were used to connect the clock body and battery terminal through a trigger device (sub-mini SPDT lever switch; $2.69 each) and soldered in place to prevent disconnection (Figure 2-1). The length of wires can be altered to fit project needs. For example, when using the device for an above-ground artificial nest, wires can be
extended so the clock is on the ground while the trigger and nest are several meters high. A #2-size ideal butterfly clamp ($0.04 each) was made into a treadle and attached via soldering and a wire crimp to the trigger device. The wires were attached so that when the trigger was depressed (egg in place) the battery was not connected. Once the trigger was released by removing the egg, the electric circuit was completed and the clock started at 1200 hrs and 1 July (start time and date differ by clock brand and should be checked). The clock display indicated the number of days, hours, and minutes that passed since the trigger was released (depredation event). The clock was placed into a plastic container to protect it from the weather. Wires were passed through a hole cut into the container that was sealed with epoxy to prevent water damage. The wires and container were spray-painted green, brown, and beige for camouflage. The trigger device was attached using 2 screws (#6 x 0.25 in Phillips pan head sheet metal screws; $0.04 each) to the bottom half of a heavy duty plastic knife to provide stability (Figure 2-2). Once familiar with the technique, it took less than 10 minutes to wire each clock. Battery life extended over 1 year with clocks in continuous use (i.e. trigger released).

Field Trial

Forty-eight clocks were placed out in a grid pattern at the Green Canyon Ecology Station of Utah State University (Logan, Utah) in August 2007. I used medium-sized white chicken eggs purchased from the grocery store. One fresh egg was placed on each treadle (Figure 2-3). Over the course of 3 days (27–29 Aug 2007), each nest was “depredated” by a person other than myself. The exact time and date of the “depredation event” was recorded, but I was not provided this information until later. I checked all
nests on 31 August 2007 and recorded the date and hour on the clock, as well as the actual time. I subtracted the depredation period from the nest check time to estimate when the “depredation” event occurred.

After I estimated the time of each depredation event, I was informed when the actual event took place. I then compared the estimated “depredation” time to the actual time of the event to determine the accuracy of the timing device. Failure rate for the clocks was calculated. Failure was defined as any instance when the difference between the calculated and actual time was > 1 hour.

RESULTS

Of 48 total clocks, 2 failed due to loose wiring that could be corrected through more rigorous soldering and 1 failed due to unknown causes (94% success). The remaining clocks averaged a time difference of 4.6 minutes (SE = 0.33), with a maximum difference of 8 minutes. This difference is attributable to variation in the accuracy of individual watches (mine versus that of the individual who “depredated” the nests). There was no precipitation during the testing period and wind speed varied from 0 to 29 km/hr. This clock has worked well under variable weather conditions during predator research in North Dakota\(^1\), where it had a similar success rate (92%) as under the more controlled conditions of this study.

DISCUSSION

Field trials showed that my clocks were very accurate, with time differences between actual and recorded depredation events ≤ 8 minutes. There are several benefits

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\(^1\) See Chapter 3
to knowing the actual time that a nest is depredated including more accurate nest survival estimates, and insight into nest predators and their activity patterns.

Normally, precise nest survival rates are hard to obtain in nesting studies. Daily nest checks increase the probability that a nest will be depredated; therefore an interval of at least 5 days between visits is generally recommended (Major 1990, Esler and Grand 1993). To estimate when the depredation event took place, investigators usually use the median date in the nest check interval (Mayfield 1975, Klett et al. 1986). My clock design eliminates the need for estimation, providing a more robust measure of nest survival rate. Additionally, this device allows investigators to lengthen the time between nest visits while providing a precise measure (within a few minutes) of the timing of the predation event.

Investigator-induced depredations are often a concern in nesting studies. The thought being that researchers may increase depredation risk through depositing odor trails to nests, disturbing vegetation around the nest site, or being observed at the nest site by a predator (Strang 1980, Götmark et al. 1990, Skagen et al. 1999, Bêty and Gauthier 2001). The importance of investigator-induced depredation on overall nest success remains unclear. Several studies found evidence of nest predators, both mammalian and avian, following observers (Götmark et al. 1990, Morton et al. 1993, Sloan et al. 1998). However, observer effects are inconsistent among studies and years (Bêty and Gauthier 2001, Keedwell and Sanders 2002) and are difficult to quantify. Researchers have used the direction of predator approach to a nest, comparisons of daily survival with different visitation rates, and depredation rates with human scent treatments to evaluate the impact
of investigator-induced depredation (Major 1990, Esler and Grand 1993, Whelan et al. 1994, Verboven et al. 2001, Keedwell and Sanders 2002). My timing device provides a more direct test of investigator-induced depredation by showing if depredation events are more likely to happen close to when a researcher visits a nest. If predators are watching observers or following observer scent trails, then nests may be depredated soon after the observer leaves the area.

Furthermore, these clocks can be used to explore temporal patterns in depredation risk caused by weather phenomena. A predator’s ability to locate a nest using olfaction is affected by humidity, temperature, wind speed, and atmospheric turbulence (Conover 2007). Previous studies reported a negative relationship between rainfall and nest survival, but they relied on averaging rainfall over the entire incubation period (Roberts et al. 1995, Roberts and Porter 1998). Roberts and Porter (1998) found that daily nest survival of turkeys (Meleagris gallopavo silvestris) was negatively associated with the departure from average daily rainfall summed over the nesting season. While this sort of analysis indicates a potential link between weather conditions and predator activity, the timing device allows us to determine predator responses to particular weather events. Use of my timing device will allow researchers to evaluate weather conditions at the time of depredation to determine if there are consistent meteorological conditions that increase the risk of predation.

Recruitment in many avian species is reduced due to high rates of nest depredation. Wildlife biologists and researchers who are studying or managing this problem have been hampered by their inability to determine the time of day when nests
are most vulnerable to depredation. My timing device can provide this information when used with artificial nests. The timing device is simple to make, inexpensive (around $13 each), and accurate. Through using this device, researchers can improve daily nest survival estimates, evaluate the impact of investigator-induced depredation in their research area, and study predator activity patterns.

LITERATURE CITED


Figure 2-1: A picture of the inside of the digital clock within a plastic container showing attachment points for the new wires; stars indicate solder points.
Figure 2-2: A diagram of the treadle attached to the trigger device, including a plastic knife which is pushed into the ground for stability.
Figure 2-3: An egg placed on the treadle at the Green Canyon Ecology Station, Logan, Utah.
CHAPTER 3

SPATIO-TEMPORAL ASPECTS OF NEST INITIATION AND NEST DEPREDATION ON UPLAND WATERFOWL NESTS AND SIMULATED DUCK NESTS IN NORTH DAKOTA.

ABSTRACT  Nest success in waterfowl is low in some areas of the Prairie Pothole Region where the primary factor causing nest failure is depredation. I evaluated the spatial and temporal patterns of nest depredation on 248 waterfowl nests and 88 simulated waterfowl nests in North Dakota over the 2006 and 2007 nesting seasons. I found no evidence that predators were able to locate adjacent nests using an area-restricted approach to foraging or that density-dependent depredation was occurring. Surprisingly, meteorological conditions impacted nest depredation; artificial nests were more likely to be depredated when either temperature or dew point was high. My data indicate meteorological conditions, such as temperature and dew point impact the vulnerability of simulated waterfowl nests to depredation. I hypothesize that these meteorological conditions improve the ability of predators to locate nests using olfaction.

INTRODUCTION

Nest success and recruitment are major factors in population maintenance of waterfowl. Without successful reproduction, species cannot maintain or increase their population. For this reason, wildlife and land managers devote much effort towards increasing nest success in waterfowl (West and Messmer 2004). Still, nesting success of waterfowl is low in some parts of the Prairie Pothole Region and predators are largely
responsible (Duebbert and Lokemoen 1976, Greenwood 1986, Losito et al. 1995, Cowardin et al. 1998, Pietz et al. 2003, Emery et al. 2005, Drever and Clark 2007). Numerous studies have evaluated factors influencing nest depredation through the use of both natural waterfowl nests and artificial nests. While many of these factors, such as habitat characteristics, predator communities, and nest-site vegetation, have been explored, spatio-temporal patterns in waterfowl nest depredation have been under-studied (Crabtree et al. 1989, Pietz et al. 2003, Drever et al. 2004, Jiménez et al. 2007).

One spatial aspect of nest depredation that has received attention is density-dependent depredation (i.e., higher nest depredation in areas with greater nest densities). Potential mechanisms for density-dependent nest depredation include predators foraging for a longer time in profitable patches (area-restricted search) and predators forming a search image of a nest after encountering one (Tinbergen et al. 1967, Bell 1990). Many predators have been shown to respond to nest density, including crows (Corvus spp.), gulls (Larus spp.), raccoons (Procyon lotor), and striped skunks (Mephitis mephitis; Page et al. 1983, Sugden and Beyersbergen 1986, Nams 1997, Schmidt and Whelan 1998). If density-dependent depredation occurs, then the fate of nest pairs spaced close together should be similar to each other and depredation events should be linked in time while those pairs separated by greater distances would be different. Furthermore, evolutionary principles indicate that a duck should avoid building its own nest close to pre-existing waterfowl nests if density-dependent depredation is an important factor, as doing so would reduce the contribution of the individual to the overall gene pool.
Another spatio-temporal aspect of nest depredation that has been examined is the increase in depredation rates for both artificial and natural nests as the nesting season advanced (Caccamise 1978, Jobin and Picman 1997, Ackerman et al. 2004, Emery et al. 2005). This pattern could result from an influx of juvenile predators searching for nests as the season progresses or from older predators developing better search images of nests. Search-image formation increases foraging efficiency of striped skunks and has been shown to increase the distance at which they can detect a nest (Bell 1990, Nams 1997). Corvids are capable of remembering the location of depredated nests and returning later to those same patches to forage (Sugden and Beyersbergen 1986, Sonerud and Fjeld 1987). This behavior may result in higher depredation rates as the season progresses. However, some studies have found that waterfowl nest success increases as the season progresses (Cowardin et al. 1985, Greenwood et al. 1995, McKinnon and Duncan 1999). They attributed this increase to additional cover from both new growth and the residual cover present from past years.

Spatio-temporal patterns in depredation may be related to meteorological events that facilitate predator foraging. Low atmospheric turbulence (low variability in wind speed and direction) and atmospheric stability allow odors from nests to remain at detectable concentrations over a larger area (Heinemann and Wahanik 1998, Vickers 2000, Moore and Crimaldi 2004). Increased temperature and humidity enhance the release of odorants from birds and their nests, increasing the probability that a predator will locate the nest (Regnier and Goodwin 1977, Conover 2007). Therefore, an increase in temperature, atmospheric stability, or water vapor content in the air or a decrease in
wind turbulence should make foraging more efficient for predators that use olfactory cues to locate nests (Shivik 2002, Conover 2007).

The purpose of this paper was to evaluate the spatial and temporal patterns of both waterfowl nest initiation and survival in North Dakota. I predicted that: 1) waterfowl would place nests far away from each other, 2) the fate of nests which were close together would be more related than nests farther away, and 3) certain meteorological conditions (such as higher temperature, dew point, and less variability in wind direction) which enhance the foraging efficiency of olfactory predators would increase nest depredation rates.

STUDY AREA

This study occurred within the Prairie Pothole Region of North Dakota (Stewart and Kantrud 1974). I utilized Alice, Avocet Island, Becker, Billings Lake, Breakey, Edwards, Erickson, Evers, Fingal, Gaier, Gette, Gunder, Jamestown College, Jeglum, Lost Island, Major, Miller, Ohnstad, Old Aalalen, Phil Aus, Pintail, Shaw, Stinkeoway, Storhoff, Tolstad, Tompkins, Wengeler, and Zimmerman waterfowl production areas (WPAs) managed by the United States Fish and Wildlife Service (USFWS). These sites were located in Barnes, Cass, Cavalier, Griggs, Ramsey, Steele, and Stutsman counties. The WPAs occurred within an agricultural matrix, mainly of cereal, oilseed, and hay fields. WPAs ranged in size from 33 to 948 ha. Plant species common on these WPAs included smooth brome (*Bromus inermis*), wheatgrass (*Agropyron* spp.), switchgrass (*Panicum virgatum*), needlegrass (*Stipa* spp.), alfalfa (*Medicago sativa*), sweetclover (*Melilotus* spp.; Greenwood 1986, Choromanski-Norris et al. 1989).
Predator removal had not occurred in the last 12 months on any WPA used. In addition, selected WPAs were >17 km from predator removal areas. Duck nest predators observed in these areas included American crows (*Corvus brachyrhynchos*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), ground squirrels (*Spermophilus* spp.), raccoons, red foxes (*Vulpes vulpes*), striped skunks, and weasels (*Mustela* sp.).

I selected WPAs that contained shelterbelts (planted tree rows) and were ≥3 km from other shelterbelt sites ($\bar{x} = 14.5$ km). Twelve of these sites contained north-facing shelterbelts (tree-row ran from east to west), and 10 contained west-facing shelterbelts (tree-row ran from north to south). I only examined 1 shelterbelt per WPA. Around each shelterbelt, I searched for nests in a rectangular area whose length was identical to the shelterbelt and whose width was >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). These distances are within the area where wind flow was altered by the presence of the shelterbelt (Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991; Figure 3-1). Total search area per shelterbelt site ranged from 2 to 22 ha.

I paired each shelterbelt site with a random site of similar size that was void of trees (open-field site). To be considered an open-field site, an area had to be the same size as its paired shelterbelt site and had to be > 100 m from any shelterbelt. If possible, each open-field site was located within the same WPA as its paired shelterbelt site. In 6 cases, no suitable site was present in the same WPA, and the open-field site was placed
on the nearest suitable WPA. These open-field sites were between 5 and 17 km from their paired shelterbelt site.

The study period (May through July 2006 and 2007) had an average monthly rainfall of 7.2 cm. The mean temperature per month was 14° C for May, 19° C for June, and 23° C for July. The region was drier and hotter than the 30-year average between May and June 2006, with an 11-cm deficit in precipitation and 2° C increase in temperature from normal. During my 2007 field season, it was wetter and hotter than the 30-year average; there was 7 cm more precipitation than average, and it was over 1° C warmer than normal (National Oceanic and Atmospheric Administration 2008).

**METHODS**

**Natural Nests**

I searched all sites for nests of upland-nesting waterfowl (Anatidae) every 3 to 5 weeks from May to July. Each shelterbelt site and its paired open-field site were always searched within 1 day of each other. I utilized chain dragging to search the sites systematically by dragging a 30-m chain between 2 all-terrain vehicles (ATVs; Higgins et al. 1969). When the chain flushed a hen, I stopped the ATVs, walked over to where the bird flushed, and searched for a nest. I recorded the GPS location of each nest. I determined the developmental stage of eggs and their expected hatch date using the Weller method of candling (Klett et al. 1986). Nesting species was determined from the appearance of the flushed hen, feathers, down, and egg characteristics. I placed a 1-m tall stake 4 m directly north of the nest to aid in relocation.
Nests were inspected every 7-10 days, and I used egg membranes and shell remnants to determine nest fate (Klett et al. 1986). I wore rubber boots and gloves when inspecting nests to reduce the deposition of human scent at the nests. I considered a nest to be successful if ≥1 egg hatched. Hatching was indicated by presence in the nest bowl of a membrane detached from the shell and in one piece. The nest was designated as depredated if the membranes were ripped into many pieces and still connected to shell fragments. For depredated nests, I estimated the depredation date as the median date between the last intact nest-check and the date of discovery of the depredated nest.

**Artificial Nests**

My artificial nests mimicked upland waterfowl nests and were placed in the field between May and June 2006 and 2007. I used medium-sized white chicken eggs, and rinsed them off with tap water before use to reduce artificial scent. I wore rubber boots and gloves during egg handling and nest set up to reduce human scent deposition. I excavated a shallow nest bowl and lined it with grass and straw. To restrict overhead visibility, I folded vegetation over the nest. One fresh egg was placed in each nest. I positioned the fresh egg on a timer-device. If the egg was depredated, this timer recorded the time and date of the depredation event to the minute. The nests were marked with a 1-m tall stake, identical to natural nests. I also recorded the location of the artificial nest using GPS technology. Three nests were placed within each shelterbelt site: one was located on the leeward side within 2 times the height of the shelterbelt (2H), one between 2H and 8H on the leeward side, and one on the windward side within 3H of the

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1 Described in Chapter 2
shelterbelt. Additionally, one nest was placed within the open-field site. Locations for artificial nests were selected by forming a grid within the placement area. I then randomly selected a grid cell for nest location. Once within the cell, I randomized a distance (number of steps) and direction for the nest. I checked nests every 7-10 days. The egg and timer-device were removed after 21 days or a depredation event. For artificial nests, I defined a depredated nest as one where the egg had been punctured, cracked, or removed from the nest.

I collected meteorological conditions on the day of the depredation event (hereafter referred to as depredation day) for artificial nests from public weather stations throughout the state (MesoWest 2008). For comparison, I randomly selected a day between when I constructed the nest and when it was depredated (persistence day). I used weather data from the nearest public weather station to each site. Distances between the sites and the nearest weather station ranged from 11 to 79 km ($\bar{x} = 30$ km). I collected data on the instantaneous temperature, dew point, wind speed, and wind direction closest to the hour of depredation on both the depredation and persistence days. I also determined the average temperature, dew point, wind speed, and wind direction during each depredation day and persistence day. Finally, I calculated the standard deviation in wind speed and the dispersion in wind direction over the days of depredation and persistence.

**Statistical Analyses**

*Nest initiation.*— I used an ANOVA to determine if the date of nest initiation (Julian Day) varied among duck species. If there was a difference ($P \leq 0.05$), I used post-hoc
means comparisons (Tukey’s Honestly Significant Difference Test [Tukey HSD]) to
determine the relationship among species (Zar 1999). To determine if there were spatial
and temporal relationships in nest initiation, I compared the distance between nests in
relation to when the nests were initiated. I used the Pythagorean metric on the Universal
Transverse Mercator coordinates (represented as $X_i$ and $Y_i$) of the nest locations to
calculate distance ($\sqrt{((X_1 - X_2)^2 + (Y_1 - Y_2)^2)}$; Longley et al. 2005). For each site, I ordered
nests by their initiation date (i.e. the first nest laid on a site would be nest 1, the second
nest would be nest 2, …, the last nest laid on a site would be nest $N$, with $N =$ number of
nests on that site). I used an ANOVA to determine if the distance between the following
pairs of nests were different: Nests 1 and 2, Nests 1 and 3, Nests 2 and 3, Nests 1 and $N$
- 2, Nests 2 and $N$-1, and Nests 3 and $N$. To meet model assumptions, distance was
transformed using the fourth root (Zar 1999). If waterfowl were spacing their nests apart
at initiation, nests laid early should be farther apart than nests which were laid later.

Next, I limited my analysis to sites where nests 1 and 2 were <7 days apart to
account for potentially confounding effects from the date of initiation. I used a t-test
(pooled method; Zar 1999) to see if the distance between nests 1 and 2 was greater than
the distance between nests 1 and $N$, as would be expected if waterfowl were spacing nests
apart.

*Survival of natural nests.*— I used an ANOVA to determine if the date of depredation
(Julian Day) differed among species. If there was a difference, I used Tukey HSD to
determine the relationship among waterfowl species (Zar 1999). I also looked at the
relationship between nest density and Mayfield nest success of natural nests (Mayfield
I classified nest density (the number of nests per hectare of searched area) on WPAs as low (< 0.56), mid-low (0.56 to 1.10), mid-high (1.10 to 1.75), or high (> 1.75). These categories were based on the 4 quartiles of the total dataset. Then I compared the values of Mayfield nest success for each density class using an ANOVA on ranked data. The Mayfield method of calculating nest success accounts for bias in nest success estimates caused by the decreased probability of researchers locating nests depredated early in their incubation period (Mayfield 1961). It does so by explicitly accounting for the observation period of the nests (period from discovery by the researcher to nest termination; Mayfield 1961).

I found no difference in Mayfield nest success among species ($\chi^2_6 = 10.87, P = 0.08$), so I pooled species in subsequent analyses. To determine if there were spatial and temporal relationships in the number of days a natural nest survived (i.e. exposure days from initiation through hatching or depredation) within a WPA, I compared the difference in exposure days between pairs of nests to the distance separating the 2 nests. If predators were utilizing area-restricted searches, nests located close together should have more similar fates, and in particular more similar exposure days, than nests located farther apart. If predators utilize area-restricted searching to hunt for nests, those nests near depredated nests should have a greater risk of depredation and fewer exposure days, while nests located near successful nests would be more likely to survive longer (Tinbergen et al. 1967, Bell 1990). Therefore, I evaluated whether nest pairs separated by shorter distances were more similar in the number of exposure days than those separated by greater distances. For this analysis, the distance between pairs of nests were
categorized into 5 different classes (0-25 m, 25-50 m, 50-75 m, 75-100 m, 100-1000 m). Each nest was paired to a randomly selected nest within each distance class. The difference in exposure days was calculated for each pair. I used an ANOVA on ranked data to compare the difference in exposure days among distance classes separately for each year. I also investigated the relationship between nearest neighbor distance and fate of the nests. I used a mixed model with WPA included as a random factor and fate (both nests successful, both depredated, or mixed fate) as the explanatory factor for the nearest neighbor distance between pairs of nests (Oehlert 2000). I used the fourth root of distance to meet normality and homoscedasticity assumptions.

To determine if there was a larger-scale spatial relationship among WPAs, I compared the difference in exposure days between pairs of nests located on WPAs different distance classes apart (1-10 km, 10-25 km, 25-50 km, and > 50 km) to pairs of nests located on the same WPA (100-1000 m). I used separate ANOVAs for each year. No suitable transformations were found for the data, so I used ranked data in my ANOVAs. If an ANOVA was significant \( (P \leq 0.05) \), I used the Tukey HSD method of post-hoc means comparisons to determine the relationship among distance classes.

Temporal patterns in artificial nest depredation.— I utilized the Circular (Lund and Agostinelli 2007) and CircStats (Agostinelli 2007) packages in R 2.5.1 statistical software (R Development Core Team 2008) to analyze all circular data (time and wind direction). I calculated the mean time of depredation events and the dispersion (a measure of variation for circular statistics) for depredated artificial nests. I used Rayleigh’s test of uniformity to determine if the depredation times were evenly
distributed around the 24-hour period, or if there was a true mean time of depredation (Jammalamadaka and SenGupta 2001).

*Meteorological patterns in nest depredation.*— I used paired t-tests to evaluate whether meteorological events facilitated nest depredation (Zar 1999). I compared instantaneous temperature, wind speed, and dew point values at the time when artificial nests were depredated to the same time of day on the randomly-selected persistence day. I also compared the average temperature, wind speed, and dew point values over the persistence day to the day that the depredation event occurred. I compared the standard deviation in wind speed and wind direction (using dispersion) over the persistence day to the day that the depredation event occurred.

I used a circular ANOVA to determine if wind direction at the hour and day of depredation on an artificial nest was different from the persistence day (Jammalamadaka and SenGupta 2001). Wind data for west-facing shelterbelts was shifted 90 degrees to allow for the grouping of west and north-facing shelterbelts.

**RESULTS**

**Nest initiation**

Of the 248 total nests I found in 2006 and 2007, 16 were destroyed through human activity (e.g. mowing or investigator disturbance) or abandoned by the hens. I removed these nests from the dataset prior to analyses. The remaining 232 nests were primarily initiated by blue-winged teal (*Anas discors*), followed by mallard (*A. platyrhynchos*), gadwall (*A. strepera*), northern pintail (*A. acuta*), northern shoveler (*A. clypeata*), lesser scaup (*Aythya affinis*), and American wigeon (*Anas americana*; Figure
The average nest initiation date was 19 May during 2006 and 27 May during 2007 (Tables 3-1 and 3-2). Gadwall nests were initiated later in the year than all other species in 2006 ($F_4 = 12.01, P < 0.0001$; Table 3-1), but there was no difference in initiation date among species in 2007 ($F_7 = 1.04, P = 0.41$; Table 3-2). The first 3 nests initiated on each site were no farther from each other than they were from the last 3 nests initiated on the same site ($F_{5,96} = 0.46, P = 0.81$; Figure 3-3). Additionally, the first and second nest were no farther from each other ($\bar{x} \pm SE; 327 m \pm 101$) than the first and last nest ($418 m \pm 127; t_{26} = -0.45, P = 0.65$).

**Natural Nest Survival**

Of the 232 waterfowl nests, 114 nests were depredated. The average nest depredation date was 12 June during 2006 and 19 June during 2007 (Tables 3-1 and 3-2). There was no difference among species in date of depredation in 2007 ($F_6 = 2.02, P = 0.07$; Table 3-2), but gadwall nests were depredated later than blue-winged teal nests during 2006 ($F_4 = 4.01, P = 0.01$; Table 3-1). I found no relationship between nest density and Mayfield nest success ($F_{3,23} = 0.75, P = 0.53; r^2 = 0.09$; Figure 3-4). Mean nest density of the search area across all WPAs was 1.20 nests per hectare and ranged from 0.15 to 4.01 (SE = 0.18).

There was no relationship between the difference in exposure days of a pair of nests on the same WPA and the distance separating them during 2006 or 2007 (Table 3-3). Additionally, nearest neighbor distance was not different between successful pairs (49 m ± 5), depredated pairs (66 m ± 7), or mixed pairs (65 m ± 6; $F_{2,201} = 2.16, P = 0.12$). However, nest pairs located on the same WPA were more similar in the number of
exposure days than nests located on WPAs separated by >25 km during 2006 but not 2007 (Table 3-4).

**Temporal Patterns in Artificial Nest Depredation**

I deployed 40 artificial nests in 2006 and 48 during 2007. Of those nests, 52 survived their 21-day exposure period, 35 were depredated, and the fate of one could not be determined. I could not determine when 7 nests were depredated due to clock failure. The mean time of nest depredations was 15:55 h (dispersion = 0.32), but depredation events were distributed uniformly throughout the day (Rayleigh’s test of uniformity, $P < 0.06$). Most happened between 10:00 and 18:00 h (15 of 28 total; Figure 3-5).

**Meteorological Patterns in Nest Depredation**

For artificial nests, meteorological conditions differed between the depredation day and the persistence day for both the hour and average day temperature and dew point (Table 3-5). Temperatures at the time of a depredation event ($22.7^\circ \text{C} \pm 1.0$) were higher than at the persistence time ($19.7^\circ \text{C} \pm 0.9$) for the same artificial nest ($t_{26} = 2.73, P = 0.01$; Table 3-5). Average temperature over the depredation day ($21.8^\circ \text{C} \pm 0.7$) was also higher than the persistence day ($19.9^\circ \text{C} \pm 0.8$) for the same artificial nest ($t_{26} = 2.12, P = 0.04$; Table 3-5). Dew points both at the time and day of a depredation event ($16.1^\circ \text{C} \pm 1.0$ and $15.8^\circ \text{C} \pm 0.8$, respectively) were higher than at the time and day of persistence ($13.1^\circ \text{C} \pm 1.0, 13.8^\circ \text{C} \pm 0.8$) for the same artificial nest ($t_{26} = 2.28, P = 0.03; t_{26} = 2.13, P = 0.04$; Table 3-5). There were no differences in mean wind direction between the depredation day and persistence day for all artificial nests (Table 3-6).
DISCUSSION

Initiation

The dates of nest initiation for waterfowl species in this study correspond to the findings of other studies (Esler and Grand 1993, Krapu 2000, Sovada et al. 2000). Gadwall often nest later in the season than other species (Lokemoen et al. 1984, Krapu 2000, Gendron and Clark 2002). Gadwall might initiate nesting later in the season to take advantage of an increase in the availability of aquatic insects later in the year (Serie and Swanson 1976).

If density-dependent depredation occurs in waterfowl, hens should space their nests as far apart as possible within suitable habitat patches. However, I found no evidence that hens were doing this. Nests initiated early in the season were no farther from concurrent early nests than they were from nests initiated later in the season when the early nests would no longer be active. Evidence for density dependence on both natural and artificial waterfowl nest depredation is mixed. Both Sugden and Beyersbergen (1986) and Esler and Grand (1993) have found higher depredation rates on artificial nests when nests were located close together (30 to 40 m) than when spaced apart (>70 m). In both of these cases, crows were a primary nest predator in the high density plots (Sugden and Beyersbergen 1986, Esler and Grand 1993). Other studies have found no relationship between nearest-neighbor distances or density and nest success for both natural and artificial nests (Duebbert and Lokemoen 1976, Andrén 1991, Ackerman et al. 2004). Nest density across my study sites ranged from 0.15 to 4.01 nests per hectare ($\bar{x} = 1.20$) which is within the bounds of where density-dependent predation
has been found to occur (Esler and Grand 1993). Waterfowl may not have spaced out
their nests in my study site because they do not know where other nests are located or
because density-dependent depredation is not a problem in my area. The latter case is
supported by the lack of any relationship between nest density and the Mayfield nest
success in this study.

**Survival**

I found no evidence that area-restricted searching by predators within WPAs
affected waterfowl nest survival. There was no relationship between nearest neighbor
distance and nest fate, or between exposure days and the distance separating nest pairs on
the same WPA. Other studies have also failed to find a relationship between fate and
nearest neighbor distances (Andrén 1991, Larivière and Messier 1998a). In my study,
nests may have been far enough apart ($\bar{x} = 60$ m; median = 48 m) to negate the benefits
of area-restricted searching for predators. With large distances between nests, the
probability of a predator encountering a second nest after depredating the first would be
low.

However, I did find a relationship between the survival of nest pairs and the
distance between them at larger scales. The survival period of nest pairs located on the
same WPA was more similar than nest pairs on different WPAs separated by >25 km.
This indicates that local characteristics, such as the presence or absence of particular
predators or predator densities, may affect survival of waterfowl nests more than regional
patterns. Depredation rates on both natural and artificial nests have been shown to
decrease as their distance to the nest of either an American crow or fish crow (*Corvus*)
"ossifragus) increased (Shields and Parnell 1986, Sullivan and Dinsmore 1990). Nest pairs separated by 100 to 1000 m could potentially be within the home range of a crow, striped skunk, or red fox (Sargeant 1972, Sullivan and Dinsmore 1990, Larivière and Messier 1998b). Within the Prairie Pothole Region, the home range of female striped skunks averaged 1.39 km² and movements by females centered near dens containing young (Larivière and Messier 1998b). Additionally, red fox territories range from 6 to 8 km² and pups stay near their rearing dens for 10 to 15 weeks (Sargeant 1972). During the waterfowl nesting season in North Dakota (April to June), the daily movements of red foxes should be centered near den sites (Sargeant 1972).

I found the average time of depredation was 15:55 h with most depredations occurring between 10:00 and 18:00 h. These periods were similar to those found by Picman and Schriml (1994), who reported a peak in depredation on artificial nests in Canada between 10:00 and 20:00 h. The timing of depredation events in my study may have been driven by ground squirrels, which were numerous in my study area. Dion et al. (2003) found that the mean time for ground squirrel depredation events on artificial nests was 12:57 h in North Dakota. I had depredation events occur throughout the 24 h period. Medium-sized mammals, such as raccoons, red foxes, coyotes, and striped skunks, typically depredate artificial nests between 16:00 and 04:00 h (Picman and Schriml 1994, Larivière and Messier 2001, Dion et al 2003). These predators possibly account for overnight depredation events in my study.

I found a relationship between artificial nest depredation and meteorological conditions. Predators appear to have an easier time locating nests at higher temperatures
and dew points. As temperature increases, more odorants evaporate from an odor source, in this case the nest or incubating bird (Regnier and Goodwin 1977). Dew point is an accurate method to determine water vapor content in the air (Ahrens 2003). Water molecules compete with odorants for binding sites on the surface of the incubating hen, eggs, and nesting material causing a rapid release of odorants into the atmosphere (Regnier and Goodwin 1977, Conover 2007). These processes increase odorant concentration in the atmosphere, making the nest and incubating bird more conspicuous to foraging predators that use olfaction to locate prey (Conover 2007).

My study is the first to examine meteorological conditions at the hour of a nest depredation event, allowing greater insight into the specific conditions that improve predator foraging efficiency. Other studies have evaluated the effect of weather conditions during the day of a depredation event or over the entire incubation period (Palmer et al. 1993, Roberts et al. 1995, and Roberts and Porter 1998). Daily nest survival in turkeys (*Meleagris gallopavo*) in New York decreased when the mean temperature during the nesting period was above 18°C or when seasonal rainfall was above average (Roberts et al. 1995, Roberts and Porter 1998). Likewise, rainfall during incubation was negatively related to nesting success of turkeys in Mississippi (Palmer et al. 1993). The increase in nest depredation during warm and wet conditions was attributed to increased foraging efficiency of nest predators during those conditions (Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998). While previous evaluations of the impact of meteorological conditions on nest success in waterfowl is limited, similar relationships between wet years and low brood success and duckling
survival have been found in waterfowl (Krapu 2000, Krapu et al. 2000, Pietz et al. 2003). Further work incorporating timer-devices or alternative technologies that record the exact time of depredation for natural waterfowl nests are necessary to confirm the relationships between predator foraging and meteorological conditions.

Overall, my results with artificial nests support previous findings that predators that rely on the olfactory cues of large, ground-nesting birds have increased foraging efficiency under humid and warm conditions (Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998, Conover 2007). Even with frequent utilization of artificial nests in ecological studies, there is still argument in the literature over whether their use is justified (Faaborg 2004, Moore and Robinson 2004). Many studies assume that depredation patterns on artificial nests reflect those of natural nests in the same area. This is not always the case (Moore and Robinson 2004). Many studies have failed to find a significant relationship between nest success rates of artificial and natural nests (MacIvor et al. 1990, Guyn and Clark 1997, Wilson et al. 1998). In this study, I used artificial nests to evaluate predator activity patterns, not as an index of natural nest survival. In this case, the use of artificial nests is justified because I was not using artificial nest depredation rates as a surrogate to natural nest survival and because it provided me with information on the time of depredation.

MANAGEMENT IMPLICATIONS

Waterfowl production is modeled for harvest management decisions. While further work is needed, my results indicate that meteorological conditions could impact recruitment in ways that have not been emphasized in the past. Previous modeling efforts
focused on wetland availability throughout the nesting season (Geis et al. 1969, Miller 2000). However, approaches to harvest management that include additional environmental variables that impact reproduction and survival have been recommended in the past (Johnson et al. 1997, Miller 2000). The addition of different environmental factors, like departure from average temperature and rainfall, may improve the predictive power of models.

LITERATURE CITED


Figure 3-1: Diagram of the effect of shelterbelts on wind flow patterns around them (length of arrows reflecting relative wind velocity), adapted from Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, and Nord 1991.
Figure 3-2: Species composition of waterfowl nests found in my study areas in North Dakota during the 2006 and 2007 nesting seasons (BLWT = blue-winged teal, MALL = mallard, GADW = gadwall, NOPI = northern pintail, NSHO = northern shoveler, LESC = lesser scaup, WIGN = American wigeon, UNID = unidentified).
Figure 3-3: Distance between nests (in meters; error bars indicate SE) for pairs in order of nest initiation date (1: earliest initiation date, 2: second initiation date, …, Nr: last initiation date) for all my study sites (n=17) with at least 6 waterfowl nests in North Dakota during the 2006 and 2007 nesting seasons.
Figure 3-4: Relationship between Mayfield nest success and nest density (nests per hectare) of waterfowl nests across my study areas in North Dakota during the 2006 and 2007 nesting seasons.
Figure 3-5: Time that the egg in an artificial nest was depredated in North Dakota between May and July 2006 and 2007, with the black diamond indicating the overall mean time. Each concentric circle represents the number of eggs depredated during each hour, with 0:00 representing midnight and 12:00 being noon.
Table 3-1: Initiation and depredation dates (mean ± SE) for waterfowl nests found in my study areas in North Dakota during the 2006 nesting season.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total nests</th>
<th>Initiation date</th>
<th>Total depredated</th>
<th>Date depredated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue-winged teal</td>
<td>38</td>
<td>May 13 ± 1.5</td>
<td>17</td>
<td>June 4 ± 2.5</td>
</tr>
<tr>
<td>Mallard</td>
<td>23</td>
<td>May 13 ± 3.6</td>
<td>8</td>
<td>June 13 ± 7.1</td>
</tr>
<tr>
<td>Gadwall</td>
<td>29</td>
<td>June 1 ± 1.7</td>
<td>6</td>
<td>July 4 ± 2.8</td>
</tr>
<tr>
<td>Northern pintail</td>
<td>15</td>
<td>May 17 ± 5.2</td>
<td>4</td>
<td>June 18 ± 8.2</td>
</tr>
<tr>
<td>Northern shoveler</td>
<td>8</td>
<td>May 15 ± 5.0</td>
<td>1</td>
<td>June 3</td>
</tr>
<tr>
<td>TOTAL</td>
<td>113</td>
<td>May 19 ± 1.5</td>
<td>36</td>
<td>June 12 ± 2.8</td>
</tr>
</tbody>
</table>
Table 3-2: Initiation and depredation dates (mean ± SE) for waterfowl nests found in my study areas in North Dakota during the 2007 nesting season.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total nests</th>
<th>Initiation date</th>
<th>Total depredated</th>
<th>Date depredated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue-winged teal</td>
<td>62</td>
<td>May 25 ± 2.1</td>
<td>38</td>
<td>June 14 ± 2.4</td>
</tr>
<tr>
<td>Mallard</td>
<td>23</td>
<td>May 26 ± 4.3</td>
<td>16</td>
<td>June 20 ± 5.5</td>
</tr>
<tr>
<td>Gadwall</td>
<td>16</td>
<td>May 31 ± 3.0</td>
<td>11</td>
<td>June 27 ± 4.4</td>
</tr>
<tr>
<td>Northern pintail</td>
<td>5</td>
<td>May 18 ± 7.6</td>
<td>2</td>
<td>June 8 ± 14.5</td>
</tr>
<tr>
<td>Northern shoveler</td>
<td>8</td>
<td>May 29 ± 5.9</td>
<td>7</td>
<td>June 25 ± 6.5</td>
</tr>
<tr>
<td>Lesser scaup</td>
<td>3</td>
<td>June 12 ± 3.0</td>
<td>3</td>
<td>July 4 ± 5.8</td>
</tr>
<tr>
<td>American wigeon</td>
<td>1</td>
<td>May 20</td>
<td>0</td>
<td>NA</td>
</tr>
<tr>
<td>Unidentified</td>
<td>1</td>
<td>May 22</td>
<td>1</td>
<td>June 15</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>119</strong></td>
<td><strong>May 27 ± 1.5</strong></td>
<td><strong>78</strong></td>
<td><strong>June 19 ± 2.0</strong></td>
</tr>
</tbody>
</table>
Table 3-3: Comparison of differences (mean ± SE) in number of exposure days for pairs of waterfowl nests separated by different distances when both nests are within the same WPA in North Dakota during the 2006 and 2007 nesting seasons, and the results of ANOVAs comparing differences among distance classes.

<table>
<thead>
<tr>
<th>Distance Class</th>
<th>Number of Pairs</th>
<th>Exposure Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25 m</td>
<td>21</td>
<td>6.33 ± 1.50</td>
</tr>
<tr>
<td>25-50 m</td>
<td>48</td>
<td>6.77 ± 0.94</td>
</tr>
<tr>
<td>50-75 m</td>
<td>57</td>
<td>7.89 ± 1.04</td>
</tr>
<tr>
<td>75-100 m</td>
<td>71</td>
<td>6.00 ± 0.85</td>
</tr>
<tr>
<td>100-1000 m</td>
<td>104</td>
<td>5.18 ± 0.60</td>
</tr>
</tbody>
</table>

**ANOVA**  \( F_{4,296} = 1.87 \) \( P = 0.12 \)

<table>
<thead>
<tr>
<th>Distance Class</th>
<th>Number of Pairs</th>
<th>Exposure Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25 m</td>
<td>27</td>
<td>8.70 ± 1.22</td>
</tr>
<tr>
<td>25-50 m</td>
<td>47</td>
<td>10.43 ± 1.26</td>
</tr>
<tr>
<td>50-75 m</td>
<td>65</td>
<td>9.38 ± 0.88</td>
</tr>
<tr>
<td>75-100 m</td>
<td>59</td>
<td>9.63 ± 0.90</td>
</tr>
<tr>
<td>100-1000 m</td>
<td>117</td>
<td>9.23 ± 0.73</td>
</tr>
</tbody>
</table>

**ANOVA**  \( F_{4,310} = 0.23 \) \( P = 0.92 \)
Table 3-4: Comparison of differences (mean ± SE) in the number of exposure days of waterfowl nest pairs separated by different distances across WPAs in North Dakota during the 2006 and 2007 nesting season, and the results of ANOVAs comparing differences among distance classes. Significant differences between distance classes are indicated by different letters.

<table>
<thead>
<tr>
<th>Distance Class</th>
<th>Number of Pairs</th>
<th>Exposure Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100-1000 m</td>
<td>104</td>
<td>5.18 ± 0.60(^A)</td>
</tr>
<tr>
<td>1-10 km</td>
<td>66</td>
<td>5.77 ± 0.82(^{AB})</td>
</tr>
<tr>
<td>10-25 km</td>
<td>109</td>
<td>5.82 ± 0.59(^{AB})</td>
</tr>
<tr>
<td>25-50 km</td>
<td>112</td>
<td>7.83 ± 0.71(^B)</td>
</tr>
<tr>
<td>&gt;50 km</td>
<td>112</td>
<td>7.74 ± 0.67(^B)</td>
</tr>
<tr>
<td>ANOVA</td>
<td></td>
<td>(F_{4,498} = 3.98) (P = 0.004)</td>
</tr>
<tr>
<td>2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100-1000 m</td>
<td>117</td>
<td>9.23 ± 0.73</td>
</tr>
<tr>
<td>1-10 km</td>
<td>53</td>
<td>10.11 ± 1.00</td>
</tr>
<tr>
<td>10-25 km</td>
<td>93</td>
<td>11.13 ± 0.79</td>
</tr>
<tr>
<td>25-50 km</td>
<td>100</td>
<td>8.48 ± 0.53</td>
</tr>
<tr>
<td>&gt;50 km</td>
<td>119</td>
<td>10.29 ± 0.70</td>
</tr>
<tr>
<td>ANOVA</td>
<td></td>
<td>(F_{4,477} = 1.57) (P = 0.18)</td>
</tr>
</tbody>
</table>
Table 3-5: Comparison of meteorological conditions (mean ± SE) between the depredation event hour and day and a random persistence day for the same depredated artificial nests in North Dakota from May through July, 2006 and 2007; and the results of a paired t-test comparing those values.

<table>
<thead>
<tr>
<th></th>
<th>Depredation Day</th>
<th>Persistence Day</th>
<th>$P$ - value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hour Temperature</strong></td>
<td>22.7 ± 1.0</td>
<td>19.7 ± 1.0</td>
<td>$t_{26} = 2.73$  $P = 0.01$</td>
</tr>
<tr>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day Temperature</strong></td>
<td>21.8 ± 0.7</td>
<td>19.9 ± 0.8</td>
<td>$t_{26} = 2.12$  $P = 0.04$</td>
</tr>
<tr>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hour Wind Speed</strong></td>
<td>3.9 ± 0.4</td>
<td>4.7 ± 0.4</td>
<td>$t_{26} = -1.26$ $P = 0.22$</td>
</tr>
<tr>
<td>ms$^{-1}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day Wind Speed</strong></td>
<td>3.9 ± 0.3</td>
<td>4.5 ± 0.4</td>
<td>$t_{26} = -1.32$ $P = 0.20$</td>
</tr>
<tr>
<td>ms$^{-1}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Wind Speed SD</strong></td>
<td>1.6 ± 0.1</td>
<td>1.6 ± 0.1</td>
<td>$t_{26} = 0.29$  $P = 0.77$</td>
</tr>
<tr>
<td>ms$^{-1}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day Dispersion</strong></td>
<td>0.8 ± 0.1</td>
<td>0.8 ± 0.1</td>
<td>$t_{26} = -0.13$ $P = 0.90$</td>
</tr>
<tr>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hour Dew Point</strong></td>
<td>16.1 ± 1.0</td>
<td>13.1 ± 1.0</td>
<td>$t_{26} = 2.28$  $P = 0.03$</td>
</tr>
<tr>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day Dew Point</strong></td>
<td>15.8 ± 0.8</td>
<td>13.8 ± 0.8</td>
<td>$t_{26} = 2.13$  $P = 0.04$</td>
</tr>
<tr>
<td>°C</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3-6: Comparison of wind direction (mean ± dispersion) between the depredation event hour and day and a random persistence day for the same depredated artificial nests in North Dakota from May through July, 2006 and 2007; and the results of a circular ANOVA comparing the persistence day to the depredation day. Wind direction is given as the compass bearing of the direction from which the wind was blowing, with 0° indicating a wind from the North.

<table>
<thead>
<tr>
<th></th>
<th>Depredation Day</th>
<th>Persistence Day</th>
<th>$P$ - value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind Direction Hour</td>
<td>203° ± 0.26</td>
<td>197° ± 0.26</td>
<td>$F_{1,48} = 0.04$</td>
</tr>
<tr>
<td>Wind Direction Day</td>
<td>197° ± 0.43</td>
<td>175° ± 0.18</td>
<td>$F_{1,48} = 0.49$</td>
</tr>
</tbody>
</table>
CHAPTER 4
THE INFLUENCE OF VISUAL AND OLFACTORY CONCEALMENT ON
DUCK NEST SELECTION AND SUCCESS

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. I located waterfowl nests, monitored
them until termination (hatched or depredated), and collected both visual and olfactory
concealment characteristics of nest 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 ($\bar{x} = 81\%$)
than random sites ($\bar{x} = 75\%$), 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 my study area because the dominant nest predators, including raccoon (Procyon lotor)
and striped skunk (Mephitis mephitis), primarily utilize olfactory cues to locate nest sites.
INTRODUCTION

For birds, the selection of nest sites is an important decision. Evolutionary and ecological principles suggest that 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, birds should attempt to conceal their nests from predators, but different predators use differing means to locate nests. The two main methods that predators use to locate nests utilize visual and olfactory cues. Predators may use both types of cues while foraging, but they usually rely more heavily on one 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.

Generally, visual predators are more dependent on visual cues when locating food sources. This method is easier to understand because humans also rely heavily on visual cues. Visual cues to nest location include parental behavior (such as flushing), the 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. In addition to behavioral modifications, selection of certain site characteristics can reduce visual cues. Vegetative cover should increase 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 (Schrank 1972, Sugden and Beyersbergen 1987, Guyn and Clark 1997, Jobin and Picman 1997).

Unlike visual predators, olfactory predators rely mainly on olfactory cues for locating food sources. Important sources of odorants from the nest include the feces, the eggs, and the incubating bird (Stoddart 1980, Burtt and Ichida 2004). Olfactory predators forage by traveling the landscape until they recognize an odor cue from a food source. Once recognized, predators find the odor source by following the odor’s concentration gradient or traveling upwind (Stoddart 1980, Jolly and Jolly 1992).

Risks from olfactory predators can be reduced by lowering their likelihood of detecting and tracking odors. 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 could reduce odors associated with the nest by removing or ingesting the fecal sacs of their nestlings. These behaviors are found in many species. For example, eastern bluebirds (Sialia sialis) carry fecal sacs an average of 91 m from the nest (Lang et al. 2002). Additionally, eastern bluebirds, American crows (Corvus brachyrhynchos), and Florida scrub jays (Aphelocoma coerulescens) often place fecal sacs from nests on elevated sites, such as trees, fence posts, or electric wires (McGowan 1995, Lang et al. 2002). This activity may provide added benefit by keeping the fecal sac’s odor plume
above the height where a predator can detect an odor. 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 2003).

Changes in wind patterns caused by surface features should influence an olfactory predator’s ability to locate nests. 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 sooner (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 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 outcome. I utilized shelterbelts (planted tree-rows) to provide a range of olfactory concealment characteristics through altering wind flow (Figure 4-1; Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). I predicted that birds 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.

STUDY AREA

This study was conducted within the Prairie Pothole Region of North Dakota that 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 (USFWS) in Barnes, Cass, Cavalier, Griggs, Ramsey, Steele, and Stutsman counties. 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. Smooth brome (Bromus inermis), wheatgrass (Agropyron spp.), switchgrass (Panicum virgatum), needlegrass (Stipa spp.), alfalfa (Medicago
sativa), sweetclover (Melilotus spp.) were common plant species on the areas (Greenwood 1986, Choromanski-Norris et al. 1989). These WPAs ranged from 33 to 948 ha, and they were usually embedded in an agricultural matrix of cereal, oilseed, and hay production. I selected WPAs that contained shelterbelts and only searched 1 shelterbelt per WPA. Shelterbelt height ranged from 6.3 to 26.6 m (\( \bar{x} = 12.6 \)). Shelterbelt areas were separated from each other by \( \geq 3 \) km (\( \bar{x} = 14.5 \) km to the nearest shelterbelt area). I searched for nests along the length of the shelterbelt and out to at least 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; Figure 4-1). I 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 between 5 and 17 km from their corresponding shelterbelt area.

Duck nest predators observed in these areas included American crows, badgers (Taxidea taxus), coyotes (Canis latrans), ground squirrels (Spermophilus spp.), raccoons,
red foxes (*Vulpes vulpes*), striped skunks, and weasels (*Mustela* sp.). Predator removal programs had not been conducted on any WPA in >12 months and the WPAs were >17 km from areas conducting predator removal.

The average rainfall throughout the study period (May through July 2006 and 2007) ranged from 3.6-11.4 cm per month. Temperatures ranged from a mean of 14°C for the month of May to 23°C for July. Between May and June 2006, the region was drier and hotter than the 30-year average; there was an 11 cm deficit from average precipitation and it was 2°C warmer than normal. During the 2007 field season, it was wetter and hotter than average; there was a 7 cm surplus from average precipitation, and it was over 1°C warmer than the 30-year average. In fact, May 2007 was the fourth wettest May on record since 1875 (NOAA 2008).

**METHODS**

**Nest Searching**

I searched all shelterbelt areas and OF areas for nests of upland-nesting waterfowl (Anatidae) every 3 to 5 weeks from May to July of each year. Each field was searched twice in 2006 and 3 times in 2007. Shelterbelt areas and their OF areas were searched within 1 day of each other. I 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). When a bird was flushed, I stopped the ATVs, walked over to where the bird flushed, and searched for a nest. When I found a nest, I recorded its GPS location. I used the Weller method to candle eggs in the nest to determine their stage of development and expected hatch date (Klett et al. 1986). I determined nesting species
from the appearance of the flushed hen, feathers, down, and egg characteristics. I placed a 1-m tall stake 10 m directly north of the nest to aid in relocation of the nest.

I inspected nests every 7-10 days to determine nest fate. I 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). If the egg’s membrane was in one piece and not connected to the shell, I considered the nest hatched. If the membrane was ripped into many pieces and still connected to shell remnants, I considered the nest depredated.

**Visual Concealment Characteristics of Nest Sites**

After a nest was terminated (was no longer being incubated), I collected information on the visual concealment characteristics of nest sites and their paired random sites. 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 4-1). 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, I 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, I averaged Robel pole readings (minimum height that the pole was visible when placed in the nest bowl) when I 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). I 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 a 10 cm x 10 cm board on which 100 1-cm² squares were marked in a checkerboard pattern. I determined lateral concealment of the nest by placing the cover board vertically on the nest or random site and, while standing 4 m away, observing the number of cells on the cover board that were obscured by vegetation (Jones 1968).

**Olfactory Concealment Characteristics of Nest Sites**

The olfactory concealment characteristics of each nest site were determined after nest termination using 2 sonic anemometers (Campbell Scientific, Logan, Utah) that measured wind speed in 3 dimensions. I concurrently measured wind speed at a nest and a 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 a second for 30 min. 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, or isolated trees) 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’s (U) indicated
the mean wind speed over the recording period in the streamwise direction. Mean of all w’s (W) indicated the vertical wind speed over the recording period, with positive values for updrafts and negative values for downdrafts. I 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 (σ_x + σ_y + σ_z). I 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, I 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 4-1) and would not necessarily reflect waterfowl nest selection. I compared the characteristics of each OF nest site to the characteristics at its paired random site in the same OF.

I found a total of 248 nests over 2006 and 2007. However, time constraints of atmospheric measurements required that I select a subset of nests for data collection. In 2006, I randomly selected 1 nest from each of 3 distance classes at 6 shelterbelt areas (Figure 4-1). I 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, I randomly selected 1 successful and 1 depredated nest at each of 3 distance classes at 12 shelterbelt areas and from their respective OF areas. I collected visual concealment characteristics on a total of 46 nests because some shelterbelt and OF areas did not contain both successful and depredated nests. Mowing occurred prior to collection of olfactory characteristics at 7 nest sites. Therefore, I 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*; Table 4-1).

**Statistical Analyses**

Due to small sample sizes, species were pooled for analyses unless otherwise specified. I 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 I used a Wilcoxon signed rank test to compare nest sites to paired random sites (Zar 1999). I analyzed blue-winged teal nests in the same manner to determine if visual concealment characteristics were species-specific. To determine whether nest sites differed from their paired random sites in olfactory concealment characteristics, I 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 I used a Wilcoxon signed rank test.
There was no difference in nest success among species ($\chi^2_3 = 9.47$, exact $P = 0.09$), so species were pooled for comparisons between successful and unsuccessful nests. I 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). I used a Mann-Whitney test for lateral concealment because the data were not normally distributed (Zar 1999). I 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 ($U$), I used a Mann-Whitney test. I 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.

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 4-2). There was no difference ($P > 0.05$) for any other visual concealment characteristic, i.e. overhead concealment, Robel reading, or maximum vegetation height (Table 4-2). Blue-winged teal nest sites had shorter maximum vegetation height (0.83m ± 0.04) than random sites (0.92m ± 0.03; $P = 0.04$; Table 4-3). There was no difference for any other visual concealment characteristic of blue-winged teal nests (Table 4-3).
Olfactory concealment characteristics between OF area nests and their paired random sites did not differ \((P > 0.05; \text{Table 4-4})\).

**Nest Site Success**

Of the 59 nests where I 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 4-5). Of the 51 nests where I measured olfactory concealment characteristics across all areas (shelterbelt and OF areas), 22 were successful and 29 were depredated. Successful nests had less of a difference in lateral dispersion \((\sigma_u)\) between themselves and their paired random sites \((0.002 \pm 0.017)\) than depredated nests \((0.056 \pm 0.018; t_{49} = 2.12, P = 0.04; \text{Table 4-6})\).

**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 visual predator on the ground to locate nests. My 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). In particular, Livezey (1981) found blue-winged teal and northern shoveler nested in shorter, less dense cover than mallard and gadwall. Unfortunately, small sample sizes resulting from the constraints of atmospheric data collection necessitated pooling data by species. I had a sufficient number of blue-winged teal nests to analyze their selection of visual concealment characteristics separately. In this case, I found that blue-winged teal selected for shorter maximum vegetation height than random sites but showed no selection for lateral concealment. These results are consistent with previous findings that teal select for microhabitat characteristics at nest sites, in particular short-grass cover (Livezey 1981). Teal may nest in shorter vegetation due to an increased ability to detect approaching predators (Götmark et al. 1995).

**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 Klvaña 2004), while others investigating the same characteristics have found no effect (Schiek 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 (Clark and Nudds 1991, Rangen et al. 1999). In areas where visual predators dominate, visual concealment should be related to
nest success (Sugden and Beyersbergen 1987, Clark and Nudds 1991). In areas where the primary nest predators are mammals that rely on olfactory cues to locate nests, such as this study area, one would expect that visual concealment would not be strongly related to nest success (Clark and Nudds 1991). This is consistent with both my results and other studies where the primary predators responsible for nest depredations were determined (Rangen et al. 1999).

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 less of a difference in lateral dispersion between themselves and their paired random sites than depredated nests. Lateral dispersion is the variability in both wind speed and direction in streamwise flow and can be generated by wind flow 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 the resulting wider odor plume aids a predator in locating the 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 my 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 my study area documented several predator species foraging within a patch over the course of a single night (Jiménez et al. 2007). A landscape with a diverse predator assemblage using multiple foraging techniques increases the benefit of random nest site selection that makes “safe” locations less predictable to predators and reduces the ability of predators to develop search images of likely nest locations (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 between 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 (Schrank 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).

My study has a low sample size which may have obscured differences between species in selection characteristics, especially olfactory concealment characteristics. However, it remains useful because this study is one of the first to investigate olfactory concealment of waterfowl nests. I 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). Dense nesting cover 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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Distance from shelterbelt

Distance Class 1: Updrafts
Distance Class 2: Slow Wind
Distance Class 3: High Turbulence

Figure 4-1: Diagram of the effect of shelterbelts on wind flow patterns around them (length of arrows reflecting relative wind velocity), adapted from Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, and Nord 1991.
Table 4-1: Species composition of waterfowl nests used in this study and of all nests found in my study areas in North Dakota during the 2006 and 2007 nesting seasons.

<table>
<thead>
<tr>
<th>Species</th>
<th>Olfaction selection</th>
<th>All other analyses</th>
<th>Total over study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue-winged teal</td>
<td>7</td>
<td>32</td>
<td>108</td>
</tr>
<tr>
<td>Gadwall</td>
<td>4</td>
<td>7</td>
<td>47</td>
</tr>
<tr>
<td>Lesser scaup</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Mallard</td>
<td>5</td>
<td>13</td>
<td>49</td>
</tr>
<tr>
<td>Northern pintail</td>
<td>0</td>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td>Northern shoveler</td>
<td>0</td>
<td>1</td>
<td>19</td>
</tr>
<tr>
<td>American widgeon</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Unidentified</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>17</strong></td>
<td><strong>59</strong></td>
<td><strong>248</strong></td>
</tr>
</tbody>
</table>
Table 4-2: 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.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Nest $\bar{x} \pm SE$</th>
<th>Random location $\bar{x} \pm SE$</th>
<th>$t_{57}$</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overhead concealment (%)</td>
<td>50.5 ± 3.6</td>
<td>41.5 ± 4.4</td>
<td>1.18</td>
<td>0.08</td>
</tr>
<tr>
<td>Lateral concealment (%)</td>
<td>81.3 ± 2.7</td>
<td>74.7 ± 2.9</td>
<td>244</td>
<td>0.05</td>
</tr>
<tr>
<td>Robel reading (m)</td>
<td>0.33 ± 0.02</td>
<td>0.31 ± 0.01</td>
<td>1.35</td>
<td>0.18</td>
</tr>
<tr>
<td>Tallest vegetation (m)</td>
<td>0.89 ± 0.03</td>
<td>0.94 ± 0.02</td>
<td>−174.5</td>
<td>0.13</td>
</tr>
</tbody>
</table>
Table 4-3: 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.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Nest $\bar{x} \pm SE$</th>
<th>Random site $\bar{x} \pm SE$</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overhead concealment (%)</td>
<td>46.3 ± 4.2</td>
<td>36.3 ± 5.9</td>
<td>$t_{30} = 1.62$, $P = 0.12$</td>
</tr>
<tr>
<td>Lateral concealment (%)</td>
<td>77.5 ± 3.9</td>
<td>73.4 ± 4.0</td>
<td>$t_{30} = 0.69$, $P = 0.50$</td>
</tr>
<tr>
<td>Robel reading (m)</td>
<td>0.31 ± 0.02</td>
<td>0.30 ± 0.02</td>
<td>$t_{30} = 0.46$, $P = 0.65$</td>
</tr>
<tr>
<td>Tallest vegetation (m)</td>
<td>0.83 ± 0.04</td>
<td>0.92 ± 0.03</td>
<td>$t_{30} = -2.19$, $P = 0.04$</td>
</tr>
</tbody>
</table>
Table 4-4: Olfactory characteristics of OF 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 OF nests with their paired random sites.

<table>
<thead>
<tr>
<th></th>
<th>OF nest $\bar{x} \pm SE$</th>
<th>Paired site $\bar{x} \pm SE$</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U$</td>
<td>0.425 ± 0.035</td>
<td>0.402 ± 0.041</td>
<td>$S_{15} = 16.50$ $P = 0.46$</td>
</tr>
<tr>
<td>$W$</td>
<td>−0.021 ± 0.005</td>
<td>−0.002 ± 0.007</td>
<td>$t_{15} = -1.87$ $P = 0.08$</td>
</tr>
<tr>
<td>$\sigma_u$</td>
<td>0.266 ± 0.022</td>
<td>0.244 ± 0.025</td>
<td>$t_{15} = 1.61$ $P = 0.13$</td>
</tr>
<tr>
<td>$\sigma_w$</td>
<td>0.175 ± 0.013</td>
<td>0.176 ± 0.018</td>
<td>$t_{15} = 1.27$ $P = 0.22$</td>
</tr>
<tr>
<td>$T$</td>
<td>0.748 ± 0.054</td>
<td>0.715 ± 0.680</td>
<td>$t_{15} = 1.60$ $P = 0.13$</td>
</tr>
<tr>
<td>$U^*$</td>
<td>0.263 ± 0.015</td>
<td>0.245 ± 0.025</td>
<td>$t_{15} = 1.02$ $P = 0.32$</td>
</tr>
</tbody>
</table>
Table 4-5: 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.

<table>
<thead>
<tr>
<th></th>
<th>Successful $\bar{x} \pm SE$</th>
<th>Depredated $\bar{x} \pm SE$</th>
<th>$P$ - value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overhead concealment (%)</td>
<td>53.2 ± 5.4</td>
<td>48.5 ± 4.8</td>
<td>$t_{57} = -0.65$  $P = 0.52$</td>
</tr>
<tr>
<td>Lateral concealment (%)</td>
<td>83.0 ± 4.2</td>
<td>80.0 ± 3.5</td>
<td>$Z_{57} = 0.88$  $P = 0.38$</td>
</tr>
<tr>
<td>Robel reading (m)</td>
<td>0.32 ± 0.02</td>
<td>0.34 ± 0.02</td>
<td>$t_{57} = 0.64$  $P = 0.52$</td>
</tr>
<tr>
<td>Tallest vegetation (m)</td>
<td>0.84 ± 0.05</td>
<td>0.92 ± 0.03</td>
<td>$t_{57} = 1.58$  $P = 0.12$</td>
</tr>
</tbody>
</table>
Table 4-6: 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.

<table>
<thead>
<tr>
<th></th>
<th>Successful $\bar{x} \pm SE$</th>
<th>Depredated $\bar{x} \pm SE$</th>
<th>$P$ - value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U$</td>
<td>$-0.002 \pm 0.026$</td>
<td>$0.069 \pm 0.034$</td>
<td>$Z_{49} = -1.19$, $P = 0.23$</td>
</tr>
<tr>
<td>$W$</td>
<td>$-0.017 \pm 0.009$</td>
<td>$-0.019 \pm 0.007$</td>
<td>$t_{49} = -0.15$, $P = 0.88$</td>
</tr>
<tr>
<td>$\sigma_u$</td>
<td>$0.002 \pm 0.017$</td>
<td>$0.056 \pm 0.018$</td>
<td>$t_{49} = 2.12$, $P = 0.04$</td>
</tr>
<tr>
<td>$\sigma_w$</td>
<td>$0.007 \pm 0.012$</td>
<td>$0.016 \pm 0.010$</td>
<td>$t_{49} = 0.55$, $P = 0.59$</td>
</tr>
<tr>
<td>$T$</td>
<td>$0.012 \pm 0.040$</td>
<td>$0.116 \pm 0.039$</td>
<td>$t_{49} = 1.82$, $P = 0.07$</td>
</tr>
<tr>
<td>$U^*$</td>
<td>$0.032 \pm 0.026$</td>
<td>$-0.004 \pm 0.027$</td>
<td>$t_{49} = -0.96$, $P = 0.34$</td>
</tr>
</tbody>
</table>
CHAPTER 5
INFLUENCE OF SHELTERBELTS ON ARTIFICIAL AND NATURAL WATERFOWL NEST DEPREDATION IN NORTH DAKOTA

ABSTRACT  I evaluated the effects of shelterbelts within Waterfowl Production Areas (WPAs) on waterfowl nest density and success in North Dakota during the 2006 and 2007 nesting seasons. These shelterbelts alter wind flow, creating updrafts on the windward side (updraft zone), slow winds immediately on the leeward side (calm zone), and increased turbulence farther downwind of the shelterbelt (turbulent zone). While shelterbelts should reduce the risk of nest depredation by olfactory predators through increased turbulence, shelterbelts could also increase the presence of predators and facilitate nest depredation by avian predators. I found that nest density (nests per hectare) was higher away from shelterbelts in the open-field zone (mean ± SE; 1.02 ± 0.08) than in the calm zone (0.22 ± 0.17). Additionally, Mayfield nest success for waterfowl decreased as shelterbelt height increased. Other shelterbelt characteristics, like porosity and orientation, did not affect artificial nest success, natural nest success, or waterfowl nest density. While I found little evidence of shelterbelts impacting waterfowl nest success, isolated surface features increased the odds of nest depredation. The comparative reduction in the probability of depredation for nests near shelterbelts compared to nests located near isolated features may be due to a reduction in foraging efficiency of olfactory predators caused by shelterbelts.
INTRODUCTION


The presence of trees within habitat patches has received little attention in waterfowl nesting studies (Preston 1957, Gazda et al. 2002). Trees and planted tree-rows (i.e., shelterbelts) are often thought to affect duck nest success negatively. For some species, such as American crows (*Corvus brachyrhynchos*) and black-billed magpies (*Pica hudsonia*), trees provide a perch from which they can scan the surrounding area (Preston 1957, Gazda et al. 2002). Both raccoons (*Procyon lotor*) and red foxes utilize shelterbelts for resting and foraging (Fritzell 1978, Johnson and Beck 1988).
Additionally, telemetry data in North Dakota indicated that raccoons preferentially used travel lanes like shelterbelts during nocturnal foraging (Fritzell 1978).

However, shelterbelts may benefit nesting ducks by altering wind flow and increasing foraging difficulty for predators (Figure 5-1). Many duck nest predators, like raccoons and striped skunk, rely mainly on olfactory cues for locating food sources. For nests, important sources of olfactory cues include feces, chemicals secreted from the hen’s uropygial gland, and microorganisms living on her feathers (Stoddart 1980, Burtt and Ichida 2004). Olfactory predators forage by traveling within the landscape until they recognize an odor cue. Once they do so, they can follow the odor’s concentration gradient or travel upwind to find the source (Stoddart 1980, Jolly and Jolly 1992). The odor cue becomes harder to follow when wind direction varies widely, resulting in longer search times before a predator is able to locate the odor source (Shivik 2002).

Surface features, like isolated trees, increase local turbulence (Conover 2007), but shelterbelts (planted tree-rows) have a larger-scale effect than isolated trees, both up and downwind of the shelterbelt. In the upwind side of a shelterbelt, the air parcel is deflected upward and over the shelterbelt, creating updrafts (i.e., the updraft zone; Figure 5-1; Sturrock 1972, McNaughton 1988, Nord 1991). Immediately downwind of the shelterbelt (leeward side) there is a calm zone of decreased wind speed and small eddies (swirling currents of air indicative of turbulence) that develops due to drag from vegetation on the air travelling through the shelterbelt (i.e., the calm zone; Figure 5-1; Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). Beyond the calm zone, an area of large eddies and increased turbulence (i.e., the turbulent zone) forms where fast
moving air that flowed over the shelterbelt mixes with slow moving air that travelled through the shelterbelt (Figure 5-1; Heisler and DeWalle 1988, McNaughton 1988). Eventually, the differences in velocity that generate this disturbance even out and wind flow returns to its original form (McNaughton 1988). Factors that influence the strength and area of shelterbelt effects include the height of the shelterbelt, its porosity, the initial wind speed, and atmospheric stability (Heisler and DeWalle 1988).

The wind patterns in different shelterbelt zones (i.e., updraft, calm, and turbulent zones) as compared to sites far removed from shelterbelts (i.e., open-field zone) should influence an olfactory predator’s ability to find nests. Olfactory predators should have a harder time tracking olfactory cues in the updraft zone, as the odor plume may be carried by updrafts above the near ground level where the predator forages (Conover 2007). In turbulent air, the resultant odor plume may meander and change direction rapidly (Finelli et al. 1999, Moore and Crimaldi 2004). This unpredictability should make foraging in the turbulent zone more difficult for olfactory predators because scent is more patchily distributed (Vickers 2000, Moore and Crimaldi 2004). The calm zone should have easier foraging than the updraft and turbulent zone, attributable to a decrease in the occurrence and size of eddies (McNaughton 1988), making the odor plume more predictable and easier to track. Air flowing over open fields has comparatively straight or laminar flow, allowing for easier tracking of olfactory cues than any of the shelterbelt zones. Therefore nesting near shelterbelts may lead to increased nest success in areas where olfactory predators dominate.
The purpose of this research was to determine what constitutes safe nesting habitat for waterfowl in areas with shelterbelts. I compared waterfowl nest density and both natural and artificial nest success near shelterbelts to open fields and among shelterbelt zones.

**STUDY AREA**

I utilized WPAs managed by the United States Fish and Wildlife Service located within Barnes, Cass, Cavalier, Griggs, Ramsey, Steele, and Stutsman counties, North Dakota. These areas are within the Prairie Pothole Region of North Dakota (Stewart and Kantrud 1974). The WPAs ranged from 33 to 948 ha and were located within an agricultural landscape. The vegetation on the WPAs typically included needlegrass (*Stipa* spp.), smooth brome (*Bromus inermis*), switchgrass (*Panicum virgatum*), wheatgrass (*Agropyron* spp.), alfalfa (*Medicago sativa*), and sweetclover (*Melilotus* spp.; Greenwood 1986, Choromanski-Norris et al. 1989).

I used 28 WPAs: Alice, Avocet Island, Becker, Billings Lake, Breakey, Edwards, Erickson, Evers, Fingal, Gaier, Gette, Gunder, Jamestown College, Jeglum, Lost Island, Major, Miller, Ohnstad, Old Aalalen, Phil Aus, Pintail, Shaw, Stinkeoway, Storhoff, Tolstad, Tompkins, Wengeler, and Zimmerman. I observed the following duck nest predators in these areas: American crows, coyotes (*Canis latrans*), ground squirrels (*Spermophilus* spp.), raccoons, red foxes, striped skunk, and weasels (*Mustela* sp.). Predator removal had not occurred within the last year on any WPA used and these WPAs were > 17km from active removal areas.
I searched WPAs that contained shelterbelts and only searched 1 shelterbelt area per WPA. There were 12 north-facing shelterbelts sites and 10 west-facing shelterbelt sites, all located ≥3 km from other shelterbelt sites (\(\bar{x} = 14.5\) km). I searched for nests along the length of the shelterbelt; including an area at least 3 times the height of the shelterbelt (3H) on the windward side of the belt (north or west side) and 8H on the leeward side (south or east side). I selected these distances because this area has altered wind flow due to the presence of the shelterbelt (Figure 5-1; Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). The search area ranged from 2-22 ha per shelterbelt site. I paired shelterbelt sites with random sites of similar size that were void of trees (open-field sites). Open-field sites were > 100 m from any shelterbelt and were the approximate size of the shelterbelt search area. Search areas for open-field sites were approximately the same dimensions as the search area of their paired shelterbelt sites. If possible, I placed each open-field site within the same WPA as its paired shelterbelt site. When no suitable area was present (6 times), the open-field site was placed on the nearest suitable WPA (5-17 km separation). There were no differences in visual obstruction measurements, using Robel readings, among shelterbelt zones (updraft, calm, turbulent, and open-field; \(F_{2,52} = 2.47, P = 0.07\); Esler and Grand 1993).

**METHODS**

**Nest Searching**

I systematically searched all sites for nests of upland nesting waterfowl (Anatidae) by dragging a 30-m chain between 2 all-terrain vehicles (ATVs) from May to July of 2006 and 2007 (Higgins et al. 1969). When a hen was flushed, I stopped the
ATV, walked to the approximate location, and searched for a nest. If a nest was found, I recorded its location using the global positioning system (GPS) and determined the stage of development of eggs through the Weller method of candling (Klett et al. 1986). Nesting species was determined from the appearance of the flushed hen, feathers, down, and egg characteristics. To aid in nest relocation, I placed a 1-m tall stake 4 m north of the nest. I searched all sites twice in 2006 and 3 times in 2007, at an interval of 3 to 5 weeks. Each shelterbelt site and its paired open-field site were searched within 1 day of each other.

**Artificial Nests**

To create an artificial nest, I excavated a shallow nest bowl and lined it with dried or fresh grass collected from the immediate area. I placed 1 medium-sized white chicken egg on the treadle of a timer that recorded the time and date of any depredation event¹. Nests were not covered with nesting material because doing so would interfere with the timer mechanism. Instead, vegetation was folded over the nest to restrict overhead visibility. I recorded the location of the artificial nests using GPS technology. Identical to natural nests, I placed a 1-m tall stake directly north of the artificial nest at a distance of 4 m to aid in relocation.

I placed 1 nest on each open-field site (open-field zone) and 3 nests within each shelterbelt site. One shelterbelt nest was placed within 2H on the leeward side (calm zone). I placed another nest between 2H and 8H on the leeward side (turbulent zone). I placed the last shelterbelt nest on the windward side of the shelterbelt within the updraft

¹ described in Chapter 2
zone. I conceptually created a grid within each zone and randomly selected a grid cell for the artificial nest location. The exact location for the artificial nest was determined through randomizing a distance (number of steps) and direction within the grid cell.

**Nest Checking Protocol**

I inspected both artificial and natural nests every 7-10 days. While checking nests, I wore rubber boots to minimize human scent deposition. I differentiated between depredation events and hatching in natural nests using membrane and egg shell remnants. If a membrane was in 1 piece and not connected to the shell, I considered the nest successful (≥ 1 egg hatched). If the membranes were broken and still connected to shell remnants, I considered the nest depredated (Klett et al. 1986). Artificial nests were considered depredated if the chicken egg was broken or removed from the nest bowl. If no depredation occurred after 21 days, the egg and timer-device were removed, and the artificial nest was considered successful.

**Shelterbelt Characteristics**

I recorded the location (Universal Transverse Mercator coordinates) and orientation (north-facing or west-facing) of shelterbelts using GPS technology. Shelterbelts were designated as north-facing if the tree-row ran from east to west and as west-facing if the tree-row ran from north to south. Shelterbelt height was determined with a tangent-height gauge and meter tape.

Shelterbelt porosity was calculated as a ratio between the lowest leeward wind velocity \( U_{\min} \); 2H on the leeward of the shelterbelt) and the unobstructed wind velocity \( U_o \); 5H on the windward side of the shelterbelt; Bean et al. 1975). Wind velocities were
simultaneously measured using 2 sonic anemometers (Campbell Scientific, Logan, Utah) at a height of 1.25 m from a random location 2H on the leeward side and from that random location 5H on the windward side, creating a line between the locations that was perpendicular to the shelterbelt. The anemometers measured wind speed once per second over a span of 5 minutes. I used the central-most 2 minute period within the 5-minute interval to calculate the average wind speed for a particular location. I did not use the entire 5 minute period to ensure that investigators were away from the anemometers and not affecting measurements. This process was done at 3 different random locations to obtain a mean porosity index for each shelterbelt. Bean et al. (1975) found that porosity was the main parameter in determining the degree of wind reduction by a shelterbelt. Therefore, the percent wind reduction achieved by a shelterbelt gives a measure of the porosity that is comparable among shelterbelt sites.

**Statistical Analyses**

_Nest density and shelterbelts._— I evaluated the relationship between shelterbelt characteristics within WPAs and waterfowl nest density. Years were pooled because there was no difference in density between years ($F_{1,19} = 0.17, P = 0.68$). Nest density was calculated as the total number of nests in a shelterbelt zone divided by the area of the zone. I used a mixed model with site included as a random factor (Oehlert 2000). My first model explored the effect of shelterbelt orientation and zone on nest density. When there was a difference ($P \leq 0.05$), I used post-hoc means comparisons (Tukey-Kramer adjusted $P$-value) to determine the relationship among zones (Dunnett 1980). I transformed nest density using the cube root to meet homoscedasticity and normality
assumptions. To determine if distance and position relative to the shelterbelt was important or if it was solely proximity to trees that affected density, I pooled nest density data within the turbulent, calm, and updraft zones into a single shelterbelt zone and compared nest density in the shelterbelt zone to the open-field zone. I still included orientation as an additional explanatory factor. In this case, density was transformed by the square root to meet model assumption. My third model evaluated the effects of shelterbelt characteristics (porosity and height) on nest density. Given that porosity should have a curvilinear relationship to the strength and area of shelterbelt effects on wind flow, I included the quadratic term for porosity (porosity$^2$; Moysey and McPherson 1966, Plate 1971). I transformed nest density using the cube root to meet homoscedasticity and normality assumptions.

Artificial nest success and shelterbelts.— There was no difference in the percent of artificial nests that were depredated between years ($\chi^2_1 = 3.21, P = 0.07$), so years were pooled for the analyses. I used a generalized linear mixed model (binary distribution; logit model) with site included as a random factor, to investigate the relationship between shelterbelt characteristics and artificial nest success (0 = depredation, 1 = survived exposure period; McCullagh and Nelder 1989). In my first model, the explanatory variables included shelterbelt zone and orientation. For the second model, I randomly picked 1 of the 3 zones (updraft, calm, or turbulent) as a pair for the open-field nest on each WPA. This was done to determine if the presence of a shelterbelt near an artificial nest, instead of a nest’s distance and position within the shelterbelt zones, was an important factor in artificial nest success. For my third model, I evaluated the effect of
porosity and shelterbelt height on artificial nest success, and included the quadratic term for porosity. In all models, I checked for multicollinearity through correlations and regression modeling of the explanatory variables (Zar 1999).

**Natural nest success and shelterbelts.**—I evaluated the relationship between characteristics within WPAs and waterfowl nest survival using mixed models with site included as a random factor. I calculated nest success for each shelterbelt zone using the Mayfield method. Years were pooled for analyses because there was no difference in nest success on WPAs containing shelterbelts between years ($F_{1,19} = 1.51, P = 0.23$). There was also no difference among duck species in the percent of nests that survived ($\chi^2_6 = 10.87$, exact $P = 0.08$), so species were pooled. For my first model, the explanatory factors included shelterbelt orientation and zone. Next, I pooled the turbulent, calm, and updraft zone into 1 shelterbelt zone and reran the analyses to determine if relative proximity to the shelterbelt (shelterbelt zone versus open-field zone) was a factor in determining natural nest success. Finally, I looked at porosity, including its quadratic term, and height. In all 3 models, I transformed density using the square root to meet model assumptions.

**Relative impact of shelterbelt zone and nest-site characteristics on nest success.**—I employed generalized linear mixed models (binomial distribution; logit model) to evaluate the impact of several factors on the probability that an individual nest would be successful. I included site as a random factor in all cases. For the zone model, I included zone, orientation, shelterbelt height, porosity, and the quadratic term for porosity as explanatory variables. For the nest-site model, distance to nearest object, whether the
nearest object was a shelterbelt or an isolated surface feature (lone tree, utility pole, or snag), and the interaction between distance and identity were included as potential explanatory variables. Within each group, I checked for multicollinearity using correlations and regressions.

RESULTS

Nest Density and Shelterbelts

I found 247 nests within 27 WPAs. I found no waterfowl nests on 1 WPA, and this WPA was deleted from further analyses. Nest densities within WPAs ranged from 0.15 to 4.01 nests per hectare (mean ± SE; 1.2 ± 0.2).

On those 21 sites with shelterbelts, the orientation of the shelterbelt did not affect nest density ($F_{1,60} = 1.57, P = 0.22$), but shelterbelt zone did ($F_{3,60} = 3.28, P = 0.03$; Figure 5-2). Waterfowl nest densities were significantly higher in the open-field zone (1.02 ± 0.08) than in the calm zone (0.22 ± 0.17; $t_{60} = 3.00$, adjusted $P = 0.02$). There were no other differences among zones. When I compared all shelterbelt zones to open fields, there were no differences in nest density between them (shelterbelt versus open field; $F_{1,20} = 3.36, P = 0.08$) or shelterbelt orientation ($F_{1,20} = 1.67, P = 0.21$). When looking at the effects of porosity and shelterbelt height, I included 17 WPAs because I had no porosity values for Billings Lake, Breakey, Old Aalalen, and Zimmerman WPAs. Porosity ($F_{1,50} = 0.12, P = 0.73$), the quadratic effect of porosity ($F_{1,50} = 0.04, P = 0.84$), and shelterbelt height ($F_{1,50} = 0.03, P = 0.86$) did not impact waterfowl nest density.
Artificial Nest Success and Shelterbelts

I deployed a total of 88 artificial nests during 2006 and 2007 (40 and 48, respectively). Of those nests, 52 survived their exposure period, 35 were depredated, and the fate of 1 could not be determined. Artificial nest survival within WPAs was not affected by shelterbelt orientation ($F_{1,63} = 0.22, P = 0.64$) or zone ($F_{3,63} = 0.36, P = 0.78$). When I randomly selected 1 artificial nest from the shelterbelt site to compare with the paired open-field nest, shelterbelt orientation ($F_{1,21} = 0.01, P = 0.92$) and zone (shelterbelt versus open-field; $F_{1,21} = 0.92, P = 0.35$) did not affect the log odds of artificial nest success. Of the 18 sites where I measured the porosity of shelterbelts, the log odds of artificial nest survival was not affected by porosity ($F_{1,53} = 0.02, P = 0.90$), the quadratic term for porosity ($F_{1,53} = 0.00, P = 0.95$), or shelterbelt height ($F_{1,53} = 0.21, P = 0.65$).

Natural Nest Success and Shelterbelts

Of the 247 total nests found in 2006 and 2007, 16 were destroyed through human activity (e.g. mowing or investigator disturbance) or abandoned by the hens. I removed these nests from the data set prior to analyses. The remaining 231 nests were initiated by blue-winged teal (Anas discors; 99 nests), mallard (A. platyrhynchos; 46 nests), gadwall (A. strepera; 45 nests), northern pintail (A. acuta; 20 nests), northern shoveler (A. clypeata; 16 nests), lesser scaup (Aythya affinis; 3 nests), American wigeon (Anas americana; 1 nest), and 1 unidentified waterfowl. Of the 21 WPAs with a shelterbelt, mean nest success was 0.28 (SE = 0.07).

Shelterbelt orientation ($F_{1,35} = 0.38, P = 0.54$) and shelterbelt zone ($F_{3,35} = 1.05, P = 0.38$) did not impact nest success (Figure 5-3). After pooling the shelterbelt zones into
a single shelterbelt zone, orientation ($F_{1,14} = 0.19, P = 0.67$) and zone ($F_{1,14} = 0.18, P = 0.68$) still did not affect nest success. On the 17 WPAs where I measured the porosity of shelterbelts, porosity ($F_{1,35} = 1.39, P = 0.25$) and the quadratic term for porosity ($F_{1,35} = 1.13, P = 0.29$) did not affect nest success. Shelterbelt height did significantly affect nest success ($F_{1,35} = 4.77, P = 0.04$; Figure 5-4). The coefficient estimate for height was -0.04 (SE = 0.02), meaning that, holding all other factors constant, every 1 m increase in height of the shelterbelt decreased nest success by 0.04.

**Relative Impact of Shelterbelt Zone and Nest-site Characteristics on Nest Success**

For the 213 nests on 17 WPAs where I measured shelterbelt porosity, the log odds of nest success were not related to shelterbelt orientation ($F_{1,193} = 1.39, P = 0.24$), height ($F_{1,193} = 2.96, P = 0.09$), porosity ($F_{1,193} = 0.29, P = 0.59$), the quadratic term for porosity ($F_{1,193} = 0.08, P = 0.77$), or zone ($F_{3,193} = 0.23, P = 0.87$; Table 5-1). The odds of nest success when a shelterbelt was the nearest object to a nest was 2.6 times higher than when the nearest object was an isolated surface feature ($F_{1,184} = 3.90, P = 0.05$; Table 5-2). Additionally, successful nests were farther from the nearest object (175 m ± 14) than depredated nests (136 ± 14; $F_{1,184} = 5.45, P = 0.02$). For every 1 m increase in distance to the nearest object, the probability of a nest being successful increased by a factor of 1.01.

**DISCUSSION**

I found little evidence that shelterbelts impacted waterfowl nest density. Average nest density on WPAs containing shelterbelts (1.2 nests per hectare ± 0.2) is within the range of other nesting studies in the Prairie Potholes (0.1 to 6.3 nest per hectare: Kirsch
1969, Higgins 1977, Duebbert and Lokemoen 1980, Higgins et al. 1992, Jiménez et al. 2007). I found that nest densities were higher in the open-field zone (1.02 ± 0.08) than in the calm zone of shelterbelts (0.22 ± 0.17). Nesting in the calm zone could increase depredation risk from predators using both modalities (olfaction and vision) for foraging. Visual predators, such as American crows, can use shelterbelts as perches when looking for nest cues in the surrounding area (Preston 1957). Olfactory predators could also have an easier time foraging in the calm zone, relative to the turbulent and updraft zones. This zone has lower wind speed and turbulence than the surrounding zones, increasing the concentration of odorants and maintaining detectable concentration levels over a larger area (McNaughton 1988, Vickers 2000, Shivik 2002, Moore and Crimaldi 2004, Conover 2007). That should make foraging easier for olfactory predators in the calm zone because a higher concentration of odorants would increase the chance of detecting and locating the nest or the incubating bird (Conover 2007). The cumulative effects of increased risk from both types of predators in the calm zone may be why ducks did not nest in as high densities as in the open-field zone, where the primary risk should be from olfactory predators because there are no perches for visual predators.

While ducks did not nest in as high densities in the calm zone as in the open-field, the probability of an individual nest surviving was not affected by shelterbelt characteristics or by the shelterbelt zone in which the nest was located. Additionally, the mean nest success (Mayfield estimate) on sites containing shelterbelts (\(\bar{x}=0.28\)) was within the range found in North Dakota by other studies (0.01-0.62; Greenwood 1986, Sovada et al. 1995, Jiménez et al. 2007). The only shelterbelt characteristic that affected
waterfowl nest success was the height of the shelterbelt. For every 1 m increase in shelterbelt height, the nest success over that WPA decreased by 0.03.

While I found little evidence of shelterbelts impacting nest success of waterfowl, nests near isolated surface features (e.g., lone trees, snags, and utility poles) had a higher probability of being depredated than nests near shelterbelts. These results are supported by previous studies that found decreased nest success for waterfowl and ring-necked pheasants (*Phasianus colchicus*) in areas with trees and shrubs (Snyder 1984, Gazda et al. 2002). These surface features can be utilized as vantage points by avian nest predators and also may provide suitable nesting habitat for nest predators like crows or magpies (Preston 1957, Sullivan and Dinsmore 1990, Gazda et al. 2002). Artificial waterfowl nests closer to crows’ nests had higher depredation rates than those located farther from crows’ nests (Sullivan and Dinsmore 1990). In addition, isolated surface features do not generate as much turbulence as shelterbelts; thus, olfactory predators should have an easier time locating nests near isolated features than nests near shelterbelts (Shivik 2002, Conover 2007).

Based on my data, I hypothesize that shelterbelts reduce nest depredation from olfactory predators but increase depredation pressure from avian predators, while isolated features only increase depredation pressure from avian predators. Shelterbelts increase turbulence in the surrounding area (Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991), and turbulence decreases the foraging efficiency of olfactory predators by making odor cues harder to track (Vickers 2000, Shivik 2002, Moore and Crimaldi 2004). The increase in the probability of nest success for nests near
shelterbelts compared to those near isolated features (2.6 times more likely) found in this study may be due to a reduction in foraging efficiency of olfactory predators possibly caused by shelterbelts.

Given that nest predators within the Prairie Potholes differ in foraging habitat, temporal patterns of activity, and searching modalities (olfactory versus visual), defenses against 1 predator may make a nest more vulnerable to other predators, as in the case of shelterbelts (Choromanski-Norris et al. 1989, Sovada et al. 2000, Larivière and Messier 2001, Kuehl and Clark 2002, Dion et al. 2003). Shelterbelts both increase and decrease depredation risk from different predator groups. Risk due to olfactory predators should be reduced by shelterbelts because locating nests is more difficult under the increased turbulence generated by them (Shivik 2002, Conover 2007). Simultaneous to this reduction, shelterbelts could also increase the presence of predators by providing denning/nesting sites or serving as travel lanes, and facilitate foraging by visual predators by providing vantage points (Preston 1957, Fritzell 1978, Dekker 1987, Johnson and Beck 1988, Gazda et al. 2002). The lack of an overall shelterbelt effect on nest success in this study may result because these conflicting pressures counter balance each other. This hypothesis is supported by the greater probability of nest predation when nests are near isolated features versus shelterbelts. Isolated features do not generate high levels of turbulence but provide a vantage point for avian predators (Preston 1957, Conover 2007). The overall impact of shelterbelts should differ depending on the predator composition of an area. While shelterbelts may have no effect or even increase waterfowl nest success in
areas where olfactory predators dominate (such as indicated in this study), nest success may be reduced by shelterbelts if avian nest predators are abundant.

**LITERATURE CITED**


Figure 5-1: Diagram of the effect of shelterbelts on wind flow patterns around them and shelterbelt zone position (length of arrows reflecting relative wind velocity), adapted from Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, and Nord 1991.
Figure 5-2: Relationship between nest density (nests per hectare of searched area), shelterbelt zone, and orientation across my study areas (n = 21) in North Dakota during the 2006 and 2007 nesting seasons. The standard error for nest density in zones was used for the error bars.
Figure 5-3: Relationship between Mayfield nest success, shelterbelt zone, and orientation of natural waterfowl nests across my study areas (n = 21) in North Dakota during the 2006 and 2007 nesting seasons. The standard error for zone nest success was used for the error bars.
Figure 5-4: Relationship between Mayfield nest success and shelterbelt height (in m) across my study areas (n = 17) in North Dakota during the 2006 and 2007 nesting seasons.
Table 5-1: Counts of successful and depredated natural waterfowl nests across shelterbelt zones and shelterbelt orientation on my study areas (n = 21) in North Dakota during the 2006 and 2007 waterfowl nesting seasons.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Orientation</th>
<th>Successful Nests</th>
<th>Depredated Nests</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Updraft</td>
<td>West-facing</td>
<td>8</td>
<td>12</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>North-facing</td>
<td>17</td>
<td>11</td>
<td>28</td>
</tr>
<tr>
<td>Calm</td>
<td>West-facing</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>North-facing</td>
<td>5</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Turbulent</td>
<td>West-facing</td>
<td>8</td>
<td>13</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>North-facing</td>
<td>12</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Open-field</td>
<td>West-facing</td>
<td>25</td>
<td>27</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>North-facing</td>
<td>39</td>
<td>36</td>
<td>75</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>115</td>
<td>116</td>
<td>231</td>
</tr>
</tbody>
</table>
Table 5-2: Counts of successful and depredated waterfowl nests with different nearest objects on my study areas in North Dakota during the 2006 and 2007 nesting seasons.

<table>
<thead>
<tr>
<th></th>
<th>Successful</th>
<th>Depredated</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shelterbelt</td>
<td>59</td>
<td>55</td>
<td>114</td>
</tr>
<tr>
<td>Isolated Feature</td>
<td>40</td>
<td>52</td>
<td>92</td>
</tr>
<tr>
<td>Total</td>
<td>99</td>
<td>107</td>
<td>208</td>
</tr>
</tbody>
</table>
CHAPTER 6
CONCLUSIONS

Nest success and recruitment are major factors in the population maintenance of waterfowl. Even with management efforts directed at improving nest success of waterfowl, it remains low in some parts of the Prairie Pothole Region primarily due to nest depredation (Duebbert and Lokemoen 1976, Greenwood 1986, Losito et al. 1995, Cowardin et al. 1998, West and Messmer 2004, Emery et al. 2005, Drever and Clark 2007). To reduce nest depredation, birds should attempt to conceal their nests from predators. However, different predators use differing means to locate nests. The 2 main methods that predators use to locate nests utilize either visual or olfactory cues. Predators may use both types of cues while foraging, but they usually rely more heavily on one or the other (Wells and Lehner 1978). The characteristics that determine depredation risk at a nest site should depend on the methods predators use to locate nests.

Many duck nest predators, like raccoons (*Procyon lotor*) and striped skunk (*Mephitis mephitis*), rely mainly on olfactory cues for locating food sources. Olfactory predators forage by traveling within the landscape until they recognize an odor cue. Once they do so, they can follow the odor’s concentration gradient or travel upwind to find the source (Stoddart 1980, Jolly and Jolly 1992). The odor cue becomes harder to follow when wind direction varies widely, resulting in longer search times before a predator is able to locate the odor source (Shivik 2002). Low atmospheric turbulence (little variability in wind speed and direction) and high atmospheric stability allow odors from nests to remain at detectable concentrations over a larger area (Heinemann and
Wahanik 1998, Vickers 2000, Moore and Crimaldi 2004). Increased temperature and humidity enhance the release of odorants from incubating birds and their nests, increasing the probability that a predator will locate the nest (Regnier and Goodwin 1977, Conover 2007). Therefore, an increase in temperature, atmospheric stability, or water vapor content in the air or a decrease in wind turbulence should make foraging more efficient for predators that use olfactory cues to locate nests (Shivik 2002, Conover 2007).

Surface features, like isolated trees, increase turbulence near the feature (Conover 2007), but shelterbelts (planted tree-rows) have a larger-scale effect than isolated trees, both upwind and downwind of the shelterbelt (Sturrock 1972, McNaughton 1988, Nord 1991). Factors that influence the strength and area over which a shelterbelt impacts wind flow include the height of the shelterbelt, its porosity, the initial wind speed, and atmospheric stability (Heisler and DeWalle 1988). The wind patterns around shelterbelt sites as compared to the open-field sites should influence an olfactory predator’s ability to find nests. Olfactory predators should have a harder time tracking olfactory cues near shelterbelts because they generate updrafts and turbulence (Sturrock 1972, Heisler and DeWalle 1988, McNaughton 1988, Nord 1991). Therefore nesting near shelterbelts may lead to increased nest success in areas where olfactory predators dominate.

Predators that use vision should be unaffected by meteorological conditions and wind flow patterns. In this case, trees and shelterbelts should decrease duck nest success because they may serve as vantage points for avian predators. For some species, such as American crows (Corvus brachyrhynchos) and black-billed magpies (Pica hudsonia), trees provide a perch from which to scan the surrounding area (Preston 1957, Gazda et al.)
2002). Trees also serve as a nesting substrate. Depredation rates on both natural and artificial nests have been shown to decrease as their distance to the nest of either an American crow or fish crow (C. ossifragus) increases (Shields and Parnell 1986, Sullivan and Dinsmore 1990).

In my study, I investigated several components of waterfowl nest-site selection and success on sites with shelterbelts in North Dakota during the 2006 and 2007 nesting seasons. I focused on the effects from characteristics that would impact the foraging efficiency of olfactory and visual nest predators.

First I evaluated the spatial and temporal patterns of nest depredation on 248 waterfowl nests and 88 simulated waterfowl nests. I found no evidence that predators were able to locate adjacent nests using an area-restricted approach to foraging or that density-dependent depredation was occurring. However, artificial nests were more likely to be depredated when either temperature or dew point was high. Temperature and dew point increase evaporation and the release of odorants into the atmosphere, making the nest and incubating bird more conspicuous to olfactory predators (Regnier and Goodwin 1977, Conover 2007). These meteorological conditions improve the ability of predators to locate nests using olfaction, thus increasing the vulnerability of waterfowl nests to depredation.

Although the impact of meteorological conditions on artificial nest success indicated that olfactory predators were important in my study area, waterfowl selected nest sites based on visual, not olfactory, concealment characteristics. They selected nesting sites with greater lateral concealment than random sites. However, no visual
concealment characteristic was predictive of nest success. The only difference between successful and depredated nests consisted of lateral dispersion, an olfactory concealment characteristic.

Finally I found that nest density (nests per hectare) was higher away from shelterbelts than near them. Additionally, natural nest success decreased near shelterbelts as shelterbelt height increased. Other shelterbelt characteristics, like porosity and orientation, did not affect artificial nest success, natural nest success, or waterfowl nest density. While shelterbelts should reduce the risk of nest depredation by olfactory predators through increased turbulence (Conover 2007), shelterbelts could also increase the presence of predators and facilitate nest depredation by visual predators (Preston 1957, Gazda et al. 2002). The lack of an overall effect of shelterbelts on nest success may be due to counter balancing depredation pressure from multiple predators.

My results emphasize the importance of considering predator foraging methods when managers try to improve the nest success of ducks. Given that nest predators within the Prairie Potholes differ in foraging habitat, temporal patterns of activity, and searching modalities (olfaction versus vision), defenses against 1 predator could make a nest more vulnerable to other predators, as in the case of shelterbelts (Choromanski-Norris et al. 1989, Sovada et al. 2000, Larivière and Messier 2001, Kuehl and Clark 2002, Dion et al. 2003). The overall impact of shelterbelts should differ depending on the predator composition of an area. While shelterbelts may increase waterfowl nest success in areas where olfactory predators dominate, nest success may be reduced by shelterbelts if avian nest predators are abundant.
The relationship between visual concealment and success of natural nests is another example of the importance of considering predator foraging methods. 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 (Schiek and Hannon 1993, Howlett and Stutchbury 1996, Brua 1999, Burhans and Thompson 2001). In areas where visual predators dominate, visual concealment should be related to nest success (Sugden and Beyersbergen 1987). However, when the primary nest predators are mammals that rely on olfactory cues to locate nests, such as this study area, one would expect that visual concealment would not be strongly related to nest success.

Increasing nesting success of waterfowl is a primary focus of wildlife and land managers throughout North America (West and Messmer 2004). In considering management alternatives, such as the removal of shelterbelts from Waterfowl Production Areas, land managers need to consider the composition of the local predator community. Other management strategies, such as the creation of dense nesting cover (DNC), can be modified to provide concealment against both visual and olfactory predators. Dense nesting cover can increase heterogeneity by providing areas with different visual and olfactory concealment characteristics in the same patch if it provides differing levels of surface roughness across the planted area (i.e. patches within the DNC vary in height; Lapointe et al. 2000, Conover 2007). In the past, studies have focused on visual characteristics over olfactory ones. But more attention to the olfactory concealment of nests is clearly warranted given that the primary nest predators in many locations are

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PUBLICATIONS
