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Upland nesting waterfowl population responses to predator reduction in North Dakota

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UPLAND NESTING WATERFOWL POPULATION RESPONSES TO PREDATOR
REDUCTION IN NORTH DAKOTA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

by
Matthew R. Pieron
B. S., Mount Union College, 1999
M.S., Eastern Kentucky University, 2003
May 2010

DEDICATION

I got some terrible Chinese take-out the other day. The fortune in the cookie read “behind every able man there are always other able men.” If I am able, it’s largely due to the more than able men who shaped my life. My grandfathers, Vernon R. Pieron (Grampa; 1922–2008) and Dudley J. Masters (Pop; 1928–2004), taught me to catch fish, shoot pool and whiskey, raise hell, laugh till it hurts, be stubborn, work hard, love my family, not give up, finish what I start, and be my own person. My father, James R. Pieron, has always been my biggest fan and supporter; even when I was way to stubborn, raised too much hell, shot too much whiskey, put off work to catch fish, or leaned towards giving up. This dissertation is for my Grampa, Pop, and Dad.

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ABSTRACT

Population growth for mallards (*Anas platyrhynchos*), and presumably other upland nesting ducks, in the Prairie Pothole Region is most sensitive to nest success, and nest success is most strongly influenced by predation. I evaluated the efficacy of reducing predator populations to improve nest success and increase local breeding populations of upland nesting ducks on township-sized (93.2 km²) management units in eastern North Dakota, USA, during 2005–2008. I also examined potential territorial limitations on local population growth for mallards. Trappers annually removed an average of 245 predators per trapped site. I monitored 7,489 nests on 7 trapped and 5 nontrapped sites, and I found nest success to be 1.4–1.9 times greater on trapped sites, depending on year. I surveyed an average of 621 wetlands twice annually and observed 3,674 blue-winged teal (*A. discors*), 3,227 mallard, 2,287 gadwall (*A. strepera*), 1,539 shoveler (*A. clypeata*), and 679 pintail (*A. acuta*) breeding pairs. I found little evidence that local breeding populations of upland nesting ducks increased following predator reduction. Defense of territories, which may limit local population growth, was most frequent during settling and declined as greater portions of local mallard populations commenced nesting. Territorial defense was strongly correlated to the ratio of breeding pairs to available wetland habitat, such that sites with higher pair densities had greater frequencies of territorial behavior. Hence, defense of territories may function to limit local breeding populations. Though predator reduction provides managers with an effective tool to improve nest success at large spatial scales, they should not rely on the practice to increase local breeding populations.

CHAPTER 1. INTRODUCTION

The Prairie Pothole Region (PPR) is the most important habitat for production of North American ducks (Bellrose 1980, Batt et al. 1989). Conversion of grassland to cropland in this region has resulted in a fragmented and structurally diversified landscape, which, in turn, has altered the composition, distribution, abundance, and foraging efficiency of predators (Cowardin et al. 1983, Sargeant et al. 1993, Sovada et al. 2000, Phillips et al. 2003). Large predators, such as wolves (*Canis lupus*), were replaced by more abundant medium-sized species such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*; Sargeant et al. 1993, Greenwood et al. 1995, Sovada et al. 2001). More recently, major changes have taken place in the distribution and abundance of canids in the PPR; coyote (*C. latrans*) populations have expanded since the 1970s, whereas red fox populations have declined since the mid-1990s (Sovada et al. 1995; D. Fecske, North Dakota Game and Fish Department, unpublished data). Population growth for mallards (*Anas platyrhynchos*), and presumably other upland nesting ducks, originating from the PPR is particularly sensitive to breeding season vital rate changes, especially nest success (Johnson et al. 1992, Hoekman et al. 2002). Predators exert the greatest negative force on breeding season vital rates, as they cause most mortality in nesting hens and prefledged ducklings and are responsible for over 70% of nest failures in most studies (Sargeant and Raveling 1992, Sovada et al. 2001, Emery et al. 2005). Increased predation as a result of habitat alteration is partially responsible for dabbling duck nest success declines during the past century (Beauchamp et al. 1996, Drever et al. 2007).

In recent decades, managers attempting to improve waterfowl production have primarily used indirect measures to decrease nest predation, with much emphasis on increasing nesting cover (Klett et al. 1988, McKinnon and Duncan 1999, Williams et al. 1999). However, sociopolitical and economic pressures often limit the ability of managers in the PPR to provide the amounts of grassland cover necessary to ensure high nesting success (Rohwer et al. 2004; C. Dixon, United States Fish and Wildlife Service [USFWS], unpublished report). In areas where nesting cover is inadequate, direct intensive predator management may be a viable method for minimizing the impacts of predation on nest success (Sovada et al. 2001). Trapping to reduce local predator populations initially yielded inconsistent results depending on methods and scale (Greenwood 1986, Sargeant et al. 1995, see review in Greenwood and Sovada 1996). Recent evaluations at 2 spatial scales (41.5 km² and 2.5 km²) reported a doubling of nest success for areas with predator reduction when compared to untreated areas in North Dakota (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006). In light of these findings, the USFWS recently recommended implementation of township-scale (93.2 km²) predator management in cropland dominated landscapes within the PPR for reducing predation on nesting waterfowl as part of a step-down plan from the Prairie Pothole Joint Venture (C. Dixon, USFWS, unpublished report). In Chapter 2, I examine the efficacy of township-scale predator reduction for improving nest survival of upland nesting ducks.

Population growth for ducks in the PPR is especially sensitive to fluctuations in nest success (Johnson et al. 1992, Hoekman et al. 2002), and reduced nest success appears to decrease breeding duck numbers in the PPR (Cowardin et al. 1983,

Greenwood et al. 1995). With this in mind, management that improves nest success (i.e. predator management) may have the potential to increase productivity and abundance of local breeding populations (Duebbert and Lokemoen 1980, Anderson et al. 1992). Numerous studies have reported that female waterfowl are philopatric to breeding locations where they nested successfully in the previous season (Johnson and Grier 1988, Lokemoen et al. 1990), and local breeding populations have been found to increase following predator removal (Duebbert and Kantrud 1974, Garrettson and Rohwer 2001). If increased duck production in predator managed areas combined with over-winter survival and philopatry leads to increased local breeding populations in subsequent years, heightened production as a product of elevated nest success may be compounded over years, lending to more cost-effective management (Garrettson and Rohwer 2001). To date there have been no extensive replicated investigations regarding breeding population densities of upland nesting ducks in years following intensive predator management. In Chapter 3, I examine whether local breeding pair abundance for each of the 5 most common upland nesting ducks in North Dakota increased following intensive predator management.

In the PPR, breeding duck densities are strongly correlated with wetland conditions (Dzubin 1969a, Pospahala et al. 1974, Johnson and Grier 1988, Cowardin et al. 1995, Viljugrein et al. 2005), and carrying capacity may be regulated by conspecific intolerance related to water-area availability (Hochbaum 1944, Dzubin 1955). The three-bird flight (TBF) is the most common form of territorial defense for mallards and other prairie nesting dabbling ducks (McKinney 1965, Seymour 1974, Humburg et al. 1978, Seymour and Titman 1978, Titman and Seymour 1981). TBFs are aerial chases that

ensue when an intruding pair enters an established pair's territory and the territorial drake pursues the intruding female, with her mate following closely behind (Hori 1963, Titman 1973). The TBF has been suggested to be an integral part of the breeding strategy that serves as a mechanism for the establishment and maintenance of territories and the subsequent expulsion of intruding pairs during settling through early incubation (McKinney 1965, Seymour and Titman 1978, Titman and Seymour 1981, Titman 1983, Anderson and Titman 1992).

Population density and habitat availability should largely dictate the frequency of territorial behavior (Dzubin 1955, 1969b). Additionally, population growth for mallards is most strongly correlated with nest success (Johnson et al. 1992, Hoekman et al. 2002); hence, areas achieving high nest success may have more pairs attempting to settle in subsequent years, and therefore, higher frequencies of TBFs. Anderson and Titman (1992) noted that minimal effort has been directed towards understanding the effects of population density on the breeding behavior of waterfowl and that more research should be conducted to assess the impact of varying population densities on spacing behavior and dispersion. In Chapter 4, I evaluate the effects of nest success in the previous season, breeding population size, available wetland habitat, and the ratio of breeding population size to available wetland habitat on the frequency of TBFs in wild breeding mallard populations.

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CHAPTER 2. EFFECTS OF LARGE-SCALE PREDATOR REDUCTION ON NEST SUCCESS OF UPLAND NESTING DUCKS

The Prairie Pothole Region (PPR) is the most important habitat for production of North American ducks (Bellrose 1980, Batt et al. 1989). Conversion of grassland to cropland in this region has resulted in a fragmented and structurally diversified landscape, which, in turn, has altered the composition, distribution, abundance, and foraging efficiency of predators (Cowardin et al. 1983, Sargeant et al. 1993, Sovada et al. 2000, Phillips et al. 2003). Large predators, such as wolves (*Canis lupus*), were replaced by more abundant medium-sized species such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*; Sargeant et al. 1993, Greenwood et al. 1995, Sovada et al. 2001). More recently, major changes have taken place in the distribution and abundance of canids in the PPR; coyote (*C. latrans*) populations have expanded since the 1970s, whereas red fox populations have declined since the mid-1990s (Sovada et al. 1995; D. Fecske, North Dakota Game and Fish Department, unpublished data). Population growth for mallards (*Anas platyrhynchos*), and presumably other upland nesting ducks, originating from the PPR is particularly sensitive to breeding season vital rate changes, especially nest success (Johnson et al. 1992, Hoekman et al. 2002). Predators exert the greatest negative force on breeding season vital rates, as they cause most mortality in nesting hens and prefledged ducklings and are responsible for over 70% of nest failures in most studies (Sargeant and Raveling 1992, Sovada et al. 2001, Emery et al. 2005). Increased predation as a result of habitat alteration is partially responsible for dabbling duck nest success declines from the 1930s to the 1980s (Beauchamp et al. 1996, Drever et al. 2007).

In recent decades, managers attempting to improve waterfowl production have primarily used indirect measures to decrease nest predation, with much emphasis on increasing nesting cover (Klett et al. 1988, McKinnon and Duncan 1999, Williams et al. 1999). Unfortunately, the amount of cover on the landscape required to meet the nest success threshold for population maintenance in the U.S. prairies appears to be near 40% (Reynolds et al. 2001), which is a lofty goal for wildlife managers in much of the PPR due to sociopolitical and economic challenges (Rohwer et al. 2004; C. Dixon, United States Fish and Wildlife Service [USFWS], unpublished report). Large-scale agricultural policies like the Conservation Reserve Program (CRP) that provide economic incentives to private landowners for converting cropland to perennial cover have positively affected nest success in the U.S. PPR (Reynolds et al. 2001, 2007). The long-term decline in nest success reported by Beauchamp et al. (1996) leveled off in the U.S. prairies by the mid-1980s and has increased recently to levels above the long-term average, which temporally coincides with implementation of the CRP (Drever et al. 2007). However, nearly 1 million acres of CRP cover in the PPR of the Dakotas were converted back to cropland in 2007 and 2008. Moreover, 60% of the current acreage enrolled in the CRP is projected to be lost by 2012 (U.S. Department of Agriculture Farm Service Agency 2008). It is likely that the benefits provided to nest success by the CRP will decline as more contracts expire from the program, so waterfowl managers may need to rely on alternative techniques to meet nest success goals.

In areas where nesting cover is inadequate, direct intensive predator management may be a viable method to minimize impacts of predation on nest success (Sovada et al. 2001). Trapping to reduce local predator populations initially yielded inconsistent results

depending on methods and scale (Greenwood 1986, Sargeant et al. 1995, see review in Greenwood and Sovada 1996). Recent evaluations at 2 spatial scales (41.5-km² and 2.5-km²) reported a doubling of nest success for areas with predator reduction when compared to untreated areas in North Dakota (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006). Hiring of professional trappers, flexible trapper work schedules, financial incentives for trapper effectiveness, and availability of trapping techniques not permitted in previous studies were cited as likely reasons for the success of predator removal in these more recent studies (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006).

The USFWS recently recommended implementation of township-scale (93.2 km²) predator management in cropland dominated landscapes within the PPR for reducing predation on nesting waterfowl as part of a step-down plan from the Prairie Pothole Joint Venture (C. Dixon, USFWS, unpublished report). My first objective was to examine the efficacy of township-scale predator reduction for improving nest survival of upland nesting ducks. My second objective was to examine the relationship between nest success and distance from the edge of trapped sites. I hypothesized that nest survival would be higher in the center of trapped sites than near the periphery. This porous border hypothesis reflected my suspicion that predator activity may be greatest at the edge of the treatment area due to predator immigration from non-trapped areas. My final objective was to examine the effects of nest age, initiation date, and species on nest survival because these variables have been important in other studies of nest success (Beauchamp et al. 1996, Emery et al. 2005, Grant et al. 2005).

STUDY AREA

I conducted my study in the drift prairie physiographic region during 2005-2007 in Benson, Cavalier, Nelson, Ramsey, Stutsman, Towner, Walsh, and Wells counties, North Dakota. Natural habitats were highly fragmented, and the region was dominated by small grain, oilseed, and row-crop agriculture. Intermixed perennial cover was present in the form of hay, pasture, and idle cover enrolled in the CRP or in federal Waterfowl Production Areas (WPAs). American crows (*Corvus brachyrhynchos*) and black-billed magpies (*Pica hudsonia*) were uncommon, whereas raptors such as red-tailed hawks (*Buteo jamaicensis*), northern harriers (*Circus cyaneus*), Swainson's hawks (*Buteo swainsoni*), and great horned owls (*Bubo virginianus*) were commonly observed (C. Martin, University of Guelph, unpublished data). Coyotes, striped skunks, raccoons, American badgers (*Taxidea taxus*), American mink (*Neovision vison*), and Franklin's ground squirrels (*Spermophilus franklinii*) were common mammalian predators of the region. Red foxes were present at much lower densities during our study than in the 1990s. Evidence of sarcoptic mange (*Sarcoptes scabiei*), which is known to reduce fox populations (Cypher 2003), began to appear in North Dakota's red fox population during the mid-1990s and continues to be persistent (Allen 1996, Sovada 2005).

METHODS

Field Methods

I conducted research on 12 township-sized (93.2 km²) study sites. Three of my sites were part of an operational predator management program initiated prior to this study, and I did not select them randomly, though they were similar to the other sites with respect to breeding pairs per km² and grassland cover, except for 1 site that had 85%

grassland cover. I randomly selected all other sites from a set of potential sites that supported >23 breeding duck pairs per km² and had moderate levels of grassland cover (~20% to 40%) in eastern North Dakota as determined from a geographic information system (GIS) based predator management decision matrix developed by USFWS Region 6 Habitat and Population Evaluation Team (C. Dixon, USFWS, unpublished report). I then visually inspected potential sites via small aircraft to confirm wetland and upland habitat composition. I randomly selected potential sites and met with landowners to discuss the possibility of working on their land. I assigned a trapped treatment to sites where I obtained $\geq 80\%$ landowner permission for trapping. I assigned a non-trapped treatment to sites that failed to meet that minimum percentage but received enough landowner permission to monitor nest success. In 2005 I evaluated 4 non-trapped sites and 6 trapped sites. I replaced 1 trapped site and 1 non-trapped site from 2005 with 1 new trapped and 1 new non-trapped site that we evaluated in 2006 and 2007.

For each trapped site, Delta Waterfowl Foundation (DWF) hired 1 professional trapper to remove mammalian predators from 15 March until 15 July. DWF paid trappers an average of \$22,000 for the 4-month period, and they received a bonus based on a sliding scale of nest success ranging from \$600 for 30% nest success to \$3,000 for nest success $\geq 90\%$. Trappers used all legal removal methods including foothold traps, body-gripping traps, snares, and shooting. Trappers checked traps at least every other day, and they killed all trapped predators. Trappers recorded the number of each predator species caught per day.

I randomly selected at least 7 nest searching plots per study site from all quarter sections where I had permission to work and that contained at least 32.4 ha of perennial

cover. I searched each plot for nests at least twice, and up to 3 times, from late April until July at approximately 3-week intervals. Two person crews dragged a chain between 2 all-terrain vehicles to locate nests by flushing attending females from 0800 to 1400 hours to maximize nest detection (Klett et al. 1986, Gloutney et al. 1993, Loos and Rohwer 2004). Once crews located a nest, they recorded the Universal Transverse Mercator (UTM) coordinates and marked the nest using a numbered wooden lathe placed 10 m from the nest and an orange metal rod (3 mm diameter, 0.95 m length) placed at the nest bowl.

Crews recorded clutch size and estimated incubation stage by candling multiple eggs upon nest discovery and every 6-10 days thereafter, until the nest was either destroyed or hatched (Weller 1956). I estimated nest initiation dates by backdating based on clutch and incubation stage. I categorized nest fates as successful (≥ 1 egg hatched), abandoned (hen absent and no advance in incubation), or destroyed. I removed nests from analyses that we were unable to relocate or that were abandoned due to investigator disturbance before the first revisit. For nests that were abandoned or destroyed due to investigator activity, flooding, or machinery after the initial revisit, I censored the last exposure interval for analysis. Hence, my measures of nest success represented 1 – probability of being destroyed by a predator.

My research was approved under the Louisiana State University Agricultural Center Animal Care and Use Committee Protocol Number AE-05-06. Predator removal and nest searching on Waterfowl Production Areas and National Wildlife Refuges were approved through USFWS special use permits DLWMD-05-008 and 62514-06-008.

Statistical Analysis

I used the logistic-exposure method to model DSR as a function of my categorical, continuous, and time-specific predictor variables (Shaffer 2004). The logistic-exposure method is a generalized linear modeling approach that models DSR for any nest during any nest-check interval as a logistic function of the values of explanatory variables for the nest during that interval, and it does not assume homogeneous DSR among and within nests (Shaffer 2004). Based on previous waterfowl literature, I identified a set of candidate variables that in combination with my treatment variable (trapped vs. non-trapped) may influence DSR of duck nests. I included year (2005, 2006, or 2007), treatment (trapped vs. non-trapped), species (American wigeon [*Anas americana*], blue-winged teal [*A. discors*], gadwall [*A. strepera*], green-winged teal [*A. crecca*], mallard, northern pintail [*A. acuta*], northern shoveler [*A. clypeata*], or lesser scaup [*Athya affinis*]) as categorical predictor variables. I also included study site nested within treatment category to account for unmeasured variation among sites. I included nest age, initiation date, and distance from the edge of the study site as continuous variables in the model. Nest age was an interval specific variable that I calculated as the average age during each exposure interval for each nest (Shaffer 2004). I also included quadratic terms for nest age, initiation date, and distance from the edge of the study site to allow for potential nonlinear effects of these 3 variables. Lastly, I included the interactions of treatment (trapped vs. non-trapped) with all continuous variables and their quadratic terms to determine if the magnitude or direction of their effect varied among treatments.

I used PROC GENMOD (SAS Institute, Cary, NC) to explore the effect of covariates on nest survival probability, and I treated each interval between visits as an observation. Because I had a small suite of independent predictor variables and sufficient data to run a full model, I began with a saturated model that I sequentially reduced using backwards elimination (Agresti 1996). I assessed model overdispersion using Pearson's χ^2 goodness-of-fit statistics from our full model, and if necessary ($\hat{c} > 1$), I retained this estimate as a scale parameter in subsequent models. I eliminated nonsignificant variables ($P > 0.05$, based on Type III generalized estimating equations) at each step, starting with the highest order interactions, until all remaining variables were significant. I retained main effects whenever they were included within a significant interaction or quadratic effect. I used LSMEANS and ESTIMATE statements to derive model-based predicted values and their associated standard errors (Shaffer and Thompson 2007). I used a 35-day exposure period to convert DSR to nest success (Klett et al. 1986) for creating some figures because nest success is a more meaningful metric than DSR for most waterfowl managers (Arnold et al. 2007).

RESULTS

Trappers removed 4,404 predators (Table 2.1). Skunks and raccoons constituted most of the trapped predators and were 38.1% and 34.5% of the total, respectively. The remaining captures included Franklin's ground squirrels (14.1%), American mink (4.5%), American badgers (3.9%), red foxes (1.9%), coyotes (1.9%), and weasels (*Mustela erminea* and *M. frenata*; 1.1%). The majority of trapped Franklin's ground squirrels occurred on 1 site as a result of differences in trapping techniques and species targeting by that trapper (D. Maw, Delta Waterfowl, personal communication).

Table 2.1. Mammalian predators removed from 93.2 km² study sites in eastern North Dakota, USA, during 15 March-15 July in 2005-2007.

Site	Year	Red fox	Coyote	Raccoon	Badger	Skunk	Mink	Weasel ^a	Squirrel ^b	Total
1	2005	0	0	83	12	118	26	9	9	257
1	2006	1	0	70	4	81	9	5	17	187
1	2007	0	0	73	3	124	10	1	55	276
2	2005	7	9	68	6	101	2	0	0	193
2	2006	0	3	113	4	61	1	0	0	182
2	2007	6	2	109	5	77	0	0	0	199
3	2005	3	1	136	11	132	32	0	10	325
3	2006	2	13	99	12	59	19	1	16	221
3	2007	0	7	60	8	79	9	1	17	181
4	2005	9	3	74	17	88	2	0	0	193
4	2006	1	7	59	8	77	0	0	0	152
4	2007	4	13	38	13	63	1	0	0	132
5	2005	6	3	26	13	97	7	20	8	180
6	2005	10	3	98	13	145	13	0	0	282
6	2006	15	8	102	15	112	16	0	0	268
6	2007	17	11	104	14	104	32	0	0	282
7	2006	1	0	122	7	78	12	0	203	423
7	2007	0	2	83	7	84	7	0	288	471
Total		82	85	1,517	172	1,680	198	47	623	4,404

^a Includes ermine (*Mustela erminea*) and long-tailed weasel (*M. frenata*).

^b Franklin's ground squirrel.

I used 7,489 nests that provided 19,810 exposure intervals for analysis. Species composition of nests was 28.5% gadwall, 25.8% blue-winged teal, 25.7% mallard, 9.6% northern shoveler, 6.1% northern pintail, 3.3% lesser scaup, 0.7% American wigeon, and 0.3% green-winged teal. In the best model, DSR was a function of an intercept, treatment (i.e., predator removal), year, site-within-treatment, species, nest age², distance from the edge², initiation date², a treatment by year interaction, a treatment by nest age interaction, and a distance by treatment interaction (Table 2.2). Overdispersion was negligible ($\hat{c} = 1.04$).

Predator reduction positively influenced DSR ($\chi^2_1 = 45.99$, $P \leq 0.001$) but the strength of this effect varied by year ($\chi^2_2 = 8.79$, $P = 0.01$). Mean (LSMEANS; \bar{X}) estimates of nest success were approximately 1.4 times higher on trapped sites than control sites in 2005 (60.1% vs. 42.6%) and 2006 (67.5% vs. 47.9%), and nearly 2 times higher in 2007 (71.8% vs. 36.6%; Fig. 2.1). The quadratic term for nest age had a pronounced effect on DSR ($\chi^2_1 = 73.75$, $P \leq 0.001$) that varied with treatment ($\chi^2_1 = 11.35$, $P \leq 0.001$): DSR was high during early egg laying, decreased through the period of laying and early incubation, but then increased until day 35 (Fig. 2.2). The quadratic initiation date term also had a strong effect on DSR ($\chi^2_1 = 69.68$, $P \leq 0.001$) but did not differ by treatment. Nest success was highest for mid-season nest initiations and was reduced for early and late season initiations (Fig. 2.3). The quadratic term for distance from the edge of the study site remained in the final model; however, its effect on DSR was weak ($\chi^2_1 = 5.44$, $P = 0.02$). Nest success appeared to remain fairly constant from the edge of trapped sites inward to 2.5 km then began to decrease until reaching its lowest level near the center of sites (Fig. 2.4). A species effect also remained in the final model ($\chi^2_7 =$

37.21, $P \leq 0.001$), and was primarily due to mallards having lower nest success than any other species ($\chi^2_1 = 19.83$, $P \leq 0.001$).

Table 2.2. Factors affecting daily survival rates of duck nests on nontrapped and trapped (predator reduced), 93.2 km² study sites in eastern North Dakota, 2005-2007. Parameter estimates, confidence intervals, and test statistics are from a reduced logistic exposure model.

Variable ^a	df	β	95% CI ^b		χ^2	P
			Lower	Upper		
Intercept	1	-8.361	-11.549	-5.109	25.91	≤ 0.001
Trapped	1	1.108	0.788	1.429	45.99	≤ 0.001
Year ^c	2	0.161			18.73	≤ 0.001
Year \times trapped	2				8.79	0.01
2005 \times trapped	1	-0.311	-0.527	-0.098	8.11	0.004
2006 \times trapped	1	0.196	-0.405	0.014	3.37	0.07
Site (Treatment) ^c	10	0.009			55.47	≤ 0.001
Species	7				37.21	≤ 0.001
American wigeon	1	-0.231	-0.723	0.336	0.74	0.39
Blue-winged teal	1	-0.086	-0.246	0.069	1.16	0.28
Gadwall	1	-0.079	-0.243	0.081	0.92	0.34
Green-winged teal	1	0.160	-0.543	1.044	0.16	0.69
Lesser scaup	1	0.043	-0.245	0.343	0.08	0.77
Mallard	1	-0.360	-0.520	-0.203	19.83	≤ 0.001
Northern pintail	1	-0.085	-0.307	0.141	0.55	0.46
Initiation date ^d	1	0.183	0.137	0.229	62.30	≤ 0.001
(Initiation date) ²	1	-0.001	$8.0e^{-04}$	$5.0e^{-04}$	69.68	≤ 0.001
Nest age (days)	1	-0.079	-0.107	-0.052	31.30	≤ 0.001
(Nest age) ²	1	0.003	0.002	0.003	73.75	≤ 0.001
Nest age \times trapped	1	-0.018	0.008	-0.029	11.35	≤ 0.001
Distance	1	0.176	0.032	0.319	5.76	0.02
(Distance) ²	1	-0.038	-0.069	-0.006	5.44	0.02
Distance \times trapped	1	-0.095	-0.173	-0.016	5.61	0.02

^a I arbitrarily set the effect size for treatment = non-trapped, year = 2007, site = 12 (control), site = 6 (trapped), and species = northern shoveler to zero.

^b Represents 95% profile likelihood confidence intervals.

^c The parameter estimate displayed is the mean over all categories, with ranges as follows: year (0.000, 0.316), site (treatment; -0.400, 0.446)

^d Day 1 is 1 January.

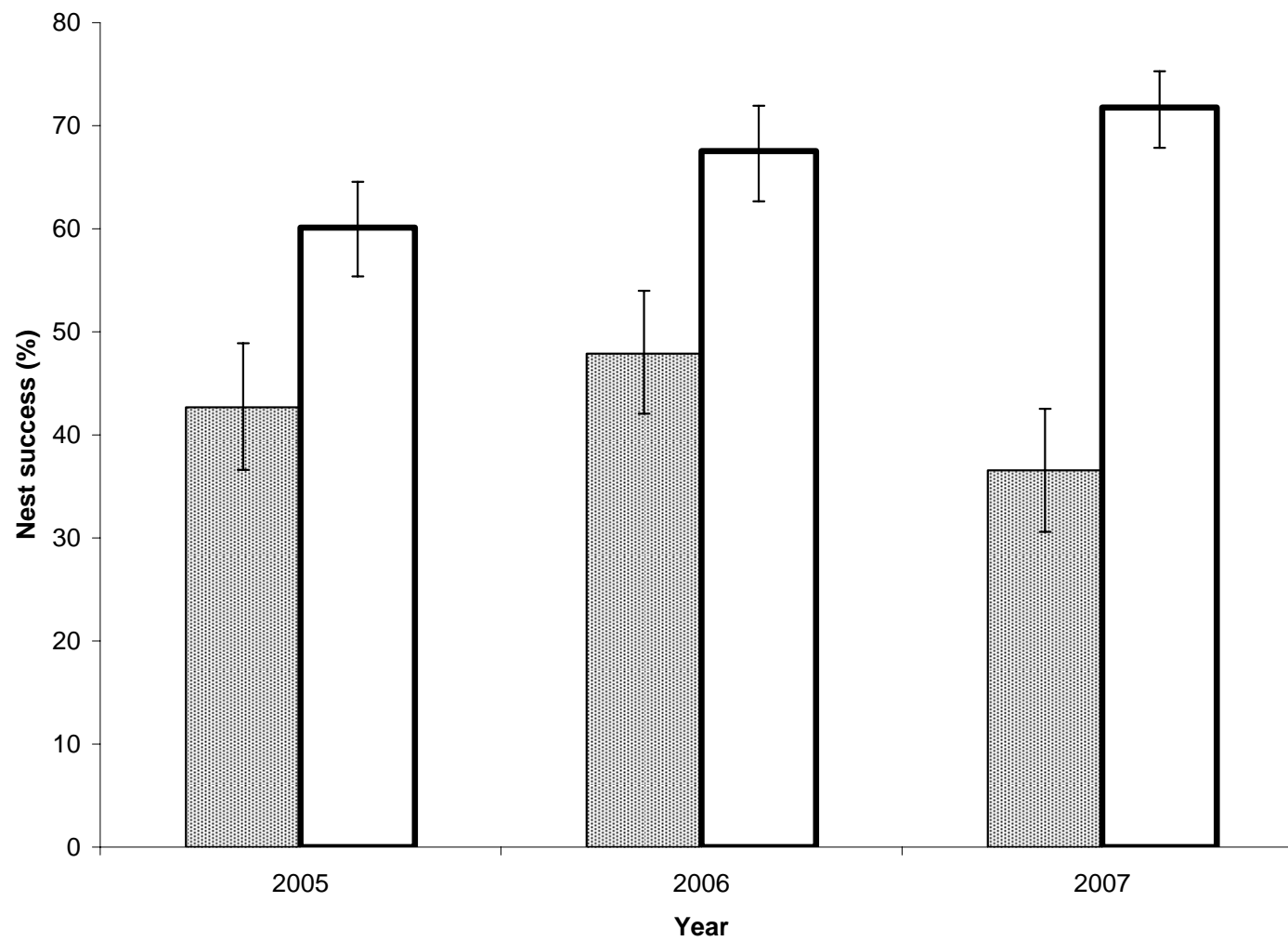


Figure 2.1. Model-based mean (LSMEANS; \bar{X}) nest success estimates and 95% confidence intervals for duck nests on trapped (white bars) and non-trapped (shaded bars) 93.2 km² study sites in eastern North Dakota, 2005-2007.

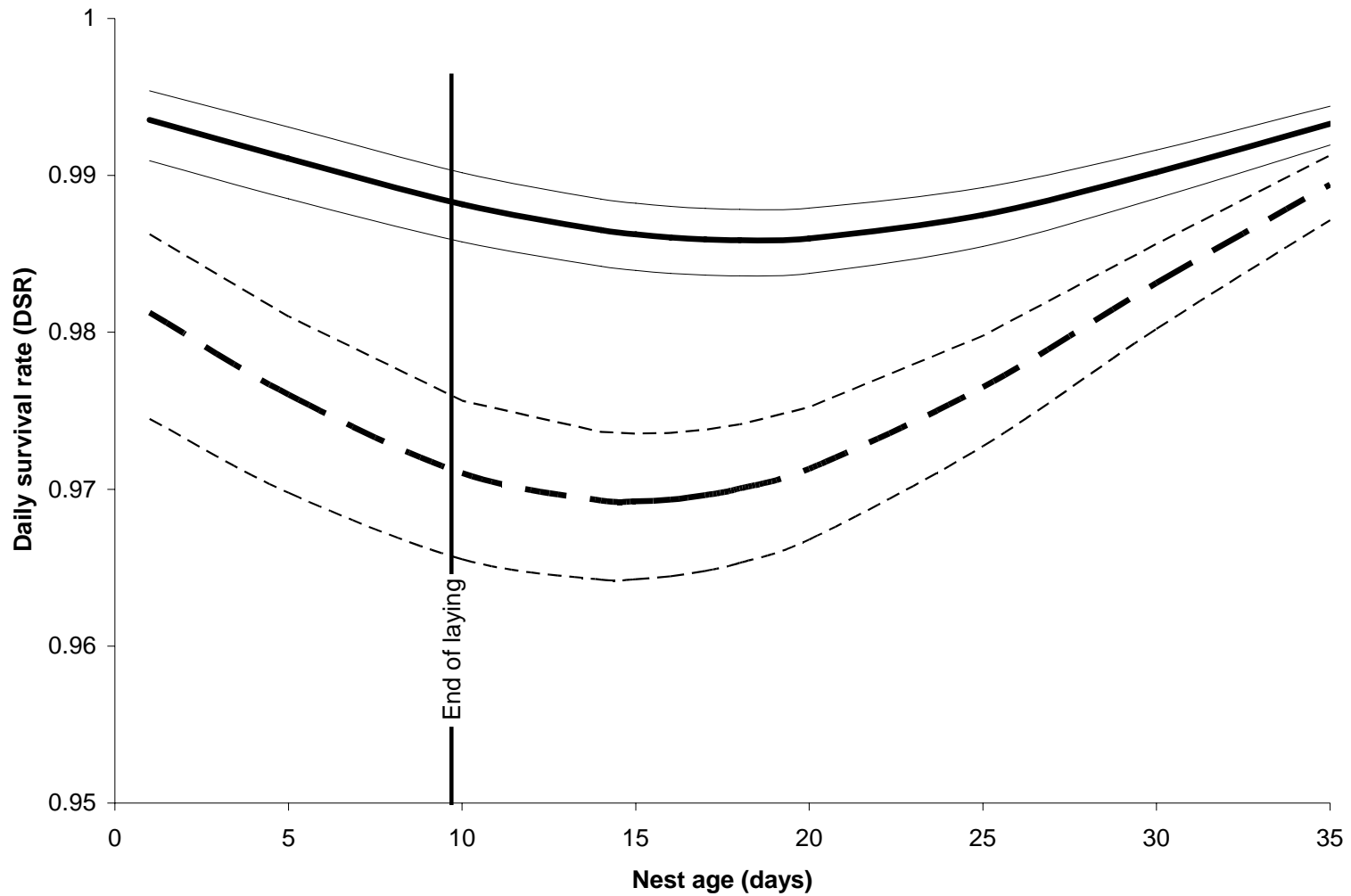


Figure 2.2. Model-based estimates of daily survival rate (DSR) for duck nests in relation to nest age on trapped (solid lines; \pm 95% confidence intervals) and non-trapped (dashed lines; \pm 95% confidence intervals) 93.2 km² study sites in eastern North Dakota, 2005-2007. I weighted years, study sites, and species equally, and I set all other covariates equal to their means. Solid vertical line represents end of laying, as determined by average clutch size of all species.

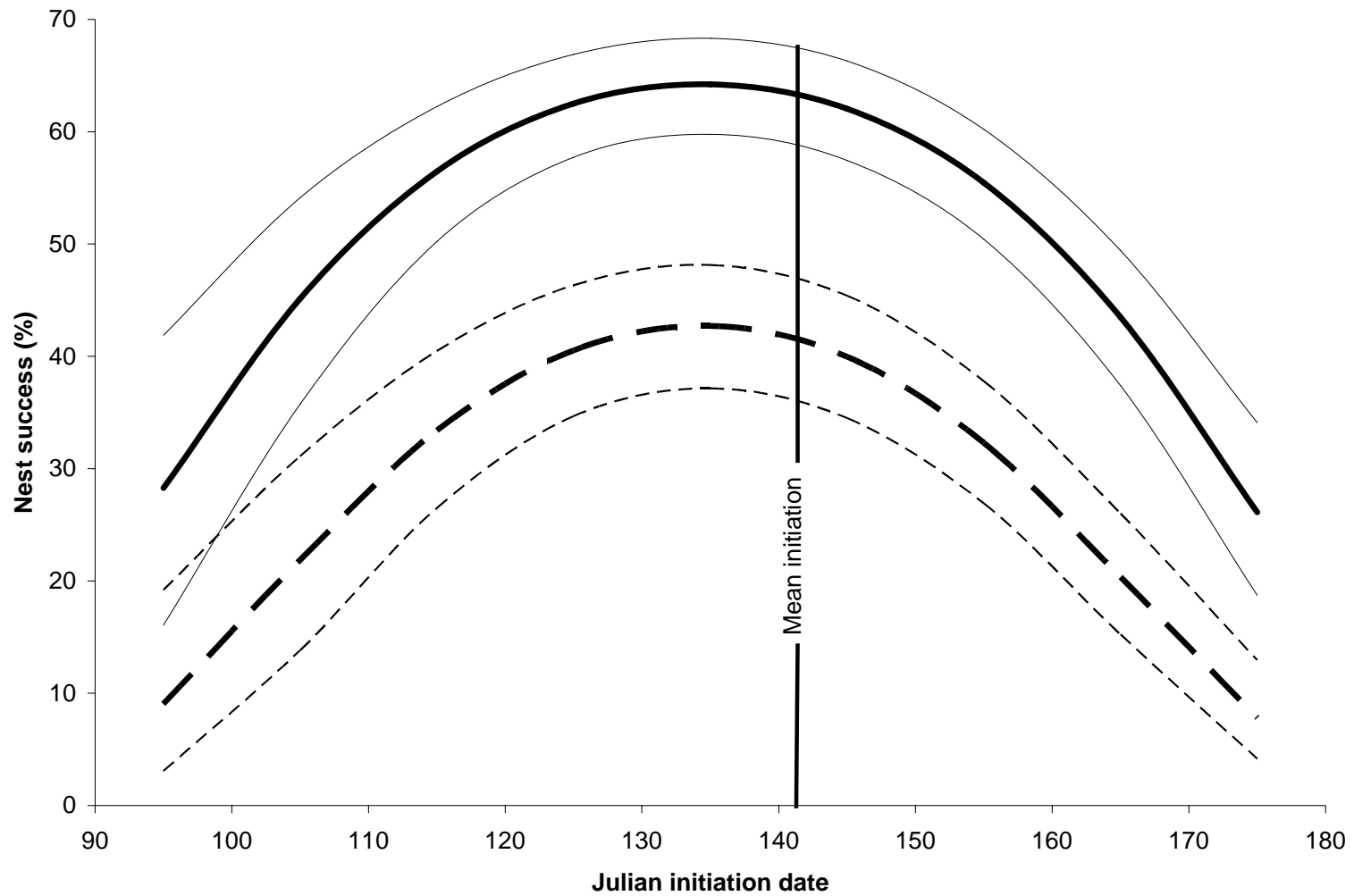


Figure 2.3. Model-based nest success estimates for duck nests in relation to nest initiation date on trapped (solid lines; \pm 95% confidence intervals) and non-trapped (dashed lines; \pm 95% confidence intervals) 93.2 km² study sites in eastern North Dakota, 2005-2007. I weighted years, study sites, and species equally, and I set all other covariates equal to their means. Solid vertical line represents mean initiation date of all nests in sample.

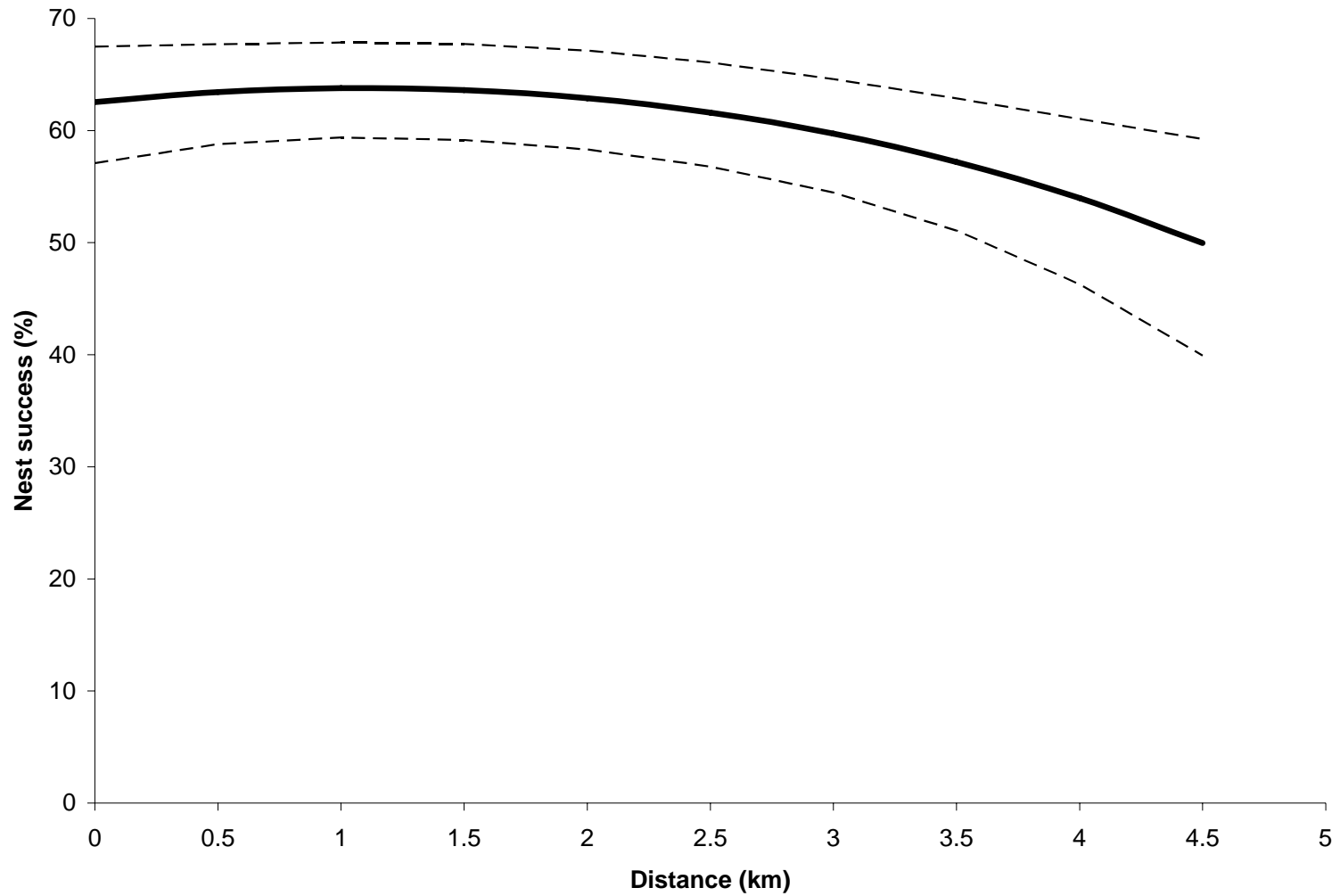


Figure 2.4. Model-based nest success estimates and 95% confidence intervals for duck nests in relation to distance (km) from the edge of 93.2 km² trapped sites in eastern North Dakota, 2005-2007. I weighed years, study sites, and species equally, and I set all other covariates equal to their means. Distance = 0 represents the edge of the site.

DISCUSSION

My hypothesis that nest success would be improved by seasonal predator reduction on township-scale management units was strongly supported in all 3 years (Fig. 1). My results were consistent with 2 previous studies that used similar payment systems and guidelines for professional trappers but at smaller spatial scales (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006). Trapped sites were 2.25 times larger than the sites that Garrettson and Rohwer (2001) evaluated, had similar effect size, but still only required one trapper salary and were therefore more cost-effective than smaller trapped sites. I was surprised that model-based DSR estimates were lower at the center of trapped sites than near the periphery (Fig. 2.4). The porous border hypothesis predicted that immigration of predators from non-trapped areas would negatively impact nest success near the periphery of trapped sites. I suspect that trappers may have shifted efforts toward the periphery of trapped sites to maximize removal of immigrating predators, thereby creating a minor sanctuary for predators in the center of sites. Although predicted nest success estimates for the center of trapped sites were 20% less than estimates at the periphery, I believe that this effect was largely unimportant because the spatial area at the center was considerably less than the spatial area towards the periphery. Proportionally, 56% of the spatial area occurred 0-1.6 km from the edge, 33% occurred 1.6-3.2 km from the edge, and only 11% occurred 3.2-4.8 km from the edge.

Several studies have found a positive linear relationship between nest age and DSR (Klett and Johnson 1982, Grand 1995, Garrettson and Rohwer 2001). However, my results were consistent with the suggestion by Grant et al. (2005) that constant survival should not be assumed among nest ages and that researchers should consider models with

nonlinear age effects when they are biologically justified (Fig. 2.2). Females spend more time at the nest each day as laying proceeds and begin nocturnal incubation 1 to 5 nights after clutch completion (Afton and Paulus 1992, Loos and Rohwer 2004). I believe that increasing female nest attendance followed by nocturnal incubation incrementally increase scent cues for the largely nocturnal mammalian nest predators, ultimately resulting in declining DSR during this period. I suspect that increasing DSR in later stages of incubation reflects early loss of nests in high risk areas and altered female behavior during later incubation (Garrettson and Rohwer 2001). Nests easily detected by predators are likely lost early in the nesting cycle, and those that survive through that initial period have increased odds of surviving to hatch (Klett and Johnson 1982, Dinsmore et al. 2002). During late incubation, hens allow predators to approach closer to nests before flushing (Forbes et al. 1994). Such behavior may present increased risk to the female, but choosing not to advertise the location of the nest may serve to protect the clutch, ultimately leading to higher DSR in late stage nests. The nest age effect was more dramatic on non-trapped sites (Fig. 2.2), most likely because reduced predator numbers on trapped sites led to decreased predation pressure on nests throughout the nesting cycle.

Several investigations have reported a seasonal increase in nest success (Grand 1995, Greenwood et al. 1995, Garrettson and Rohwer 2001), while others have documented seasonal declines in nest success for waterfowl and other avian species (Flint and Grand 1996, Arnold et al. 2007, Johnson and Walters 2008, Sandercock et al. 2008). Emery et al. (2005) found evidence for nonlinear effects of relative initiation date on DSR, but the direction of the effect varied with habitat management. I found a nonlinear relationship between nest success and initiation date, with nests initiated midseason

having the highest probability of survival (Fig. 2.3). Flint and Grand (1996) found that northern pintail nest success on the Yukon-Kuskokwim Delta in Alaska was greatest for nests initiated early in the season and approached 0% for late season initiations. Early pintail initiations were synchronous with most other waterfowl nesting activity (e.g., geese and eiders) which likely increased the probability that an individual nest would be successful (i.e., predator swamping; Flint and Grand 1996). Peak initiation for all species during my study was 21 May (day 141), which is near my highest model based estimate for nest success (Fig. 2.3). I believe that predator swamping may have been responsible for the higher nest success that I observed for mid-season initiations.

In general, my results indicate that differences in DSR between upland nesting duck species are minimal. Mallards were the exception, as they had lower DSR than all other species (Table 2.2). Previous studies have reported similar trends (Beauchamp et al. 1996, Garrettson 1999, Emery et al. 2005) and suggested that reduced DSR in mallards may be a reflection of early season nesting (Beauchamp et al. 1996, Garrettson 1999), when DSR has been documented to be low (Grand 1995, Greenwood et al. 1995, Garrettson and Rohwer 2001). However, I found a strong nonlinear relationship between initiation date and DSR, which does not support the early nesting hypothesis. Mallards engage in less risky nest defense behavior than do other dabbling ducks (Forbes et al. 1994). Such behavior leads to decreased risk for the female but increased risk to the nest and may explain the lower nest survival estimates commonly reported for mallards. I had no a priori notions about interactions of species with any of my other variables and felt that incorporating additional complexity into the model to address species effects would detract from attempts to address our main questions. However, I believe further

investigations specifically directed toward identifying causative factors for reduced DSR in mallards would be interesting.

My mean annual nest success estimates on both trapped and non-trapped sites were higher than levels reported by Garrettson and Rohwer (2001) in similar areas a decade earlier. Moreover, nest success estimates on my non-trapped sites were well above levels believed necessary for population maintenance (Cowardin and Johnson 1979, Cowardin et al. 1985). Red foxes were scarce during my study and constituted less than 2% of trapped predators compared to 26% reported by Garrettson and Rohwer (2001). During Garrettson and Rohwer's (2001) study, an average of 1.9 foxes/km² were removed from trapped sites annually as opposed to only 0.049 foxes/km² annually during my study. Additionally, during the Garrettson and Rohwer (2001) study only 0.006 coyotes/km² were trapped annually, as opposed to 0.05 coyotes/km² annually during my study. Though these are imperfect measures, they suggest that about 39 times more foxes and 8 times fewer coyotes were removed per km² per year during the Garrettson and Rohwer (2001) study than during my study. Though I did not attempt to estimate canid densities during my study, the North Dakota Game and Fish Department (NDGF) has assessed relative densities of foxes and coyotes in the drift prairie physiographic since 1990 with a spring rural mail carrier survey (Fig. 2.5; D. Fecske, NDGF, unpublished data). Fox densities have declined dramatically, while coyote densities have nearly doubled in the time between the two studies. It has been suggested that coyote populations recover more rapidly than do fox populations after mange infestation (Sovada et al. 2005), and coyotes are known to exclude red foxes from their territories (Sargeant et al. 1987, Sovada et al. 2005). Reduced red fox populations during my study

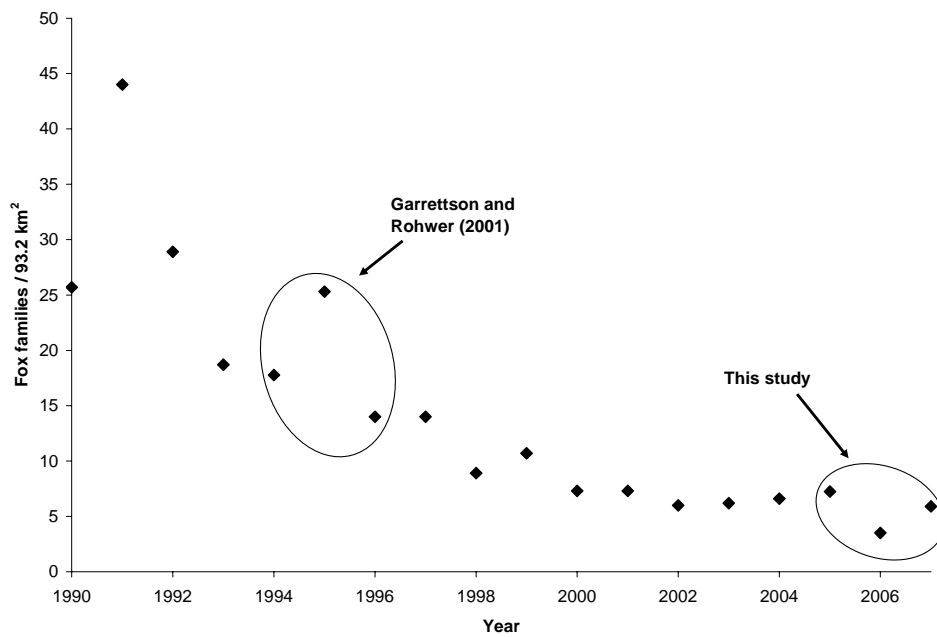
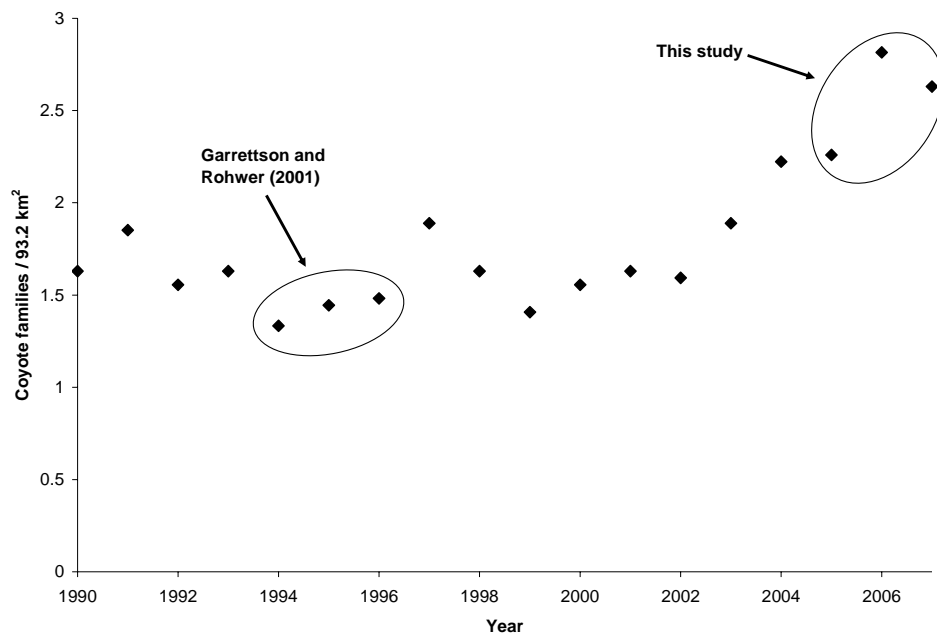


Figure 2.5. Relative densities of coyote and fox families in the drift prairie physiographic region of North Dakota from annual spring rural mail carrier surveys, 1990-2007. Selected data points are circled for comparison between this study and Garrettson and Rohwer (2001). Data provided by the North Dakota Game and Fish Department.

likely resulted from direct impacts from mange infestation confounded by foxes' inability to repopulate areas with increased coyote densities. Sovada et al. (1995) found that duck nest success was 15 percentage points greater in areas where the local canid population was dominated by coyotes compared to those dominated by red foxes. I believe that the relatively high densities of coyotes and low densities of red foxes were largely responsible for my high nest success estimates, even on non-trapped sites.

The large amount of perennial cover on the landscape may also have contributed to overall high nest success. Selection criteria for sites limited variation in percent cover between sites and eliminated my ability to test for effects of variation in percent cover on nest success. Aside from 1 control site with 11% cover and 1 trapped site with 85% cover, all sites had between 30% and 40% perennial cover. Future studies on predator management should seek to evaluate the relationship between perennial cover and nest success by selecting sites with varying percent cover or by selecting sites with less perennial cover than in my study.

Hoekman et al. (2002) reported that population growth rate (λ) for midcontinent mallards was most affected by analytic variation in nest success, but noted that as nest success increases, manipulation of duckling survival becomes more important (see Coluccy et al. 2008). Hoekman et al. (2002) further suggested that increasing female summer survival may increase λ , but improvements to female summer survival via predator reduction are unlikely when fox depredation is already low, as in my study. Though Pearse and Ratti (2004) found that predator reduction benefited duckling survival, Pearse and Lester (2007) suggested that duckling densities exceeding some critical threshold may lead to density dependant reduction in duckling survival

(Makepeace and Patterson 1980, Savard et al. 1991). Future analyses should be conducted to ascertain the benefits provided to production associated with improving nest success that is already well above levels deemed necessary for population growth.

MANAGEMENT IMPLICATIONS

Predator reduction is a valuable tool for managers seeking to improve nest success of upland nesting ducks at spatial scales much larger than previously evaluated. I recommend large-scale predator reduction be targeted towards areas with high densities of breeding ducks but low nest success. Considerable upland cover is being lost with the expiration of CRP contracts in the U.S. PPR (U.S. Department of Agriculture Farm Service Agency 2008), which may result in large regions with numerous breeding pairs but reduced nest success. Township-scale predator reduction would likely be most effective if directed towards such areas. Additionally, I encourage managers to utilize existing canid population indices (e.g., NDGF rural mail carrier survey) or to conduct their own canid surveys prior to implementation of predator reduction. Areas with high coyote and low fox densities likely are already achieving desirable nest success rates and are probably not the best locations to exhaust management resources. Lastly, I advise, to whatever extent possible, altering trapping techniques to limit the removal of coyotes from management areas.

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CHAPTER 3: DOES PREDATOR MANAGEMENT INCREASE LOCAL BREEDING POPULATIONS OF UPLAND NESTING DUCKS?

Manipulating factors that influence population trajectories is a fundamental concept of wildlife management (Duebbert and Lokemoen 1980). For upland nesting ducks in the Prairie Pothole Region (PPR), managers have primarily directed efforts towards improving nest success (Williams et al. 1999, Stephens et al. 2005). Population growth for ducks in the PPR is especially sensitive to fluctuations in nest success (Johnson et al. 1992, Hoekman et al. 2002), and reduced nest success appears to decrease breeding duck numbers in the PPR (Cowardin et al. 1983, Greenwood et al. 1995). Reynolds et al. (2001) noted that long-term declines in breeding populations (Dubovsky et al. 1997) coincided with similar declines in nest success (Beauchamp et al. 1996) for multiple duck species in the PPR during the latter half of the twentieth century. Managers attempting to elevate local nesting success have primarily relied on providing increased nesting cover (Klett et al. 1988, McKinnon and Duncan 1999, Williams et al. 1999). There is a positive relationship between the amount of grassland on the landscape and nest success (Reynolds et al. 2001, Stephens et al. 2005), and wetlands adjacent to grassland may support more breeding pairs than those embedded in cropland (Fischer 1998, Artmann et al. 2001, Reynolds et al. 2007).

Intensive management of mammalian predators has also been used to improve nesting success of upland nesting ducks (Duebbert and Kantrud 1974, Duebbert and Lokemoen 1980, Garrettson and Rohwer 2001, Pieron and Rohwer 2010). Recent investigations in the PPR have consistently reported nesting success rates for upland nesting ducks in areas receiving intensive predator management to be significantly greater than in areas without predator management (Garrettson and Rohwer 2001,

Rohwer et al. 2004, Chodachek and Chamberlain 2006, Pearse and Lester 2007, Pieron and Rohwer 2010) and well above levels necessary for population maintenance (Cowardin and Johnson 1979, Cowardin et al. 1985). Mortality of breeding females and ducklings are also critical components of production (Klett et al. 1988, Hoekman et al. 2002), and predator management can increase duckling survival (Zimmer 1996, Pearse and Ratti 2004; but see Amundson 2010) and hen survival during the brood rearing period (Pearse and Ratti 2004).

Management that effectively elevates breeding season vital rates may have the potential to increase productivity and abundance of local breeding populations (Duebbert and Lokemoen 1980, Anderson et al. 1992). In some studies, local pair numbers increased in the year following predator removal (Duebbert and Kantrud 1974, Garrettson and Rohwer 2001; but see Chodachek and Chamberlain 2006), but increased breeding populations following increased production are dependant on the extent to which females home to the same area in subsequent years (Anderson et al. 1992). Numerous studies have reported that waterfowl are philopatric to previous breeding areas (Rohwer and Anderson 1988, Anderson et al. 1992, Arnold et al. 2002), that homing is measurably elevated for females that nested successfully in the previous season (Johnson and Grier 1988, Lokemoen et al. 1990), and that females returning to sites where they nested successfully in the past have increased reproductive success (Dow and Fredga 1983, Blancher and Robertson 1985). The degree of philopatry to breeding sites varies among species in the PPR (Johnson and Grier 1988, Lokemoen et al. 1990, Anderson et al. 1992, Evrand 1999); mallards (*Anas platyrhynchos*), gadwalls (*A. strepera*) and northern shovelers (*A. clypeata*; hereafter shoveler) show stronger philopatry than northern pintails

(*A. acuta*; hereafter pintail), and blue-winged teal (*A. discors*) rarely exhibit philopatry (Johnson and Grier 1988, Lokemoen et al. 1990, Anderson et al. 1992).

If increased duck production in predator-managed areas combined with over-winter survival and philopatry lead to increased local breeding populations in subsequent years, heightened production as a product of elevated nest success may be compounded over years, lending to more cost-effective management (Garrettson and Rohwer 2001). To date there have been no extensive replicated investigations regarding breeding population densities of upland nesting ducks in years following intensive predator management. My primary objective was to determine if local breeding pair abundance for each of the 5 most common upland nesting ducks in North Dakota increased following intensive predator management. My secondary objective was to determine if breeding pair abundance was greater on wetlands adjacent to grassland than on those embedded in cropland.

STUDY AREA

I conducted my study in the drift prairie physiographic region during 2005–2008 in Benson, Cavalier, Nelson, Ramsey, Stutsman, Towner, Walsh, and Wells counties, North Dakota. Habitats were highly fragmented, and the region was dominated by small grain, oilseed, and row-crop agriculture. Intermixed perennial cover was present in the form of hay, pasture, and idle cover enrolled in the Conservation Reserve Program (CRP) or in federal Waterfowl Production Areas (WPA). Blue-winged teal, mallard, gadwall, shoveler, and pintail were the 5 most common dabbling duck species (Pagano and Arnold 2009), and breeding duck population estimates in the region ranged from 10–86% above

the long-term average during my study (Wilkins et al. 2005, 2006, 2007, Zimpfer et al. 2008).

METHODS

Field Methods

I conducted research on 12 township-sized (93.2 km²) study sites. Three of my sites were part of an operational predator management program initiated prior to this study, and I did not select them randomly. They were similar to the other sites with respect to breeding pairs per km² and grassland cover, except for 1 site that had 85% grassland cover. I randomly selected all other sites from a set of potential sites that supported >23 breeding duck pairs per km² and had moderate levels of grassland cover (~20% to 40%) in eastern North Dakota as determined from a predator management decision matrix developed by United States Fish and Wildlife Service (USFWS) Region 6 Habitat and Population Evaluation Team (C. Dixon, unpublished report). I then visually inspected potential sites via small aircraft to confirm wetland and upland habitat composition. I randomly selected potential sites and met with landowners to discuss the possibility of working on their land. I assigned a trapped treatment to sites where I obtained $\geq 80\%$ landowner permission for trapping. I assigned a non-trapped treatment to sites that failed to meet that minimum percentage but received enough landowner permission to survey breeding pairs. In 2005 I evaluated 4 nontrapped sites and 6 trapped sites. I replaced 1 trapped site and 1 non-trapped site from 2005 with 1 new trapped and 1 new non-trapped site that I evaluated during 2006–2008.

For each trapped site, Delta Waterfowl Foundation (DWF) hired 1 professional trapper to remove mammalian predators from 15 March until 15 July. Trappers used all

legal removal methods including foothold traps, body-gripping traps, snares, and shooting. Trappers checked traps at least every other day and killed all trapped predators. Trappers annually removed an average of 245 predators per trapped site, and nest success was 1.4 to 1.9 times greater on trapped sites than non-trapped sites, depending on year (Pieron and Rohwer 2010).

On each study site, I randomly selected at least 12 breeding pair survey plots, each 32 ha (800m × 400m). Within each site, plot selection was stratified between grassland and cropland to account for any differences in pair abundances that may be a function of upland habitat (Fischer 1998, Reynolds et al. 2007). Pair counts were conducted following procedures used during the USFWS's 4-square-mile (10.5 km²) breeding waterfowl survey (Cowardin et al. 1995). Technicians and I conducted surveys from 0900–1600 hours during 1 May–15 May for early nesting species such as mallards and pintails, and during 20 May–5 June for late nesting species such as blue-winged teal and gadwall. We did not conduct surveys during heavy rain, snow, fog, ice cover, or when wind speeds exceeded 32 km/hour. Two observers conducted walk-up breeding pair counts on all wetlands within each plot that were delineated by the National Wetland Inventory (NWI) and recorded all distinct social groups of ducks. I used 2 observers to increase the accuracy of surveys; one observer devoted their attention entirely to counting and announcing social groups to the other, whose sole responsibility was to record data. Some wetlands extended beyond the random plot boundaries. Such wetlands were only surveyed if I had permission to work on the adjacent land so that I could survey the entire wetland.

I used the indicated breeding pair criterion described by Cowardin et al. (1995) as slightly adjusted from Hammond (1969) and Dzubin (1969) such that pairs, lone males, and males in groups of ≤ 5 represented dabbling duck breeding pairs except for shovelers for which only distinct pairs and lone males were considered pairs. I used data from the first survey (1 May–15 May) to calculate breeding pairs for mallards and pintails, from the second survey (20 May–5 June) for blue-winged teal and gadwall, and from the survey closest to 15 May for shovelers (Reynolds et al. 2007).

Wetland and Upland Habitat Classification

I used geo-referenced aerial photographs taken during late April–early May, 2005–2008, to digitize all inundated wetlands in each site-year and to determine their area in ArcGIS 9.2 . Each basin was classified based on the deepest water zone (Stewart and Kantrud 1971) resulting in 5 wetland classes; temporary, seasonal, semi-permanent, lake, and riverine (see Reynolds et al. 2007 for detailed description of classification). After conducting extensive ground surveys of each site, I used the same geo-referenced aerial photographs to digitize upland habitats as either grassland (pasture, idle grassland, and hayland) or cropland. I then merged the digitized wetland layer with the upland layer to create a complete land classification coverage layer for each site-year. From this coverage layer, for each wetland, I was able to determine wetland classification, upland habitat association, and area.

Statistical Analysis

I first developed a series of competing regression models that related wetland area and/or perimeter to the number of breeding pairs on a given wetland for each species. Non-linear relationships between duck pairs and wetland area are common (Kantrud and

Stewart 1977, Cowardin et al. 1988), therefore I considered the relationship of wetland area in hectares (HEC) and the square root of the wetland area (\sqrt{HEC}), which served as a proxy for shoreline length (Reynolds et al. 2007), to pair abundance. I conducted separate analyses for 1) temporary wetlands, 2) seasonal wetlands, and 3) semipermanent wetlands and lakes combined. I fit models using PROC GLIMMIX (SAS Version 9.2; SAS Institute, Cary, NC) with a Poisson distribution and a log-link function, because count data are commonly Poisson distributed (Zar 1999). Further, during fitting, scaling parameters were monitored to ensure that the Poisson distribution remained the best choice. In each model, I included a fixed YEAR variable to account for annual variation in pair numbers and a random study SITE nested within TRAP category variable (trapped or not trapped) to account for unmeasured variation in pair densities among sites.

Competing models contained the following sets of fixed predictor variables:

1. YEAR, HEC, \sqrt{HEC}
2. YEAR, HEC
3. YEAR, \sqrt{HEC}

Pseudoestimation techniques are inappropriate for comparison of models in a model selection context because they do not estimate a true log likelihood (Crozier et al. 2006). Therefore, I used Laplace's method in PROC GLIMMIX (SAS Version 9.2; SAS Institute, Cary, NC) to estimate marginal likelihoods that are suitable for comparison of competing models (Schabenberger 2007). I used Akaike's Information Criterion adjusted for small sample size (AIC_c) to calculate differences between models (ΔAIC_c) and included models $< 2 AIC_c$ units from the best model during ranking (Burnham and Anderson 2002). I considered a ranked model to be competitive for drawing inference if

parameters in the top model were not a subset of the parameters in the competing model and used AIC_c weights (w_i) as a measure of evidence of support for models (Burnham and Anderson 2002).

I next used the best supported wetland area-perimeter model as a template on which to evaluate the relationship of predator management (TRAP) and upland habitat (UPHAB) to pair abundance for each species-wetland class combination. TRAP categorized wetlands within study sites that received predator management in the previous season as trapped, and wetlands within study sites that had not received predator management as nontrapped. UPHAB categorized wetlands as either adjacent to grassland or not adjacent to grassland (i.e. embedded in cropland). Competing models contained the following sets of fixed predictor variables:

1. Best template model
2. Best template model, UPHAB
3. Best template model, TRAP
4. Best template model, UPHAB, TRAP

I used the same procedure to assess model support that I used for the wetland size-perimeter models.

RESULTS

During 2005–2008 we surveyed an average of 621 wetlands twice annually and observed 3,674 blue-winged teal, 3,227 mallard, 2,287 gadwall, 1,539 shoveler, and 679 pintail breeding pairs. Models containing both HEC and \sqrt{HEC} in initial analyses relating pair abundance to wetland size-perimeter variables were clearly best for all 5 species, for each class of wetlands (Table 3.1).

The wetland area-perimeter template model performed better than any models containing TRAP and/or UPHAB for mallards on temporary ($w_i = 0.51$), seasonal ($w_i = 0.47$), and lake-semipermanent ($w_i = 0.50$) wetlands (Table 3.2). Parameter estimates and model-based estimates of mallard pair abundance from the best model for all 3 wetland types are presented in Table 3.3 and Figure 3.1, respectively.

For blue-winged teal, the best model for temporary ($w_i = 0.72$), seasonal ($w_i = 0.66$), and lake-semipermanent ($w_i = 0.64$) wetlands included UPHAB (Table 3.2). Depending on wetland class, blue-winged teal pair abundance was 1.2–2.0 times greater on wetlands adjacent to grassland than on wetlands embedded in cropland (Figure 3.2, Table 3.3).

The wetland area-perimeter template model performed best for gadwalls on temporary ($w_i = 0.49$) and seasonal ($w_i = 0.34$) wetlands (Table 3.2). The best model for lake-semipermanent wetlands included UPHAB and TRAP ($w_i = 0.43$; Table 3.2), and predicted gadwall pair abundance to be 1.2 times greater on wetlands embedded in cropland and 1.5 times greater on wetlands in predator managed sites (Figure 3.3, Table 3.3).

The wetland area-perimeter template model performed best for pintails on lake-semipermanent wetlands ($w_i = 0.52$), but the best model for temporary ($w_i = 0.68$) and seasonal ($w_i = 0.49$) wetlands included UPHAB (Table 3.2). Estimated pintail pair abundance was 2.8 and 1.2 times greater on wetlands embedded in cropland than on wetlands adjacent to grassland on temporary and seasonal wetlands, respectively (Figure 3.4, Table 3.3).

The wetland area-perimeter template model performed best for shovelers on seasonal wetlands ($w_i = 0.35$; Table 3.2). The best model for temporary wetlands included TRAP ($w_i = 0.47$; Table 3.2) and estimated 1.9 times more shoveler pairs on wetlands within predator managed sites than on wetlands in sites without predator management (Figure 3.5, Table 3.3). The best model for lake-semipermanent wetlands included UPHAB ($w_i = 0.39$; Table 3.2) and estimated 1.2 times more shoveler pairs on wetlands embedded on cropland than on wetlands adjacent to grassland (Figure 3.5, Table 3.3).

DISCUSSION

Upland Habitat and Pair Abundance

Blue-winged teal pair densities were greater on wetlands adjacent to grassland than on wetlands embedded in cropland for all wetland classes (Figure 3.2), which was consistent with prior work (Fischer 1998, Reynolds et al. 2007). The positive effect of grassland cover on blue-winged teal pair abundance may be a reflection of their tendency to nest close to water within relatively small territories (Duebbert and Lokemoen 1976, Stewart and Titman 1980, Clark and Shutler 1999) combined with their tendency to avoid nesting in cropland habitat (Klett et al. 1988, Greenwood et al. 1995).

Only blue-winged teal had greater pair densities on wetlands adjacent to grassland, which is in contrast to results presented by Fischer (1998) and Reynolds et al. (2007). The abundance of grass on the landscape may have contributed to this finding, as all but one of my sites had $\geq 30\%$ grassland cover (Pieron and Rohwer 2010). Perhaps pairs settled on cropland wetlands more readily on my study sites because grassland nesting cover was abundant and close to most wetlands in cropland. This may offer an

Table 3.1. Model selection results for models evaluating the relationship of duck pair abundance to wetland size and perimeter for the 5 most common upland nesting ducks by wetland class in eastern North Dakota, 2005-2008. Models are ranked based on Akaike's Information Criterion adjusted for small sample size (AIC_c) and model weights (w_i).

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Blue-winged teal	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	14.02	0.00
		YEAR + HEC	37.46	0.00
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	170.99	0.00
		YEAR + HEC	538.83	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	197.72	0.00
		YEAR + HEC	223.26	0.00
Gadwall	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	13.53	0.00
		YEAR + HEC	26.60	0.00
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	162.95	0.00
		YEAR + HEC	468.44	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	196.00	0.00
		YEAR + HEC	356.96	0.00

(Table continued)

(Table 3.1 continued)

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Mallard	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	0.80
		YEAR + \sqrt{HEC}	2.82	0.20
		YEAR + HEC	25.08	0.00
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	146.54	0.00
		YEAR + HEC	517.55	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	216.06	0.00
		YEAR + HEC	465.04	0.00
Pintail	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	0.86
		YEAR + \sqrt{HEC}	3.98	0.12
		YEAR + HEC	6.84	0.02
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	24.79	0.00
		YEAR + HEC	86.27	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	91.80	0.00
		YEAR + HEC	184.63	0.00

(Table continued)

(Table 3.1 continued)

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Shoveler	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	0.94
		YEAR + \sqrt{HEC}	5.64	0.06
		YEAR + HEC	14.38	0.00
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	181.15	0.00
		YEAR + HEC	432.14	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	1.00
		YEAR + \sqrt{HEC}	126.96	0.00
		YEAR + HEC	206.42	0.00

^a Lakes and semipermanent wetlands were combined for analysis.

^b YEAR includes 2005, 2006, 2007, and 2008, HEC = wetland area inundated with water in ha, \sqrt{HEC} = square root of wetland area, which is a proxy for wetland perimeter.

Table 3.2. Model selection results for models evaluating the relationship of breeding duck pair abundance to wetland size and perimeter, predator management, and upland habitat adjacent to wetlands for the 5 most common upland nesting ducks by wetland class in eastern North Dakota, 2005-2008. Models are ranked based on Akaike's Information Criterion adjusted for small sample size (AIC_c) and model weights (w_i).

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Blue-winged teal	Temporary	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.72
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	2.09	0.25
		YEAR + HEC + \sqrt{HEC}	6.73	0.02
		YEAR + HEC + \sqrt{HEC} + TRAP	8.80	0.01
	Seasonal	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.66
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.33	0.34
		YEAR + HEC + \sqrt{HEC}	124.68	0.00
		YEAR + HEC + \sqrt{HEC} + TRAP	124.86	0.00
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.64
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.79	0.26
		YEAR + HEC + \sqrt{HEC}	4.55	0.07
		YEAR + HEC + \sqrt{HEC} + TRAP	6.22	0.03
Gadwall	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	0.49
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.43	0.24
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.94	0.18
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	3.36	0.09
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	0.34
		YEAR + HEC + \sqrt{HEC} + UPHAB	0.44	0.27
		YEAR + HEC + \sqrt{HEC} + TRAP	0.85	0.22
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.35	0.17

(Table continued)

(Table 3.2 continued)

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Gadwall	Lake-semipermanent	YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	0.00	0.43
		YEAR + HEC + \sqrt{HEC} + UPHAB	0.61	0.31
		YEAR + HEC + \sqrt{HEC} + TRAP	2.12	0.15
		YEAR + HEC + \sqrt{HEC}	2.63	0.12
Mallard	Temporary	YEAR + HEC + \sqrt{HEC}	0.00	0.51
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.22	0.28
		YEAR + HEC + \sqrt{HEC} + TRAP	3.07	0.11
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	3.29	0.10
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	0.47
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.49	0.23
		YEAR + HEC + \sqrt{HEC} + TRAP	1.70	0.20
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	3.17	0.10
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	0.50
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.76	0.21
		YEAR + HEC + \sqrt{HEC} + TRAP	1.76	0.21
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	3.52	0.08
Pintail	Temporary	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.68
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	2.05	0.24
		YEAR + HEC + \sqrt{HEC}	5.00	0.06
		YEAR + HEC + \sqrt{HEC} + TRAP	7.04	0.02
	Seasonal	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.49
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.28	0.26
		YEAR + HEC + \sqrt{HEC}	2.34	0.15
		YEAR + HEC + \sqrt{HEC} + TRAP	3.03	0.10

(Table continued)

(Table 3.2 continued)

Species	Wetland Class ^a	Model ^b	ΔAIC_c	w_i
Pintail	Lake-semipermanent	YEAR + HEC + \sqrt{HEC}	0.00	0.52
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.68	0.22
		YEAR + HEC + \sqrt{HEC} + TRAP	2.09	0.18
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	3.78	0.08
Shoveler	Temporary	YEAR + HEC + \sqrt{HEC} + TRAP	0.00	0.47
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.45	0.22
		YEAR + HEC + \sqrt{HEC}	1.50	0.22
		YEAR + HEC + \sqrt{HEC} + UPHAB	3.29	0.09
	Seasonal	YEAR + HEC + \sqrt{HEC}	0.00	0.35
		YEAR + HEC + \sqrt{HEC} + TRAP	0.43	0.28
		YEAR + HEC + \sqrt{HEC} + UPHAB	1.06	0.21
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.58	0.16
	Lake-semipermanent	YEAR + HEC + \sqrt{HEC} + UPHAB	0.00	0.39
		YEAR + HEC + \sqrt{HEC}	0.36	0.33
		YEAR + HEC + \sqrt{HEC} + UPHAB + TRAP	1.94	0.15
		YEAR + HEC + \sqrt{HEC} + TRAP	2.26	0.13

^a Lakes and semipermanent wetlands were combined for analysis.

^b YEAR includes 2005, 2006, 2007, and 2008, HEC = wetland area inundated with water in ha, \sqrt{HEC} = square root of wetland area, which is a proxy for wetland perimeter, UPHAB categorized wetlands as either adjacent to grasslands or not (embedded in cropland), TRAP categorized wetlands within study sites that received predator management in the previous season as trapped, and wetlands within study sites that had not received predator management as nontrapped.

Table 3.3. Parameter estimates and 95% confidence intervals from best regression models relating breeding duck abundance to wetland size, wetland perimeter, predator management, and upland habitats adjacent to wetlands for the 5 most common upland nesting ducks by wetland class in eastern North Dakota, 2005-2008.

Species	Wetland Class	Variable ^a			
		Hectares	$\sqrt{\text{Hectares}}$	Grass	Trapped
Blue-winged teal	Temporary	-1.500 (2.248, -0.752)	3.984 (2.731, 5.238)	0.675 (0.201, 1.145)	-----
	Seasonal	-0.258 (-0.300, -0.217)	1.718 (1.569, 1.867)	0.542 (0.443, 0.640)	-----
	Lake-semipermanent	-0.068 (-0.080, -0.057)	0.743 (0.642, 0.844)	0.177 (0.041, 0.313)	-----
Gadwall	Temporary	-3.349 (-5.576, -1.123)	5.963 (3.196, 8.730)	-----	-----
	Seasonal	-0.329 (-0.387, -0.272)	2.112 (1.904, 2.319)	-----	-----
	Lake-semipermanent	-0.052 (-0.060, -0.043)	0.846 (0.751, 0.940)	-0.168 (-0.328, -0.008)	0.376 (-0.084, 0.837)
Mallard	Temporary	-0.772 (-1.472, -0.072)	3.048 (1.889, 4.207)	-----	-----
	Seasonal	-0.268 (-0.316, -0.220)	1.840 (1.669, 2.011)	-----	-----
	Lake-semipermanent	-0.050 (-0.057, -0.042)	0.869 (0.785, 0.954)	-----	-----
Pintail	Temporary	-2.792 (-6.098, 0.515)	4.979 (0.921, 9.037)	-1.045 (-1.815, -0.276)	-----
	Seasonal	-.281 (-0.400, -0.162)	1.760 (1.360, 2.159)	-0.209 (-0.422, 0.004)	-----
	Lake-semipermanent	-0.079 (-0.099, -0.060)	1.108 (0.934, 1.283)	-----	-----

(Table continued)

(Table 3.3 continued)

Species	Wetland Class	Variable ^a			
		Hectares	$\sqrt{\text{Hectares}}$	Grass	Trapped
Shoveler	Temporary	-2.024 (-3.666, -0.382)	4.812 (2.389, 7.235)	-----	0.658 (-.080, 1.395)
	Seasonal	-0.466 (-0.548, -0.384)	2.500 (2.230, 2.768)	-----	-----
	Lake-semipermanent	-0.062 (-0.074, -0.049)	0.892 (0.763, 1.021)	-0.166 (-0.372, 0.041)	-----

^a Hectares is wetland area, $\sqrt{\text{Hectares}}$ is the square root of wetland area and is a proxy for wetland perimeter, Grass indicates the effect of grassland cover, and Trapped indicates the effect of predator management on pair abundance. I arbitrarily set the effect size for UPHAB = crop and TRAP = nontrapped to zero.

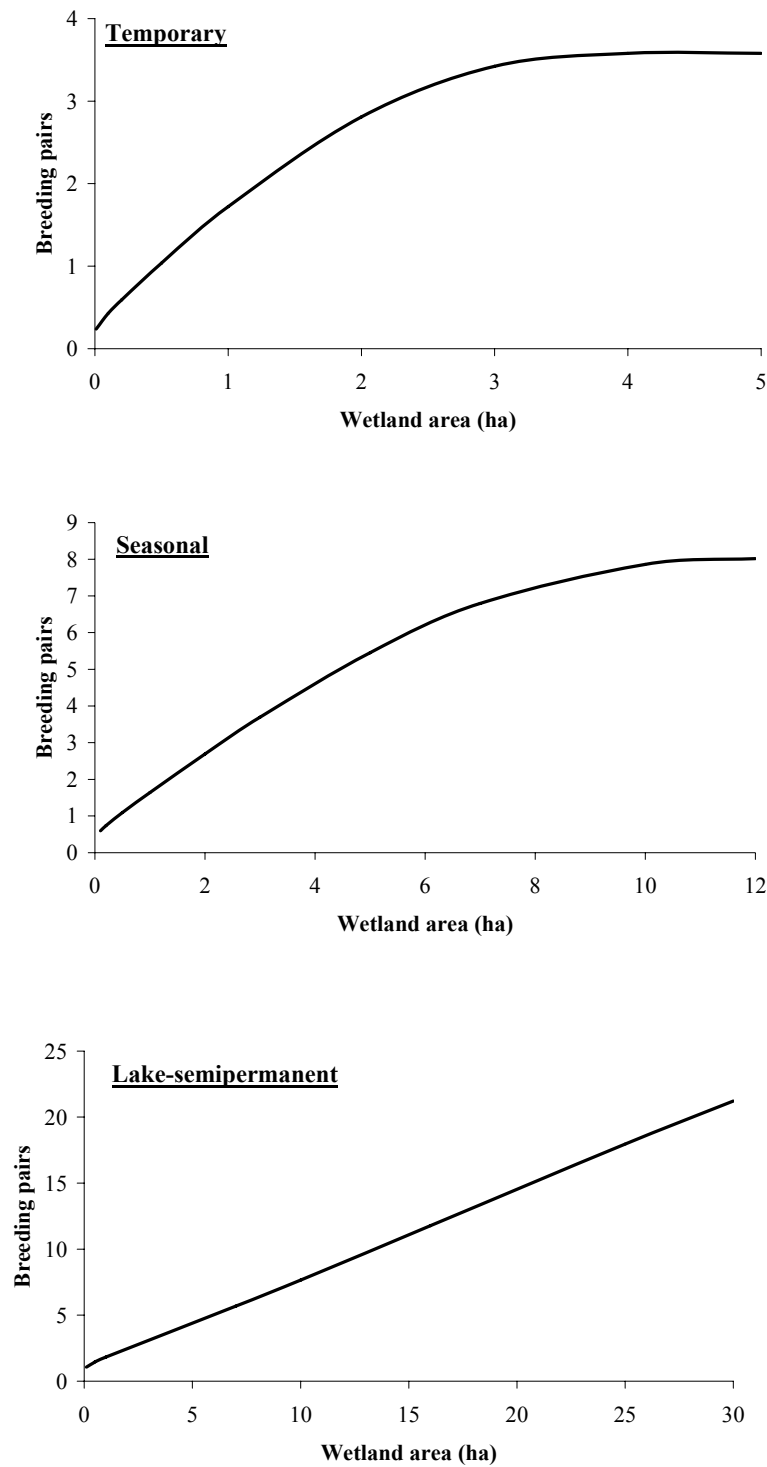


Figure 3.1. Best model-based relationships of mallard breeding pair abundance to wetland area on temporary, seasonal, and lake-semipermanent wetlands in eastern North Dakota, 2005–2008. I weighted years and study sites equally.

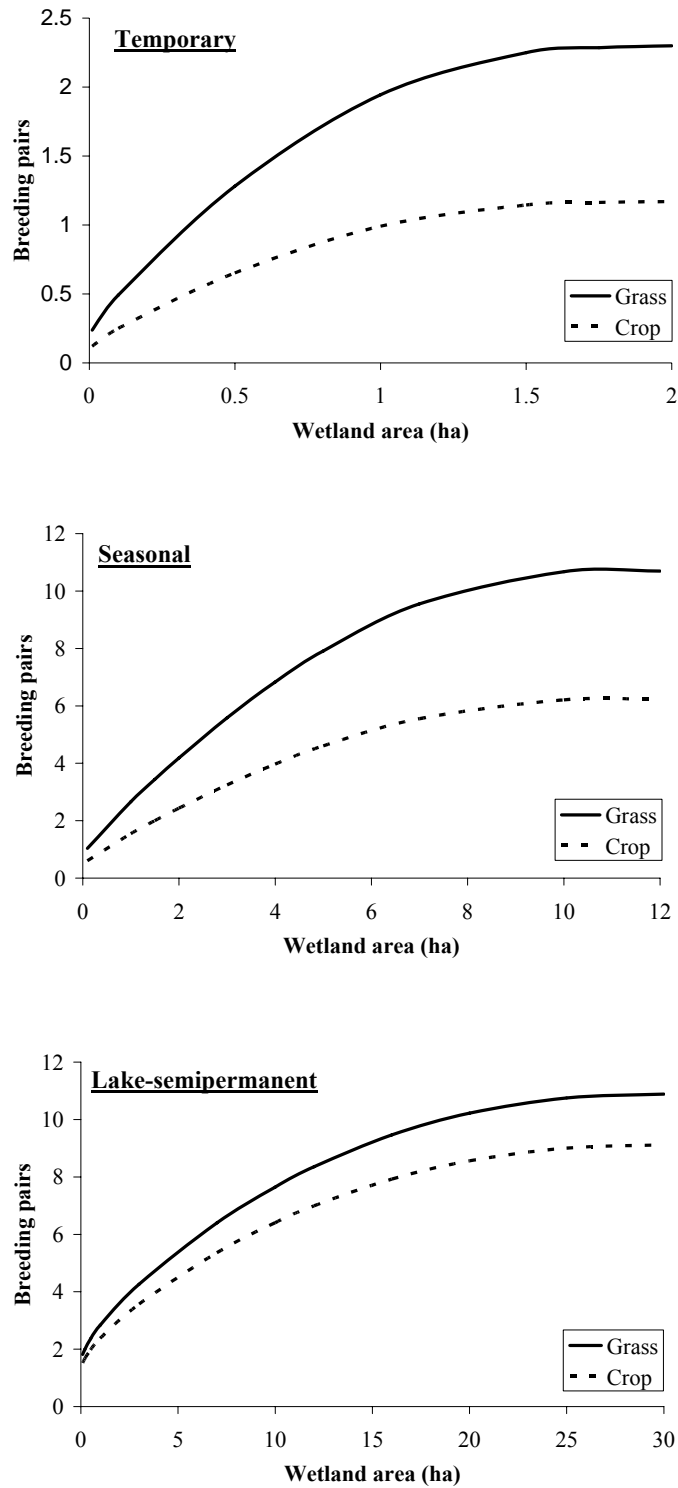


Figure 3.2. Best model-based relationships of blue-winged teal breeding pair abundance to wetland area on temporary, seasonal, and lake-semipermanent wetlands in eastern North Dakota, 2005–2008. I weighted years and study sites equally.

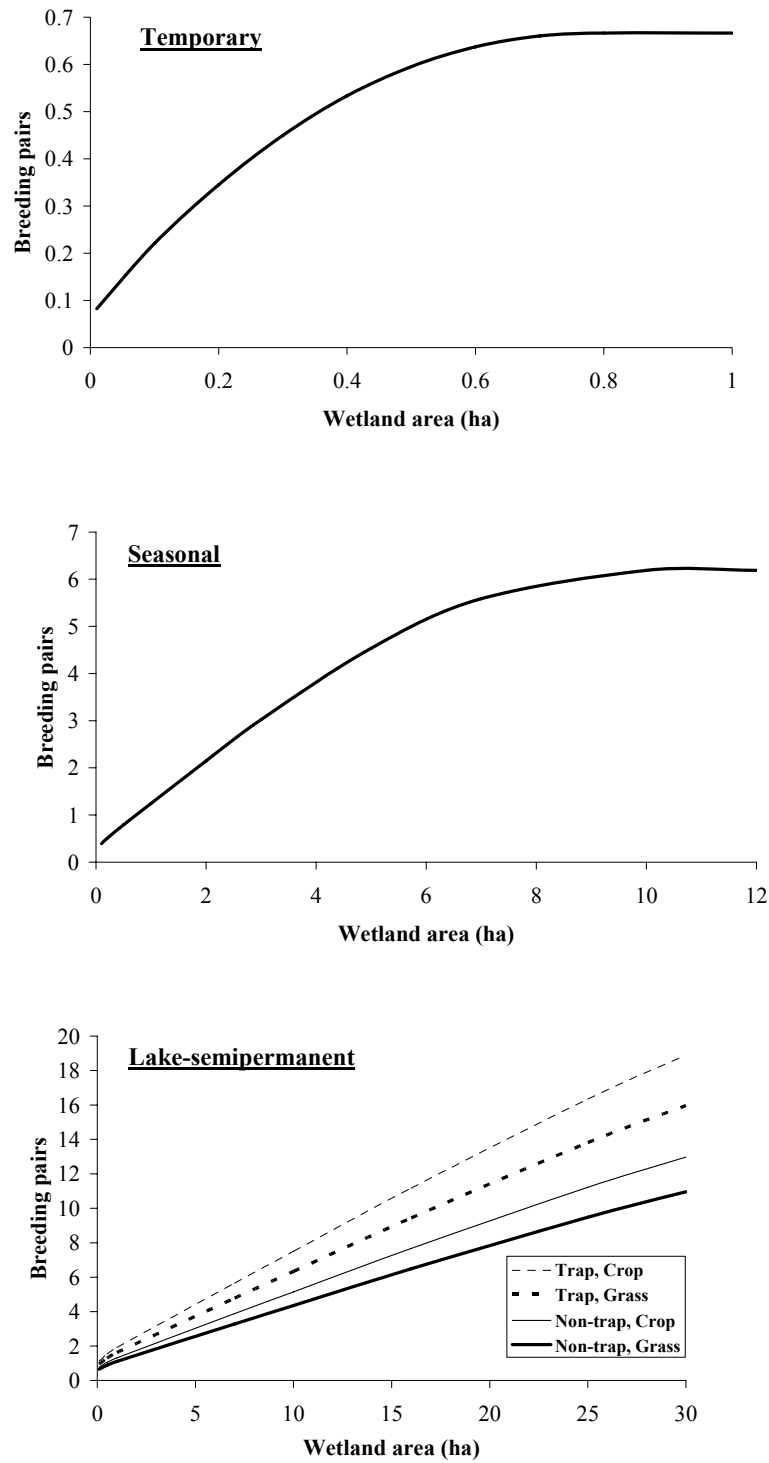


Figure 3.3. Best model-based relationships of gadwall breeding pair abundance to wetland area on temporary, seasonal, and lake-semipermanent wetlands in eastern North Dakota, 2005–2008. I weighted years and study sites equally.

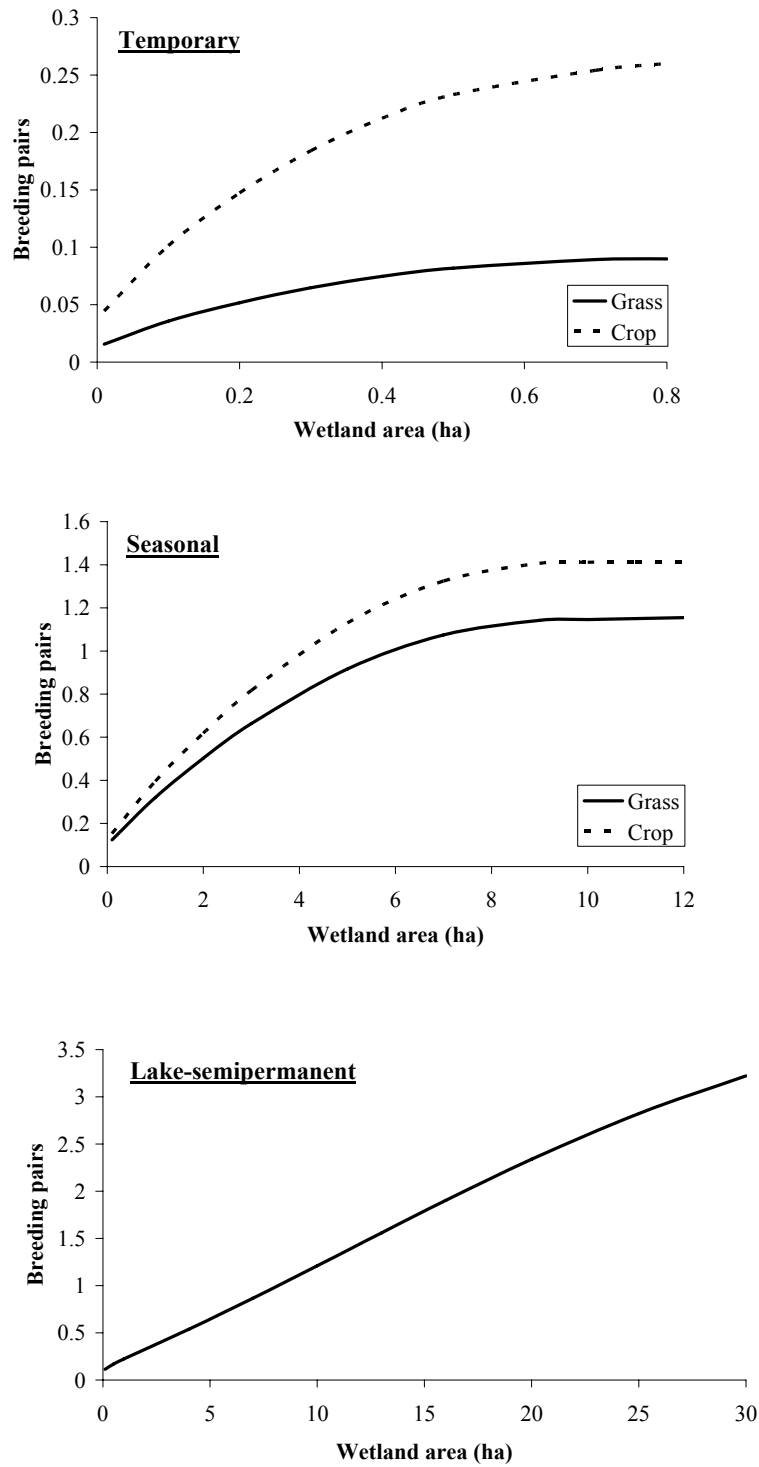


Figure 3.4. Best model-based relationships of pintail breeding pair abundance to wetland area on temporary, seasonal, and lake-semipermanent wetlands in eastern North Dakota, 2005–2008. I weighted years and study sites equally.

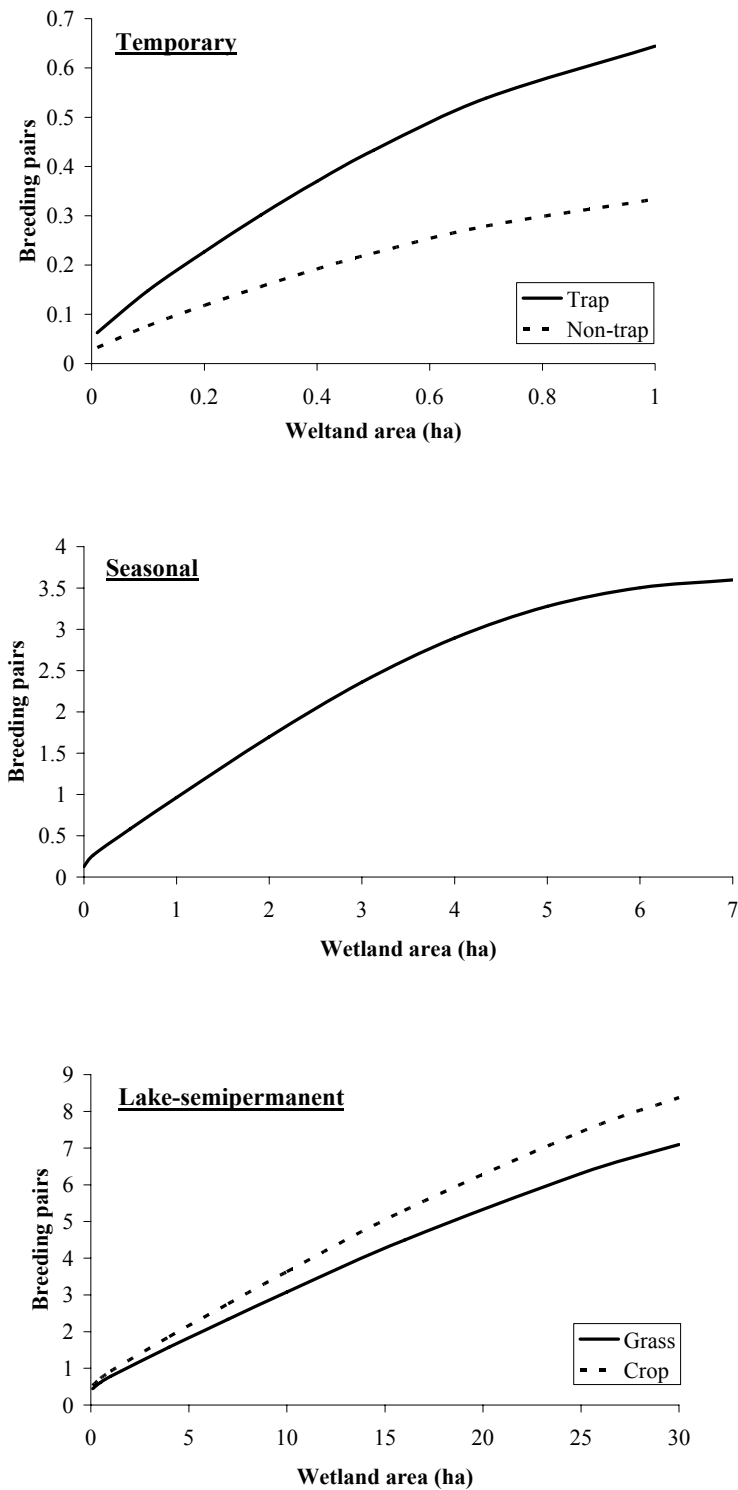


Figure 3.5. Best model-based relationships of shoveler breeding pair abundance to wetland area on temporary, seasonal, and lake-semipermanent wetlands in eastern North Dakota, 2005–2008. I weighted years and study sites equally.

explanation for the lack of positive response by pairs to wetlands adjacent to grassland, but it does not explain greater pair estimates for pintails on wetlands embedded in cropland. The finding that pintail pair abundance was greater on temporary and seasonal wetlands embedded in cropland than on those adjacent to grassland (Figure 3.4) was somewhat surprising. However, proportional use of cropped wetlands is greater for northern pintails than for any other duck species in the PPR (Stewart and Kantrud 1973, Kantrud and Stewart 1977). Also, pintails, unlike other upland nesting ducks, show no preference to nest in grassland and regularly nest in cropland (Milonski 1958, Klett et al. 1988, Greenwood et al. 1995, Richkus 2002) which may result in pintails settling at higher rates than other species on wetlands within cropland. Lastly, pintails prefer shallow, sparsely vegetated open water habitats that are subject to seasonal and annual instability (Sowls 1955, Smith 1970, Fredrickson and Heitmeyer 1988), which is more typical of wetlands within cropland than those within grassland. Predicted shoveler and gadwall pair abundance estimates were also greater on lake-semipermanent wetlands in cropland. However, the magnitude of effect was less than for pintails, and only occurred on one wetland class for each species.

Predator Management and Pair Abundance

Only 2 of 15 species-wetland class analyses indicated that pair densities increased following predator management; gadwalls on lake-semipermanent wetlands and shovelers on temporary wetlands. Even these 2 instances were equivocal, as the 95% confidence intervals for the TRAP parameter estimates bounded zero in both cases (Table 3.3). The overwhelming majority of species-wetland class analyses indicated that local breeding pair densities did not respond positively following predator management.

During prior studies in the same geographic region, Garrettson and Rohwer (2001) reported that breeding pair densities increased for most species following predator management, but Chodachek and Chamberlain (2006) found no positive effects of predator management on pair densities. My analyses of pair abundance were conducted at the wetland level, whereas Garrettson and Rohwer (2001) and Chodachek and Chamberlain (2006) analyzed pair densities per study plot. Chodachek and Chamberlain (2006) accounted for differences in wetland abundance among plots by using pond density as a covariate in their analysis, but Garrettson and Rohwer (2001) did not take wetland metrics within plots into consideration. Hence, I would caution that inference drawn from Garrettson and Rohwer's (2001) results may be misleading, especially if more wetland habitat was present on sites managed for predators.

While predator management significantly increased nest success during this study, mean nest success on nontrapped sites (43%; Pieron and Rohwer 2010) was still well above levels necessary for population maintenance (Cowardin and Johnson 1979, Cowardin et al. 1985). Hoekman et al. (2002) reported that the population growth rate (λ) for mid-continent mallards was most sensitive to variation in nest success but noted that as nest success increases duckling survival becomes a more important driver of population growth. Amundson (2010) found that predator management did not positively affect duckling survival during 2006–2007 on the same sites where I conducted my research. Improvements to exceptionally high background nesting success combined with unimproved duckling survival may have only marginally increased production on trapped sites, which would elucidate my finding that pair densities did not respond positively following predator management.

Anderson et al. (1992) noted that increased breeding populations following increased production are dependant on the extent to which females home to the same area in subsequent years. In light of this prerequisite, it is not surprising that blue-winged teal and pintail pair densities did not increase following predator management, because both species are less philopatric to breeding areas than other species and often pioneer into new breeding areas (Johnson and Grier 1988, Lokemoen et al. 1990, Anderson et al. 1992). This does not, however, explain why mallard pair densities did not increase, or why gadwall and shoveler pair densities generally did not increase following predator management. Mallards, gadwalls, and shovelers are all philopatric to breeding areas (Johnson and Grier 1988, Lokemoen et al. 1990, Anderson et al. 1992, Arnold and Clark 1996). If predator management did increase production, density-dependent settling may have forced emigration of some homing females and explain the lack of local population growth on predator managed sites. Hochbaum (1944) and Dzubin (1955) suggested that carrying capacity on the breeding grounds may result from conspecific intolerance related to water-area availability. Mallards, gadwalls, and shovelers all defend breeding territories from which conspecifics are excluded (Titman 1973, Seymour 1974, Dwyer 1975, Humburg et al. 1978, Seymour and Titman 1978, Titman and Seymour 1981). Territorial defense partially dictates the spacing of breeding pairs (Seymour and Titman 1978, Humburg et al. 1978) and may explain why mallard, gadwall, and shoveler pair densities generally did not increase following predator management.

Regardless of the mechanism, I found little evidence that local breeding populations of upland nesting ducks increased following predator management. Côte and Sutherland (1997) conducted a meta-analysis of published studies on predator

management and reported that while the practice regularly improves nesting success it does not reliably increase subsequent breeding bird populations. My results support these findings and further substantiate Côte and Sutherland's (1997) prediction that attempts to augment local breeding densities with predator management will likely be plagued by mechanistic limitations on population growth.

MANAGEMENT IMPLICATIONS

Though predator management is an effective technique for increasing nesting success of upland nesting ducks (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006, Pieron and Rohwer 2010), I would not recommend its use for attempts to increase local breeding populations, especially when nest success is already high. Managers should not operate under the assumption that increased production as a product of elevated nest success could be compounded over years. Also, I found little evidence that breeding pair densities were higher on wetlands adjacent to grassland, but this definitely does not negate the well established positive association between grassland cover and nesting success of upland nesting ducks (Reynolds et al. 2001, Stephens et al. 2005). Managers should certainly maintain and create grassland cover on the landscape, but I would suggest that protection of all wetlands, even those embedded in croplands, is important for securing ample settling habitat for breeding pairs.

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CHAPTER 4. FACTORS ASSOCIATED WITH THE FREQUENCY OF THREE-BIRD FLIGHTS IN THE MALLARD

For decades ecologists have been intensely interested in the regulation of wildlife populations, and considerable attention has been paid to territorial limitations on local breeding bird densities (Lack 1954, Brown 1969, Rodenhouse et al. 1997, 2003, Newton 1998). In the Prairie Pothole Region (PPR), breeding duck densities are strongly correlated with wetland conditions (Dzubin 1969*a*, Pospahala et al. 1974, Johnson and Grier 1988, Cowardin et al. 1995, Viljugrein et al. 2005), and carrying capacity may be regulated by conspecific intolerance related to water-area availability (Hochbaum 1944, Dzubin 1955). Dzubin (1969*b*) suggested that “densities of breeding pairs are controlled in part by the interaction of the pairs themselves, especially where optimum habitat is limited.”

In most temperate nesting ducks, females choose breeding locations (see review in Rohwer and Anderson 1988), and males defend territories from which conspecific pairs are excluded (Titman 1973, Seymour 1974, Dwyer 1975, Humburg et al. 1978, Seymour and Titman 1978, Titman and Seymour 1981). The pursuit flight, or three-bird flight (hereafter TBF), is the most common form of territorial defense for mallards (*Anas platyrhynchos*) and other prairie nesting dabbling ducks (McKinney 1965, Seymour 1974, Humburg et al. 1978, Seymour and Titman 1978, Titman and Seymour 1981). TBFs are aerial chases that ensue when an intruding pair enters an established pair's territory and the territorial male pursues the intruding female, with her mate following closely behind (Hori 1963, Titman 1973). Most frequently, the defending male returns to his point of origin after a brief chase, and the intruding pair is displaced from the defended territory (Barclay 1970, Seymour and Titman 1978, Titman and Seymour 1981,

Titman 1983). Males may benefit from defensive behavior and subsequent spacing by decreasing disturbance during copulation, restricting access to his mate, or by increasing the probability of reproductive success of his mate by protecting her food source and ensuring she can feed without harassment (Hochbaum 1944, Titman and Seymour 1981, McKinney 1973, McKinney et al. 1983, Titman 1983, Gauthier 1987). Regardless of the male's motivation, the TBF has been suggested to serve as a mechanism for the establishment and maintenance of territories and the subsequent expulsion of intruding pairs during settling through early incubation (McKinney 1965, Seymour and Titman 1978, Titman and Seymour 1981, Titman 1983, Anderson and Titman 1992).

Population density and habitat availability should largely dictate the frequency of territorial behavior (Dzubin 1955, 1969*b*). Anderson and Titman (1992) noted that minimal effort has been directed towards understanding the effects of population density on the breeding behavior of waterfowl and that more research should be conducted to assess the impact of varying population densities on spacing behavior and dispersion. The few studies that have been conducted with regard to this subject have yielded conflicting results. Frequency of TBFs was positively correlated with population density in some black duck (*A. rubripes*) and mallard populations (Humburg et al. 1978, Seymour and Titman 1978, Amat 1983), but Titman (1983) reported reduced TBF frequencies in a population of breeding mallards that was artificially inflated with hatchery-reared birds. Titman (1983) and Dzubin (1969*b*) suggested that under extreme densities territorial behavior may completely break down in breeding mallard populations. In addition to the fact that few studies have been conducted to ascertain the relationship between pair densities and territorial defense, those that have usually

considered pairs/area without taking into account available wetland habitat within that area (but see Amat 1983). Wetland habitat is likely an important source of variation to consider, given the well established relationship between pair abundance and wetland metrics (Dzubin 1969a, Pospahala et al. 1974, Johnson and Grier 1988, Cowardin et al. 1995, Viljugrein et al. 2005).

The abundance of pairs attempting to settle at a given breeding location is likely influenced by the rate of philopatry exhibited by females that nested at that location in the previous season (Anderson et al. 1992). Mallards are one of the most philopatric dabbling duck species in the PPR (Rohwer and Anderson 1988, Anderson et al. 1992, Arnold and Clark 1996), philopatry is greater for females that nested successfully in the previous season (Johnson and Grier 1988, Lokemoen et al. 1990, Majewski and Beszterda 1990), and progeny of successful females exhibit natal philopatry (Lokemoen et al. 1990, Arnold and Clark 1996). Additionally, population growth for mallards is most strongly correlated with nest success (Johnson et al. 1992, Hoekman et al. 2002). Hence, areas achieving high nest success may have more pairs attempting to settle in subsequent years, and therefore, higher frequencies of TBFs. I am aware of no studies that have explored the relationship between TBF frequency and nesting success in the previous season.

Most studies of territoriality in breeding duck populations in the PPR were conducted on relatively small study areas, were not replicated over multiple sites and/or years, and concentrated observations on relatively few marked individuals. During 2007 and 2008, I used point-count distance sampling (Thomas et al. 2002) to estimate TBF frequencies in breeding mallard populations on 5 township-sized (93.2 km²) study sites

where nest success was experimentally manipulated and 3 sites where nest success was not manipulated in northeast North Dakota (Pieron and Rohwer 2010). My first objective was to determine whether seasonal patterns in the frequency of TBFs in local populations were similar to patterns from small samples of marked individuals in prior studies. My second objective was to explore the effects of nest success in the previous season, breeding population size, available wetland habitat, and the ratio of breeding population size to available wetland habitat on the frequency of TBFs in wild breeding mallard populations.

STUDY AREA

During 2007 and 2008, I conducted research on 8 township-sized (93.2 km²) sites that were originally selected during a study evaluating the effect of predator reduction on nesting success and breeding populations of upland nesting ducks. Sites were in the drift prairie physiographic region in Benson, Cavalier, Nelson, Ramsey, Towner, and Walsh counties, North Dakota (Pieron and Rohwer 2010, Chapters 2 and 3). All sites had high wetland densities that supported >23 breeding duck pairs per km² and were dominated by agricultural land intermixed with moderate levels of grassland cover (~20% to 40%) in the form of hay, pasture, and idle cover enrolled in the Conservation Reserve Program (CRP) or in federal Waterfowl Production Areas (WPA). Mallards were one of the most common dabbling ducks on the study area (Pagano and Arnold 2009, Chapter 3), and regional population estimates for the species were 138% and 75% above the long-term average for 2007 and 2008, respectively (Wilkins et al. 2007, Zimpfer et al. 2008). On 5 of 8 sites, Delta Waterfowl Foundation hired professional trappers to remove mammalian predators from 15 March until 15 July. Nest success was 1.4 to 1.9 times greater on

trapped sites than non-trapped sites (Pieron and Rohwer 2010), but breeding mallard densities did not increase following predator management (Chapter 3).

METHODS

Field Methods

I initiated TBF surveys as soon as mallard pairs began to arrive on study sites in early April and terminated surveys in mid May. This captured the period between settling and early incubation when territorial defense is most prevalent (Dzubin 1955, Titman 1973, 1983). Within each of the 8 study sites, 15 point-count locations were spaced ≥ 1.6 km apart along road sides, which allowed for maximum coverage within study sites, yet independence of each point-count location. Points where $>25\%$ of the survey area was visually obstructed were replaced with new points. Each survey began at a randomly assigned point to avoid sampling a given point at the same time during subsequent surveys.

Point-counts, each of 15 minute duration, began at sunrise and continued until all 15 point-count locations were surveyed, which took approximately 5 hours. During a 2 minute settling period (to reduce potential observer disturbance on bird behavior) observers recorded date, time of day, wind speed (km/hr) using a Skymate SM-18 wind meter (Speedtech Instruments, Great Falls, VA), and sky condition. Sky condition was categorized as clear, partly cloudy, cloudy, fog, drizzle, or showers. Surveys were not conducted on days when severe weather conditions (heavy rain, snow, or fog) limited an observer's ability to traverse roadways or drastically reduced visibility. A single observer conducted each point-count by scanning in all cardinal directions for TBFs while standing in the bed of a pick-up truck to allow for increased visibility. Observers

recorded the distance from the location where each TBF began within distance intervals of 0–267 m, 268–533 m, 534–800 m, and >800 m. I chose these intervals because the agricultural landscape in North Dakota generally has landscape features (e.g. fence rows, grid roads, field entrances) spaced at these distances that can be used as spatial references by observers. Observers also carried aerial photographs of each point with concentric circles delineating distance intervals that further aided in assessing distances to observed TBFs (Fig. 4.1). Each observer completed surveys at all 8 study sites before rotating through the sites a second time.

Wetlands, Breeding Population Size, and Nesting Metrics

Utilizing ArcGIS 9.2, I used geo-referenced aerial photographs taken during late April–early May, 2007 and 2008, to digitize all inundated wetlands in each site-year. I classified each digitized basin based on the deepest water zone (Stewart and Kantrud 1971) and determined its area in ha. From this coverage layer, I determined the square root of the area for each wetland, which serves as a proxy for shoreline perimeter (Reynolds et al. 2007). Further, I determined the total wetland perimeter within each site-year by summing the perimeters of all wetlands in each site-year.

In Chapter 3, I developed regression models using PROC GLIMMIX (SAS Version 9.2; SAS Institute, Cary, NC) relating mallard pair abundance to wetland area and perimeter for sampled temporary, seasonal, and semipermanent and lake wetlands combined on the same study sites during 2005–2008. I used those regression equations to predict mallard pair abundance on all wetlands and then estimated total breeding mallard population size for each site-year by summing all wetland estimates from each site-year.

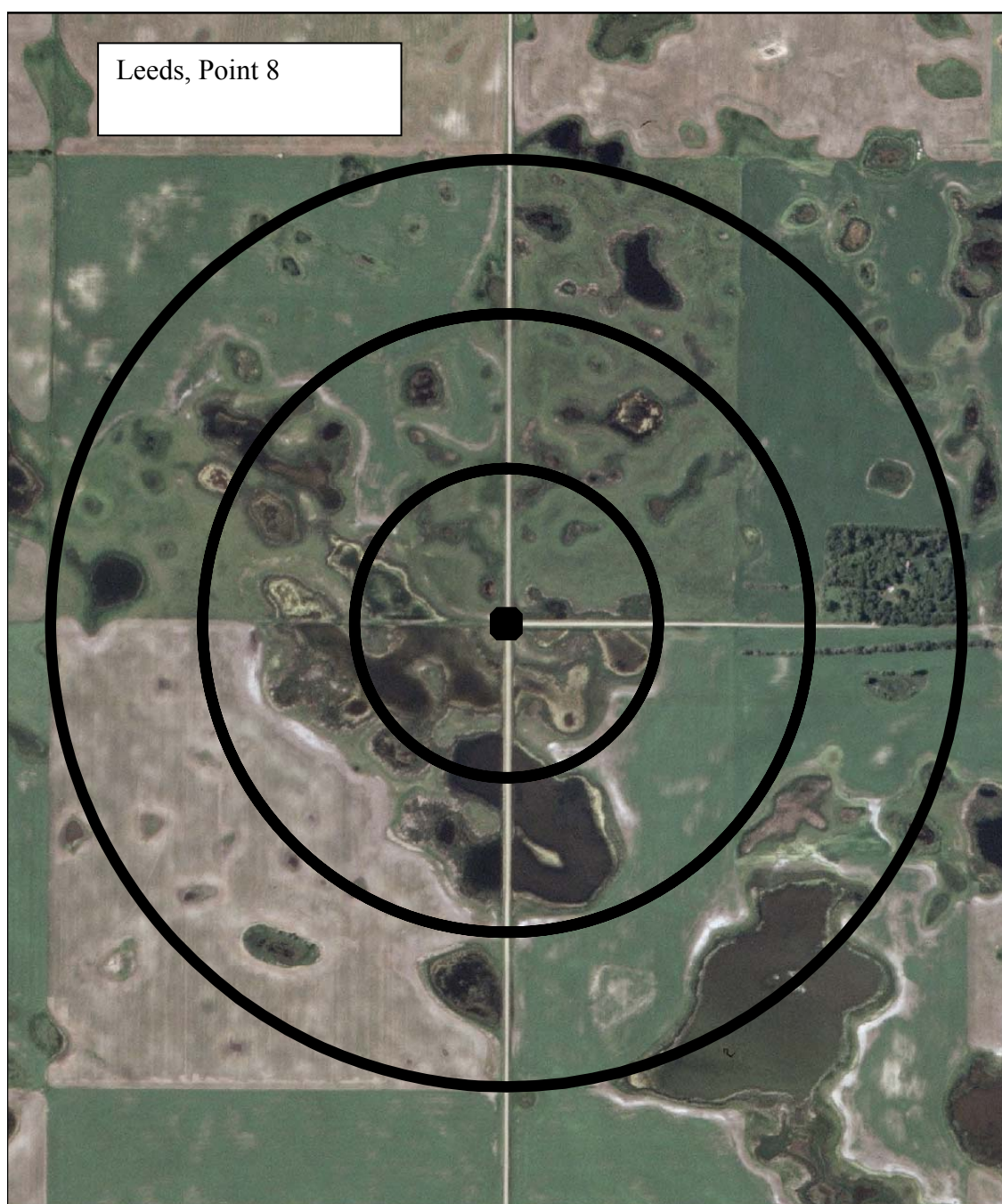


Figure 4.1. Example of map used to facilitate distance interval estimation during three-bird flight point-counts in northeast North Dakota, USA, during 2007 and 2008. Concentric circles are 267, 534, and 800 m from the survey point.

Pieron and Rohwer (2010) used the logistic exposure method (Shaffer 2004) to model daily survival rates (DSR) for upland nesting ducks on the same study sites during 2005-2007. Because Pieron and Rohwer (2010) included species, year, and site effects in their modeling, I was able to use ESTIMATE statements in PROC GENMOD (SAS Institute, Cary, NC) to derive model-based predicted values of DSR for mallards on each of my study sites for the years prior to TBF surveys (Shaffer and Thompson 2007). I then used a 35-day exposure period to convert DSR to nest success (Klett et al. 1986). Additionally, in 2007 and 2008, I monitored mallard nests on all study sites to assess nesting season chronology and estimated nest initiation dates by backdating based on clutch and incubation stage (Weller 1956).

Statistical Analysis

To ascertain potential effects of weather and study site, I initially modeled detection functions and frequencies of TBFs, pooled across years, from categorical distance data using program DISTANCE 5.0, Release 2.0 (Thomas et al. 2006). Distance sampling is a well accepted method used to estimate abundance of wildlife populations (Thomas et al. 2002, Farnsworth et al. 2005, McCallum 2005), but typically estimates the density of animals (animals/area; Buckland et al. 1993, 2001, Thomas et al. 2002). I modified typical distance-sampling methods by re-recording the same individual multiple times if that individual engaged in multiple TBFs during a survey period. Thus, I am determining the rate of a behavior not the density of individuals. Using sites (8), sky conditions (6), and wind speed as covariates, I developed 7 plausible models that contained all possible combinations of covariates and a null model. I fit detection models using half-normal base functions and cosine adjustments (Laake et al. 1993; Buckland et

al. 2001, 2004). I used Akaike's information criterion (AIC, Burnham and Anderson 2002) and visual inspection of the detection probability density graphs (Buckland et al. 2001, 2004) to select the most parsimonious of these competing models.

I estimated site-year specific frequencies of TBFs from the best detection probability model. I then used those estimates as responses in mixed general linear model (PROC MIXED; SAS Institute, Cary, NC) to identify site level variables that best explained variation in TBF frequency. I began with a saturated model that included breeding population size, total wetland perimeter, the ratio of breeding population size to wetland perimeter, last year's nest success, and year as fixed effects, and a random site variable. I sequentially reduced the saturated model using backwards elimination ($\alpha = 0.05$; Agresti 2007). To estimate variation in the response explained by a significant fixed effect, I calculated the pseudo R^2 (Littell et al. 2006) by (1) rerunning the final model without that effect while holding the random site effect at the level for the model containing the fixed effect, (2) subtracting the residual estimate for the model with the fixed effect from the residual estimate for the model without the fixed effect, and (3) dividing that difference by the residual estimate for the model without the fixed effect.

RESULTS

Each study site was surveyed at least 16 times in 2007 and 21 times in 2008, and we detected 7,334 mallard TBFs in both years combined. TBFs commenced as soon as pairs began settling and decreased as the nesting season progressed (Figure 4.2). The frequency of TBFs was greatest just after sunrise and consistently decreased through the morning (Figure 4.3).

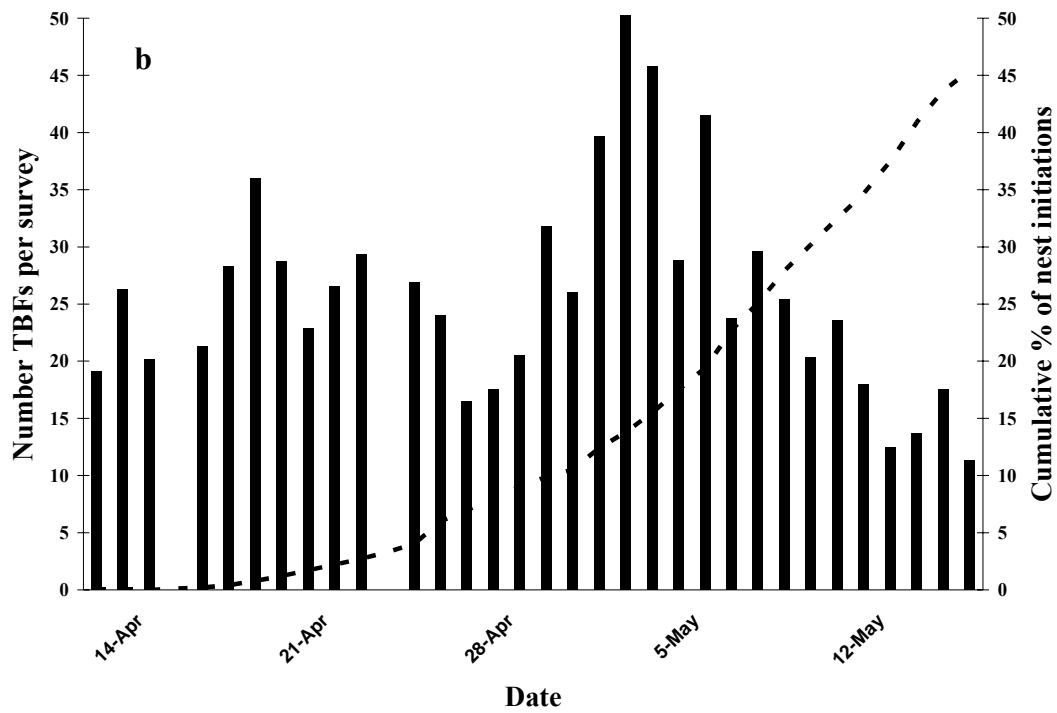
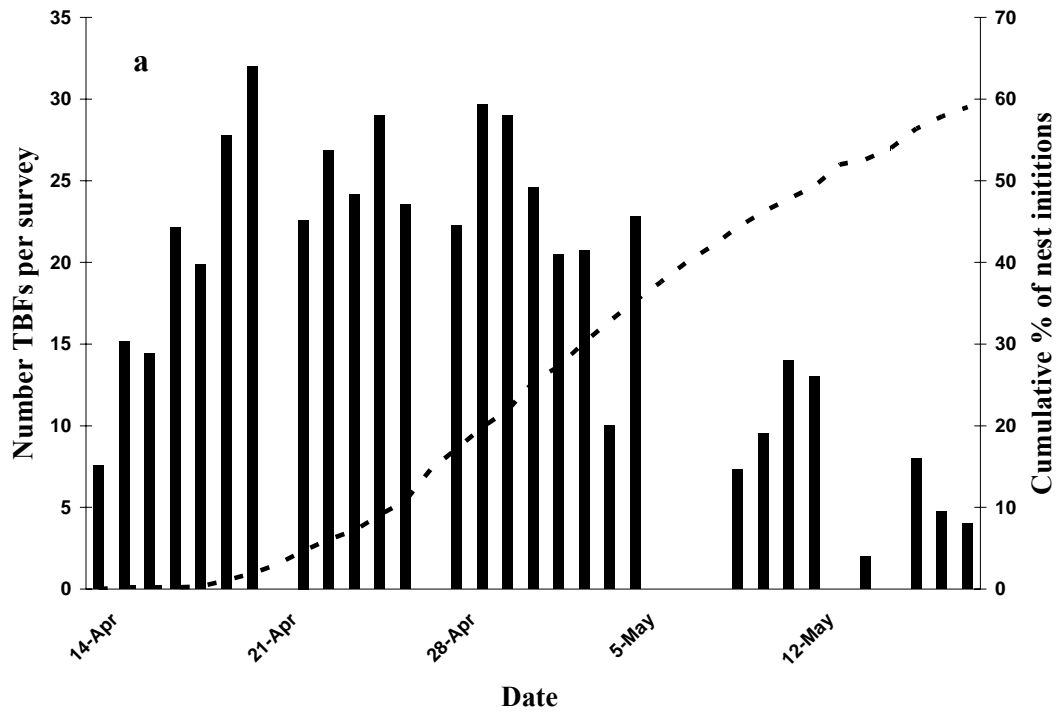


Figure 4.2. Daily number of detected three-bird flights per survey (bars) and cumulative percent of annual nest initiations (dotted line) during 2007 (a) and 2008 (b) averaged over 8, 93.2 km² study sites in northeast North Dakota, USA. Where estimates are missing, no TBF surveys were conducted due to inclement conditions.

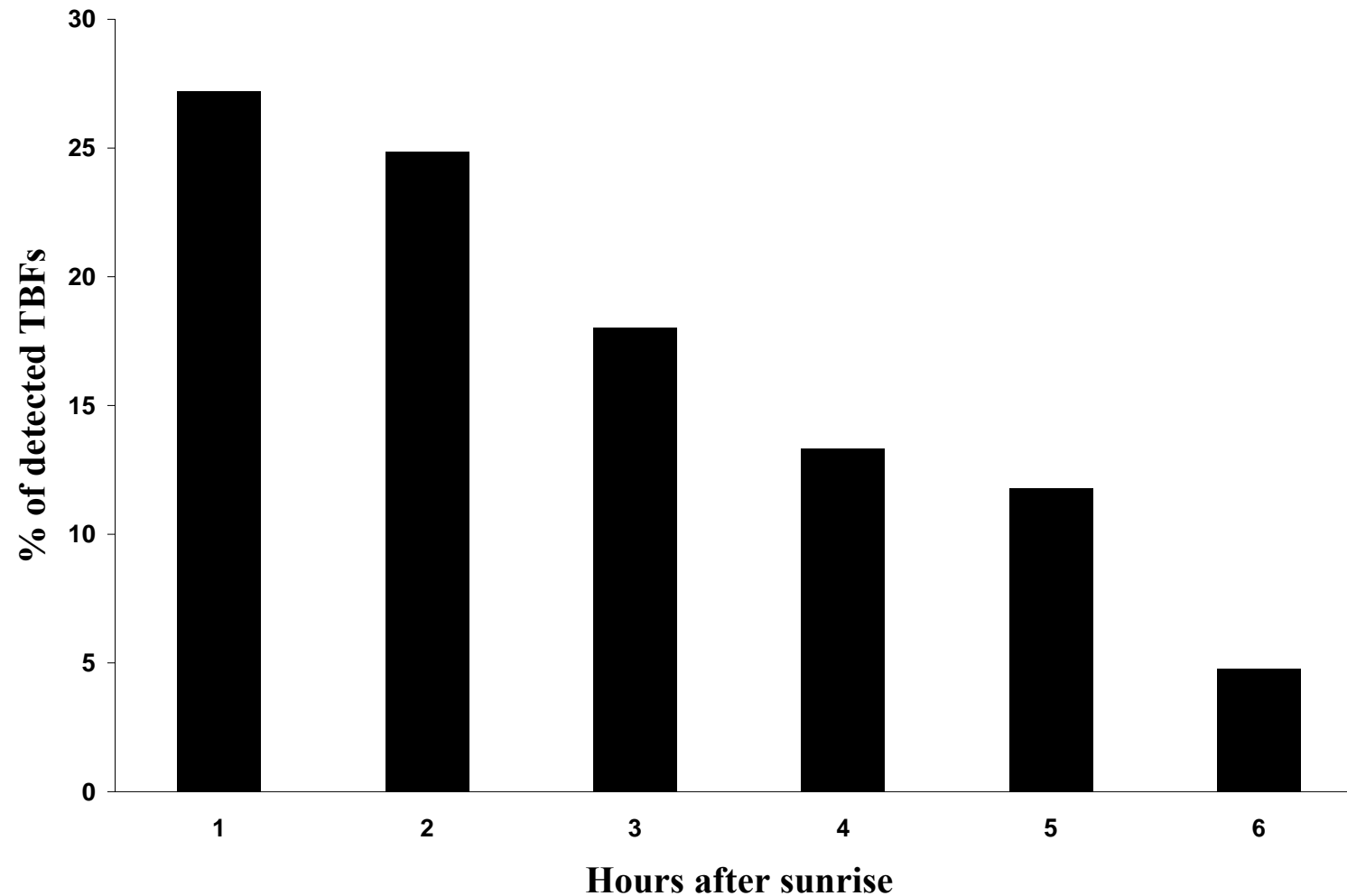


Figure 4.3. Percent of all detected three-bird flights, by hours after sunrise, during point-count surveys in northeast North Dakota, USA, during April and May, 2007 and 2008. For example, hour category 1 represents all point-counts that were initiated within 1 hour of sunrise.

The program DISTANCE model containing only wind as a covariate clearly outperformed competing models ($w_i = 0.86$), which were all $>2 \Delta AIC$ units from the best model. As wind speed increased, the detection probability for TBFs decreased ($\beta = -0.01641, \pm 0.00601$; Figure 4.4). The final reduced mixed general linear model included only the ratio of breeding population size to wetland perimeter, and predicted that the frequency of TBFs was positively correlated with breeding pair densities ($F_{1, 11.1} = 14.87$; $P = .002$; $R^2 = 0.63$; Figure 4.5).

DISCUSSION

My finding that TBFs were most frequent during early morning hours was consistent with previous studies (Titman 1973, Seymour and Titman 1978). Likely, this simply reflects the fact that ducks are most active during early morning hours (Chan and Phillips 1972), and behavioral interactions are therefore more frequent during this time. I found that TBF frequency was greatest early in the breeding season and subsided as greater portions of the population commenced nesting (Figure 4.2), which was consistent with previous reports that territorial defense is greatest from pre-laying through early incubation (Titman 1973, 1983, Dwyer 1975, Humburg et al. 1978, Seymour and Titman 1978, Titman and Seymour 1981). Heightened territorial defense by males early in the nesting season is likely associated with establishment and maintenance of an exclusive territory that limits access to his mate and provides her with an exclusive feeding area (Milne 1974, Dwyer 1975, Seymour and Titman 1978, Titman 1983, Gauthier 1987). Dissolution of mallard pair bonds generally occurs during early to mid-incubation (Dzubin 1955, Gilmer et al. 1977, Bellrose 1980; but see Losito and Baldassarre 1996) and would explain decreased territorial defense with progression of the nesting season.

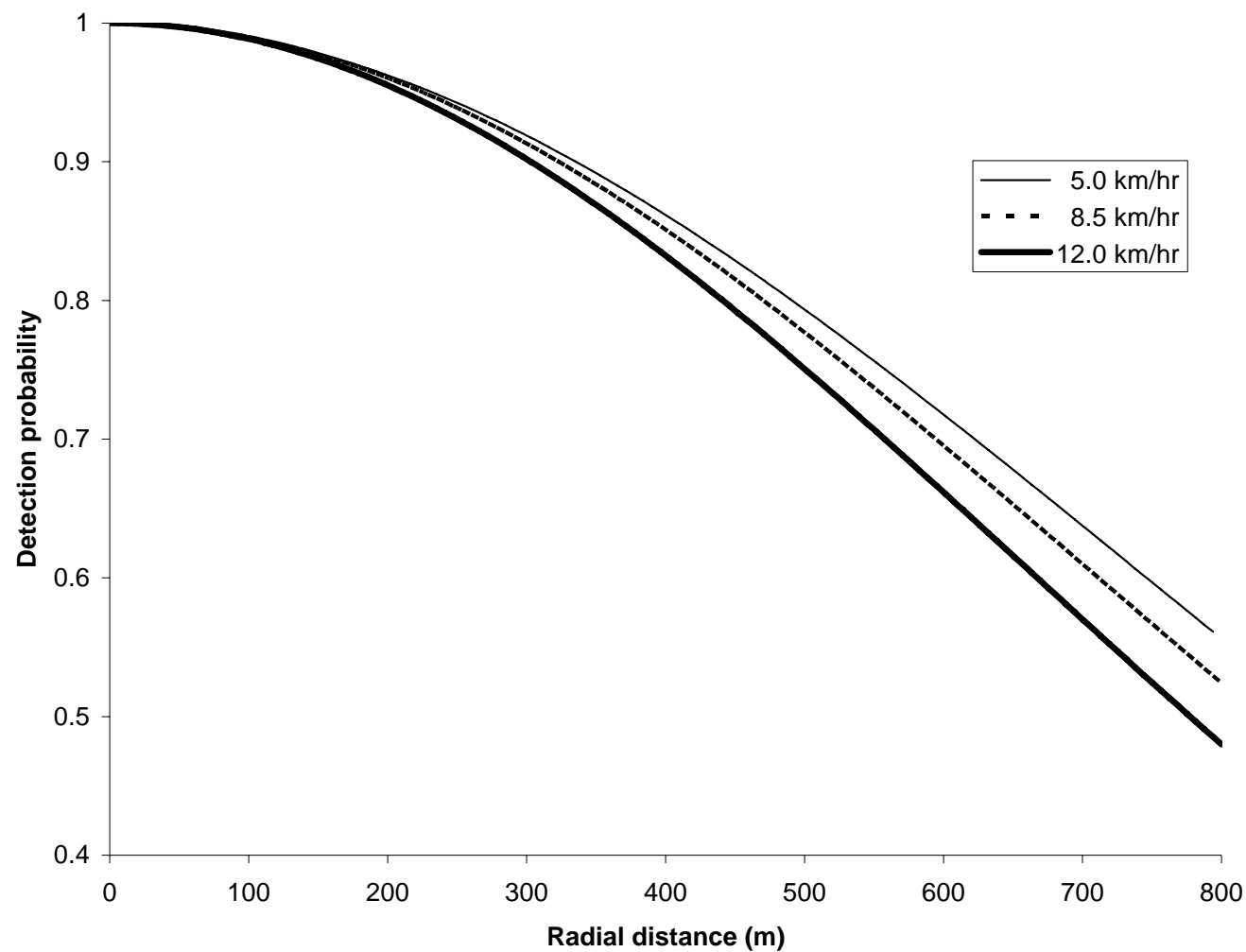


Figure 4.4. Distance and detection probability of mallard three-bird flights at varying wind speeds based on point-count survey data collected in northeast North Dakota, USA during early April–mid May, 2007 and 2008. The half-normal base function with a cosine adjustment provided the most parsimonious fit to the data.

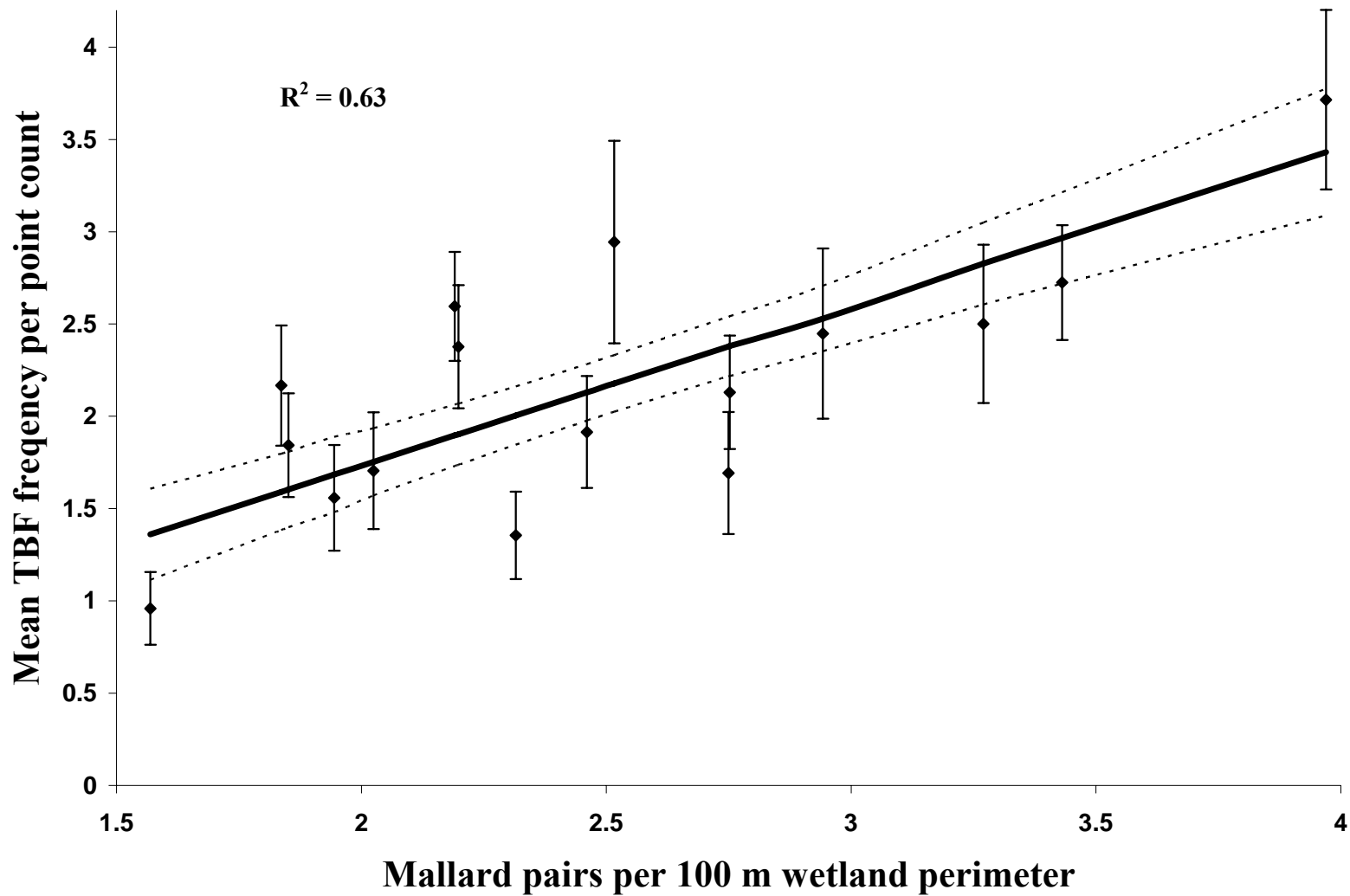


Figure 4. 5. Estimated frequencies of three-bird flights from the best DISTANCE detection probability model (black dots; ± 1 SE) and ANCOVA model-based relationship between TBF frequency and breeding pairs per wetland perimeter (solid line; ± 1 SE) for mallards in northeast North Dakota, USA, during April and May, 2007 and 2008.

I speculated that TBF frequencies may be correlated with local nest success in the previous season because population growth for mallards is strongly influenced by nest success (Johnson et al. 1992, Hoekman et al. 2002), philopatry is greater for females that nested successfully in the previous season (Johnson and Grier 1988, Lokemoen et al. 1990, Majewski and Beszterda 1990), and progeny of successful females exhibit natal philopatry (Lokemoen et al. 1990, Arnold and Clark 1996). However, I found no evidence for such a relationship. This may be a reflection of the fact that nest success was above levels necessary for population growth (Cowardin and Johnson 1979, Cowardin et al. 1985) on all sites during my study (Pieron and Rohwer 2010).

The ratio of breeding population size to wetland perimeter within sites was the only variable that remained in my final model and it explained a substantial portion of the variation in TBF frequencies ($R^2 = 0.63$; Figure 4.5). Prior studies also found a positive correlation between pair densities and the frequency of territorial behavior in mallards and black ducks (Humburg et al. 1978, Seymour and Titman 1978, Amat 1983), but only Amat (1983) considered the density of pairs per wetland area. My results were consistent with Amat's (1983) and suggest that correlations between defensive behavior and pair densities should consider pairs per available wetland habitat not pairs per upland and wetland habitat combined. This is not surprising, in light of the well established relationship between pair abundance and wetland metrics (Dzubin 1969a, Pospahala et al. 1974, Johnson and Grier 1988, Cowardin et al. 1995, Viljugrein et al. 2005).

Titman (1983) reported that territorial behavior appeared to completely break down in a breeding mallard population that was artificially inflated to 22-25 pairs/km² with hatchery-reared mallards. My study sites were 93.2 km² and supported an average

of 1,256 estimated breeding mallard pairs, or about 13.5 pairs/km². Though pair densities on my study sites were less than in the artificially inflated populations that Titman (1983) studied, they were still considerably greater than in the population he studied without artificial inflation (4-7.5 pairs/km²). I found no evidence that territorial behavior broke down under greater pair densities during my study. Rather, the frequency of territorial behavior was positively correlated with pair densities ($R^2 = 0.63$; Figure 4.5). I am aware of no studies of natural populations that corroborate Titman's (1983) findings that territoriality completely breaks down under extreme densities. In fact, territorial behavior by mallards and gadwalls (*A. strepera*) nesting in exceptionally high densities on islands in North Dakota caused pairs to establish territories up to 5 km from nesting islands (Duebbert 1966, Lokemoen et al. 1984). I would venture that Titman's (1983) results were likely attributable to, or at least confounded by, introducing hatchery reared birds into a wild population.

In conclusion, current conception is that defense of territories limits pair densities, but that densities above some threshold lead to dissolution of territorial behavior (Dzubín 1969b, Titman 1983). Making the connection between these 2 divergent hypotheses, that supposedly exist along one continuum, seems formidable. If territoriality limits local populations, how then, could a local population reach levels at which territoriality ceases to exist? It seems very difficult to unequivocally demonstrate that territoriality does limit pair densities, and I am aware of no evidence from natural populations that territoriality ceases to exist above some upper bound of density. Both hypotheses are illustrated in Figure 4.6; once the number of pairs attempting to settle in an area reaches some critical

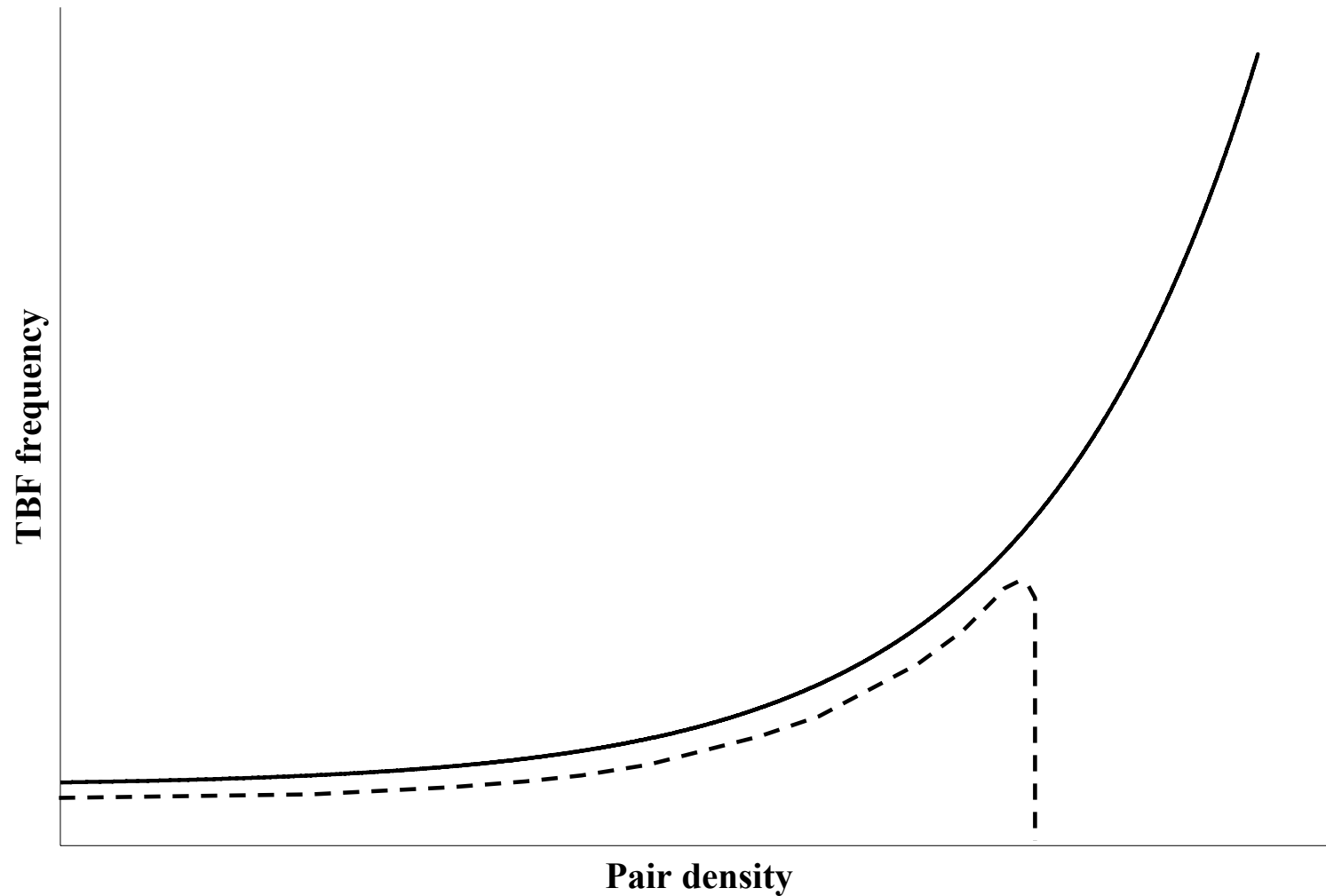


Figure 4. 6. Theoretical territorial responses of breeding mallards as the density of breeding pairs attempting to settle in limited habitat increases under two hypotheses; pair densities reach some critical threshold and the frequency of TBFs increases exponentially (solid line), or territoriality completely breaks down once pair densities reach the threshold (dashed line).

threshold then the frequency of TBFs increases exponentially, or conversely, territoriality completely breaks down. Determining the correct hypothesis would likely require studying a population that had reached such a threshold. However, such a determination would still not address whether territorial defense ultimately limits local populations. Strictly testing for effects of territoriality on pair densities would seemingly necessitate observing populations in the absence of territoriality. This seems an unlikely, if not impossible task in natural populations.

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CHAPTER 5. SUMMARY

Seasonal predator reduction on township-scale management units improved nesting success for upland nesting ducks in all years of my study. This was consistent with findings from prior evaluations that used similar payment systems and guidelines for professional trappers but at smaller spatial scales (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006). Trapped sites were 2.25 times larger than the sites that Garrettson and Rohwer (2001) evaluated, had similar effect size, but still only required one trapper salary and were therefore more cost-effective than smaller trapped sites. Predator reduction is a valuable tool for managers seeking to improve nest success and should likely be targeted towards areas with high densities of breeding ducks but low nest success. However, nest success estimates on both trapped and non-trapped sites were well above levels believed necessary for population maintenance (Cowardin and Johnson 1979, Cowardin et al. 1985). I suggest that future analyses be conducted to ascertain the benefits provided to production associated with improving nest success that is already well above levels deemed necessary for population growth.

While predator management significantly increased nest success during my study, I found little evidence that local breeding populations of upland nesting ducks increased following predator management. Hoekman et al. (2002) reported that the population growth rate (λ) for mid-continent mallards was most sensitive to variation in nest success but noted that as nest success increases duckling survival becomes a more important driver of population growth. Amundson (2010) found that predator management did not positively affect duckling survival on the same sites where I conducted my research. Improvements to exceptionally high background nesting success combined with

unimproved duckling survival may have only marginally increased production on trapped sites, which would elucidate my finding that pair densities did not respond positively following predator management. My results conform to Côte and Sutherland's (1997) prediction that attempts to augment local breeding densities with predator management will likely be plagued by mechanistic limitations on population growth. Therefore, I would not recommend its use for attempts to increase local breeding populations, especially when nest success is already high. Managers should not operate under the assumption that increased production as a product of elevated nest success could be compounded over years.

I found that three-bird flights (TBF) were most frequent early in the breeding season and subsided as greater portions of the population commenced nesting, which was consistent with previous reports that territorial defense is greatest from pre-laying through early incubation (Humburg et al. 1978, Titman and Seymour 1981, Titman 1983). Heightened territorial defense by males early in the nesting season is likely associated with the establishment and maintenance of an exclusive territory that limits access to his mate and provides her with an exclusive feeding area (Milne 1974, Seymour and Titman 1978, Titman 1983, Gauthier 1987). The ratio of breeding population size to available wetland habitat best explained variation in the frequency of TBFs. This was not surprising, given the well established relationship between pair abundance and wetland metrics (Dzubin 1969, Pospahala et al. 1974, Johnson and Grier 1988, Viljugrein et al. 2005).

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