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Jaime E. Jimenez

Utah State University

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NEST SUCCESS OF DABBLING DUCKS IN A HUMAN-MODIFIED PRAIRIE: EFFECTS OF PREDATION AND HABITAT VARIABLES AT DIFFERENT SPATIAL SCALES

by

Jaime E. Jiménez

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

Approved:

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Logan, Utah

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ABSTRACT

Nest Success of Dabbling Ducks in a Human-Modified Prairie: Effects of Predation and Habitat Variables at Different Spatial Scales

by

Jaime E. Jiménez, Doctor of Philosophy

Utah State University, 1999

Major Professors: Drs. Raymond D. Dueser and Michael R. Conover
Department: Fisheries and Wildlife

Nest success of dabbling ducks in the Prairie Pothole region of North America has been declining for the past 40 years in parallel with declines in duck populations. Low nest success seems to result from the combination of an extremely fragmented breeding ground in a human-dominated landscape with an abundant and expanding community of generalist nest predators. Studies that examined variables associated with nest vulnerability to predation have produced contradictory results, likely because of simplistic approaches, lack of spatio-temporal replication, use of artificial nests, and the effect of confounding variables. I attempted to clarify the equivocal findings of previous studies by using multiple regression to simultaneously examine the effect of several variables purportedly related to nest predation risk. I collected data on >1,800 dabbling duck nests and associated variables for 16 habitat patches (14 managed for duck production) during two nesting seasons in North Dakota.

At the habitat patch level, early and late in each breeding season, I studied the relationship of nest success and upland area, nest density, predator abundance and richness, abundance of alternative prey for predators, and visual and physical obstruction provided by the vegetation. At the spatial scale of the nest and its neighborhood, I examined the likelihood of nest predation in association to nest initiation date, year, distance from nest to a wetland and to an edge, vegetation type at the nest, visual obstruction and heterogeneity of the vegetation around the nest, duck nest species, predator abundance, and presence/absence of 5 carnivorous predators at the nest habitat patch. Nest success was generally low and highly variable in time, and among and within habitat patches. I found no relationship between nest success and any of the variables measured at the patch scale. At the nest level, only initiation date, distance to water, visual obstruction, predator abundance, and duck species had an effect. High variability in the data and the lack of patterns in the relationship of nest predation and the predictor variables precluded me from building a predictive model that explains nest success. Nest success could not be predicted, predation was incidental and risk was high, and there were no safe nest sites for hens to choose in a landscape swamped by nest predators. Nests were located randomly; therefore, there were no clues predators could use to enhance their success in finding nests.

(197 pages)

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Jaime E. Jiménez

PREFACE

Chapter 2, Effects of Environmental Variables on Prairie Duck Nest Success: A Multivariate Approach at the Landscape Level, and Chapter 3, Effects of Environmental Variables on Prairie Duck Nest Success: A Multivariate Approach at the Nest Level, will be coauthored with Michael R. Conover, Terry A. Messmer, and Raymond D. Dueser. The former will be submitted to *Ecological Applications* and the latter to the *Journal of Wildlife Management*. Chapter 4, Analysis of Nonlethal Methods to Reduce Predation on Ground-Nesting Birds and Their Nests, will be submitted to the *Wildlife Society Bulletin* with Michael R. Conover as a coauthor.

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CHAPTER 1

INTRODUCTION

Waterfowl populations in the Prairie Pothole Region (PPR) of North America declined during the last 40 years (Cowardin et al. 1985, Greenwood et al. 1995). This long-term trend is attributed to a 0.5% annual decrease in waterfowl nesting success (Beauchamp et al. 1996*a*) resulting from human-induced changes in habitat quantity (e.g., habitat loss and fragmentation, Andrén 1994, Bethke and Nudds 1995), habitat quality (Kirsch 1969, Higgins 1977), and predator abundance (U. S. Fish & Wildlife Service 1986, Klett et al. 1988, Johnson et al. 1989, Clark & Nudds 1991, Sargeant et al. 1993, Greenwood et al. 1995, Beauchamp et al. 1996*a*, 1996*b*).

The PPR is the primary duck breeding ground of North America (Bellrose 1980). Anthropogenic disturbances during the last 100 years have transformed this natural grassland/wetland landscape into a heterogeneous mosaic of discrete patches of cultivated and grazed fields (Kantrud et al. 1989, Sargeant et al. 1993, Greenwood et al. 1995). Little of the native prairie remains (Samson and Knopf 1994), and up to 95% of the surface is cultivated annually in some areas (Reynolds et al. 1994). As a result, good nesting cover for ducks has been reduced to small, isolated patches of grassland in a cropland-dominated landscape. Wetlands, which are key landscape features that attract breeding ducks (Kantrud and Stewart 1977, Krapu et al. 1983, Higgins et al. 1992) and which provide food for nesting hens and their broods (Sedinger 1992), have also been dramatically impacted by human activities through drainage, filling, and pollution (Kantrud et al. 1989, Krapu and Reinecke 1992, Batt 1996). About 90% of the wetlands have been drained (Sargeant and Raveling 1992). The modified landscape has been further impacted by a 1-by-1-mile network of roads and planted shelterbelts (Fritzell 1978, Faanes 1984), which produce a grid-like mosaic of discrete patches with sharp edges (Pasitschniak-Arts et al. 1998) and a characteristic human-imposed geometry (Krummel et al. 1987). It is not surprising that the prairie ecosystem is considered the most endangered ecosystem in the United States (Samson and Knopf 1994, 1996). Preserving the waterfowl breeding habitat in the PPR is the top priority of the North American Waterfowl Management Plan (U. S. Fish & Wildlife Service 1986).

Predation is considered the major cause of duck nest failure in the PPR (Johnson et al. 1989, Higgins et al. 1992, Sargeant and Raveling 1992). Common nest predators are medium-sized carnivores including red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*) (Urban 1970, Sargeant 1972, Duebbert and Kantrud 1974, Duebbert and Lokemoen 1980, Greenwood 1981, 1986, Klett el al. 1984, 1988, Sargeant and Arnold 1984, Sargeant et al. 1984, 1993, 1995, Cowardin et al. 1985, Kantrud et al. 1989, Trevor et al. 1991, Higgins et al. 1992, Greenwood et al. 1995, Pasitschniak-Arts and Messier 1995, Garrettson et al. 1996). These abundant opportunistic, generalist predators (Jones et al. 1985) are expanding their ranges in the PPR, apparently in response to human-induced changes in the landscape and the availability of resources (Fritzell 1978, Sargeant 1982, Sargeant et al. 1993). Predators appear to have taken advantage of abnormal concentrations of nesting ducks found on isolated fragments of suitable nesting cover, preying both on the eggs and on the incubating hens (Johnson and Sargeant 1977). In doing so, they reduce nesting success to less than 20% (e.g., mean nest success was 13-18% in 1970 and 8-12% in 1992; Beauchamp et al. 1996*a*, see also Beauchamp et al. 1996*b*). Reported nest success is lower than that necessary for maintaining a sustainable population over the long term (Cowardin et al. 1985, Johnson and Shaffer 1987, Klett et al. 1988).

In spite of the large amount of research dedicated to the study of waterfowl breeding ecology and its relationship to nest predation (see review by Sargeant and

Raveling 1992), the causal mechanisms of predator impact are not well known. Researchers have studied many variables associated with predation risk to nests. However, their results are often conflicting and consequently our understanding of the phenomenon is still poor (Clark and Nudds 1991). This is likely due, in part, to the complexity of nest predation and the many variables influencing it (Sargeant and Arnold 1984, Ebbinge 1989). Another reason may be that premature generalizations based on weak evidence and assumed mechanisms sometimes become ingrained as paradigms in the secondary literature (Paton 1994, Beck 1997). Often, studies are difficult to compare because of differences in methodology, definition of variables, predator communities, and the confounding effects of weather patterns (Clark and Nudds 1991, Greenwood et al. 1995). The problem is further exacerbated by the generally limited approach of examining one or two variables at a time with little or no spatial and temporal replication (Crabtree and Wolfe 1988, but see Donovan et al. 1997). Other complications are the disparate spatial and temporal scales of the nest predation studies and the landscape context involved (Sargeant et al. 1993, Ritchie et al. 1994, Andrén 1995, Huhta 1995, Donovan et al. 1997).

Given the logistical difficulties of assessing the success of producing fledglings as a measure of breeding success, most breeding waterfowl studies have used nest success as a surrogate. Although high nest success does not necessarily imply the production of many young, it has been shown through modeling that nest success and brood survival are the most important parameters affecting the breeding success of ducks (Johnson et al. 1992). Hence, nest success is considered a good index of waterfowl recruitment (Cowardin and Blohm 1992). In turn, nest success is largely determined by predation (Johnson et al. 1992).

Variables that have been shown to influence the vulnerability of duck nests to predation include nest concealment and structural habitat heterogeneity provided by vegetative cover (Duebbert 1969), cover composition (Klett et al. 1984), species composition and abundance of predators (Johnson et al. 1989), availability of alternative prey for nest predators (Crabtree and Wolfe 1988), habitat patch size where the nests are located (Greenwood et al. 1995), nest density (Andrén 1991), nest proximity to edges or water (Pasitschniak-Arts et al. 1998), and duck species identity (Klett et al. 1988, see also reviews by Clark and Nudds 1991, Johnson et al. 1992, Sargeant and Raveling 1992). Often, these variables operate simultaneously and at different spatial and temporal scales in determining nest fates. Nonetheless, despite the bewildering complexity of the variables affecting the vulnerability of nests to predation, the traditional approach has been to study the relationship of nest fate to single variables. Further, it is surprising that several years after the publication of the landmark paper by Clark and Nudds (1991), who pointed out the lack of generalities resulting from previous studies, no one has yet resolved the issue of complexity in nest vulnerability by considering the effects of several variables simultaneously.

The purpose of this study was to simultaneously address the effect of several variables which influence predation risk to duck nests in the agricultural prairies of North Dakota. In Chapter 2, I use a multiple regression approach to examine the effect of seven of the variables mentioned above on nest success at the scale of the landscape. My sample units are 16 different patches, most of them managed for the production of upland-nesting waterfowl. In Chapter 3, I improve the level of resolution by decreasing the spatial scale of the analysis from the patch to the nest level. I studied the influence of another set of 14 variables on nest fate with logistic regression. The strength in both chapters lies in the statistical modeling, which, as a tool, allows one to examine the association between each predictor variable and the response variable --either nest success or nest fate-- while statistically accounting for the effects of other variables. The goal of these chapters is to determine associations and to generate testable hypotheses. In Chapter 4, I present a review of nonlethal techniques to improve the recruitment of ground-nesting birds, including ducks. It describes work conducted in open habitats and evaluates the effectiveness of different methods. The content of this chapter is intended to aid wildlife managers in making decisions.

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CHAPTER 2

EFFECTS OF ENVIRONMENTAL VARIABLES ON PRAIRIE DUCK NEST SUCCESS: A MULTIVARIATE APPROACH AT THE LANDSCAPE LEVEL[1]

INTRODUCTION

Duck populations in the Prairie Pothole Region (PPR) of North America have declined during recent decades (Johnson and Shaffer 1987). This trend is attributed to a steady decrease in nesting success associated with habitat loss, fragmentation, and degradation due to human activities during the last century (Beauchamp et al. 1996*a*). Associated with this decline, duck production in the PPR dropped below population maintenance levels (Cowardin et al. 1985, Klett et al. 1988). This low recruitment is attributed to predation on nests and incubating hens by a suite of generalist predators that thrive in the human-modified landscape (Sargeant et al. 1993, Greenwood et al. 1995). These predators have increased in number and expanded their distributions, becoming the primary cause of nest losses (Sargeant and Raveling 1992, Sargeant et al. 1993, Greenwood et al. 1995).

Efforts to reverse the decline in waterfowl populations in the PPR have concentrated on improving upland nesting habitat to increase recruitment (U. S. Fish and Wildlife Service 1986, 1994). Restoration of habitat to high-density cover and nest habitat improvement have been implemented by setting aside areas and seeding them to obtain dense vegetative cover of grasses and legumes (Cowardin and Johnson 1979,

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[1] Coauthored by Jaime E. Jiménez, Michael R. Conover, Terry A. Messmer, and Raymond D. Dueser.

Duebbert et al. 1981, Klett et al. 1984, Higgins et al. 1992, see also Kantrud 1986). This action assumes that (1) hens will be attracted to nest in fields with high-density cover and (2) the complexity of the habitat will discourage predators from entering these dense patches and preying on nests and incubating hens (Higgins et al. 1992, Greenwood et al. 1995). Efforts to validate the first assumption have produced contradictory results (Clark and Nudds 1991, Clark and Diamond 1993). The latter has been assumed, but never tested (Duebbert 1969, Sargeant et al. 1984, Higgins et al. 1992, Greenwood et al. 1995).

The effect of habitat patch size (Clark and Nudds 1991) has been generally overlooked by previous studies of upland nesting ducks (for exceptions see Klett et al. 1988, Ball 1996). Nest success of breeding birds in forested landscapes varies with the size of the forest fragment (Burgess and Sharpe 1981, Andrén and Angelstam 1988, Andrén 1995). The mechanism implicated has been an increase in predation by generalist predators and in nest parasitism with decreasing patch size (Brittingham and Temple 1983, Wilcove 1985, Robinson et al. 1995). Predators and nest parasites have responded to the increase of edge (Gates and Gysel 1978, Angelstam 1986, Andrén 1992, 1994, 1995, Paton 1994, Pasitschniak-Arts and Messier 1995). Similar findings were reported by Johnson and Temple (1990) for prairie birds. However, the effects of the interaction of predation and habitat fragmentation on the reproductive success of waterfowl has not been explicitly documented in the PPR (Clark and Nudds 1991, Clark and Diamond 1993, Beauchamp et al. 1996*b*). Further, the scarce available evidence for the relationship between nest success and patch size in ducks shows mixed results (see Clark and Nudds 1991 and references therein).

Confounding and/or ignoring variables that might mediate predation risk of duck nests in a fragmented grassland could explain the inconsistency of the findings (see above). In addition to patch size, these variables include composition and abundance of the local predator community (Andrén et al. 1985, Angelstam 1986, Johnson et al. 1989, Nour et al. 1993, Sargeant et al. 1993, Greenwood et al. 1995, Sovada et al. 1995), abundance of alternative prey for the predators (Darrow 1945, Weller 1979, Angelstam et al. 1984, Phersson 1986, Crabtree and Wolfe 1988, Higgins et al. 1992, Greenwood et al. 1995, Pasitschniak-Arts and Messier 1995, Beauchamp et al. 1996*a*), the structural complexity of the habitat and nest concealment (Martz 1967, Schranck 1972, Higgins 1977, Bowman and Harris 1980, Livezey 1981, Hines and Mitchell 1983, Angelstam 1986, Sugden and Beyersbergen 1986, 1987, Crabtree et al. 1989, O'Reilly and Hannon 1989, Trevor 1989, Clark and Nudds 1991, Guyn and Clark 1997), and the density of nests (Tinbergen et al. 1967, Goransson et al. 1975, Oetting and Dixon 1975, Braun et al. 1978, Weller 1979, Duebbert and Lokemoen 1980, Hill 1984, Sugden and Beyersbergen 1986, Ratti and Reese 1988, Andrén 1991, Clark and Diamond 1993, Chamberlain et al. 1995, Nams 1997). Again, when studied in isolation, the influence of these variables on the nest success of dabbling ducks has produced mixed results.

An additional complication is the temporal component of change in these variables (Pasitschniak-Arts and Messier 1995). Indeed, temporal changes in predation pressure on duck nests have been documented (Sugden and Beyersbergen 1986, Greenwood et al. 1995). As the result of demographic processes (e.g., reproduction, mortality, dispersal), the abundance and community composition of both predators and their alternative prey change seasonally (Schultz 1965, Lysne 1991). Plant growth during the duck breeding season increases habitat structure (Martz 1967). Both the density of nesting hens and the species composition of the breeding duck community also change with time (Hill 1984, Higgins et al. 1992, Greenwood et al. 1995). Patch size may be the most constant variable. Consequently, the time *when* these variables are measured during the breeding season will likely produce different results. It is not surprising that studies evaluating nest success in relation to these variables have produced conflicting results (see Clark and Nudds 1991, Clark and Diamond 1993, and references above), again, likely as a result of focusing on a partial approach to the problem by studying environmental variables in isolation or a few of them and generally during one breeding season.

The first objective of this study was to examine the simultaneous effect of patch size and the seven confounding variables mentioned above on nesting success of upland nesting ducks in the PPR. We used a multiple regression approach, considering the eight variables simultaneously. Thus, unlike most previous studies, we assumed that more than one variable affects nest success. As a second objective, we built a model that predicts nesting success as explained by local environmental variables. We addressed the temporal dynamics of the ecosystem by using information obtained in the early and late phase of two breeding seasons. Thus, the central questions underlying this research were: (1) Is there an association between duck nest predation and local environmental variables at the landscape level related to predation in a human-modified prairie? (2) What is the importance of local environmental variables and their relationship to nesting success? (3) Is there a seasonal effect on any observed associations? (4) How well can a model that incorporates these variables predict nest success of upland nesting ducks in the PPR?

Besides improving our understanding of the complex phenomenon of predation on nests in a multivariate way, this study will benefit wildlife managers by providing them with a predictive model to guide their management of duck habitats and populations. These results should also guide future research to experimentally test the causality of the independent variables on nest success.

MATERIALS AND METHODS

Study sites

We studied nest success and measured the other variables at 15 sites during the waterfowl breeding seasons of 1997 and 1998. Study sites were located in an area of about 100 km in diameter north and east of Devils Lake in North Dakota, in the Drift Plain biogeographical province of the PPR (Stewart 1975). The region exhibited a high density of breeding waterfowl and abundant potential terrestrial predators (R. Reynolds and B. Holien pers. comm., J. Jiménez unpublished data, Garrettson et al. 1996). The landscape is highly fragmented. The 1-by-1 mile road network and planted shelterbelts produce a grid-like mosaic of patches with sharp edges (Pasitschniak-Arts et al. 1998). Up to 95% of the landscape surface is cultivated annually (Reynolds et al. 1994), primarily for the production of small grains and sunflowers (Cowardin et al. 1985). Precipitation averages 43.3 cm/year (at Edmore, N. D.), but is highly variable among years (Krapu et al. 1983). Most rain falls during spring and summer (Kantrud et al. 1989). Average minimum, mean, and maximum temperatures are -3.6, 2.9, and 9.5°C, respectively (at Edmore, N. D., Utah Climate Center).

To select the study sites, we considered all the sites in Ramsey, Cavalier, and part of Nelson Counties with dense nesting cover available during the breeding season of 1997. Dense nesting cover is considered the best available duck nesting habitat and the one that most closely resembles the original prairie vegetation (Klett et al. 1984, 1988, Higgins et al. 1992). Potential sites were not subjected to plowing, tilling, grazing, or predator control during at least the last 2 years prior to initiation of this study. Areas enrolled in the Conservation Reserve Program (CRP) and U. S. Fish and Wildlife Service Waterfowl Production Areas (WPA) and Wildlife Development Areas (WDA) met these requirements. Other criteria for site selection included abundant seasonal and temporary wetlands (Kantrud and Stewart 1977) and compact shape. Sites with large wetlands were discarded. We stratified the remaining available sites by the amount of upland area into small, medium, and large-sized patches. From each group we randomly selected 5 sites. To gain independence among sites, selected sites were located at least 5 km apart. For comparative purposes we used all but one of the same sites in 1998. Because one site was mowed in autumn 1997, it was replaced by another with similar characteristics. These sites encompassed the whole range of variability available in the area. Surface area of each site (including wetlands) and upland area was obtained from the Devils Lake Fish and Wildlife Service records and when not available, computed from aerial photographs. Upland surface area was considered the patch size estimator. Site characteristics are shown in Table 2-1, and their plant composition on Table A-1.

Estimates of all habitat, prey, and predator variables were obtained early (i.e., May-early June) and late (i.e., late June-July) during each breeding season. Splitting the breeding season into two periods is a compromise to account for temporal ecosystem-level changes and different duck breeding ecologies while still acknowledging logistic constraints of studying the system throughout the breeding season.

Estimating waterfowl nest success

As in Duebbert and Kantrud (1974) and Cowardin and Johnson (1979), we used nest success as an index of recruitment. Nest success was estimated at each site on four 16-ha blocks. Information from the four blocks was pooled by site. Sites smaller than 64 ha were surveyed entirely. Data from nests of all species were combined by site because of small sample sizes for individual species (Greenwood 1986). We employed the method developed by Higgins et al. (1977) for locating nests. Hatching date was estimated as described in Weller (1956) and Klett et al. (1986). Nest locations were marked with a bamboo stake 4 m from the nest, and the position was recorded with a hand-held GPS unit with differential correction. Nest fate was assessed as abandoned, successful, or depredated (Cowardin et al. 1985, Klett et al. 1986). Abandoned nests were not used in the analyses. The predator species that destroyed a nest often could not be determined because the evidence left by predators was inconclusive (Sargeant et al. 1998). We used nest fates and exposure days to calculate nest daily survival rates according to the Mayfield method (Mayfield 1961) as modified by Johnson (1979, see also Miller and Johnson 1978). We weighted the mean laying and incubation period of successful clutches (Klett et al. 1986) by the relative proportion of species at each site. Hatch rate, expressed as nest success, was computed from daily survival rates as described by Greenwood (1986). Nest searching was conducted three times between early-May and late-July (Miller and Johnson 1978, Sargeant et al. 1984, Higgins et al. 1992, Greenwood et al. 1995). To determine the fate, nests with known locations were visited during and between searches, and 7-15 days after the last search.

Nest success estimates were calculated separately for the fist and second half of the breeding season using the median initiation date plus the mean exposure days as the cutoff point. In what follows, these will be called early and late season, respectively. Splitting the breeding season into two periods, instead of treating time as a continuous variable, may seem arbitrary, but it was dictated by logistic constraints in sampling the other variables.

Estimating nest density

We first attempted to compute the density of nests as the ratio of the number of nests initiated to the surface of upland area searched. The number of nests initiated was computed as the ratio of the number of successful nests found to the estimated hatch rate (Miller and Johnson 1978:474). However, this procedure has two problems. Statistically it would be incorrect to calculate the independent variable, nest density, from the dependent variable nest success. Additionally, this procedure only works well within certain ranges of nest success values and will produce extreme density values if few nests were successful and nonsense values if no nest succeeded at a site. Instead, we used a more conservative approach based only on the total number of nests found. Thus, nest density at any given site will be the ratio of all nests found to the upland area searched (Duebbert 1969, Higgins 1977). Even though this estimate will present negative bias for sites with intense predation --this is the essence of the Mayfield estimator-- it correlates positively with estimates produced by the method described above (Spearman rhos for early and late seasons > 0.69, $P < 0.001$, $n = 30$). Because this estimate is a composite of the nests found over a time span, it overestimates nest density at any given time (Hill 1984). Conversely, because only a fraction of the nests are detected (Sowls 1955:102, Keith 1961:67, Gloutney et al. 1993), the estimate will underestimate nest density.

Measuring habitat variables

We estimated visual and physical obstruction at 20 random locations in each site from each of four cardinal directions. These two measures represent the difficulty that a mammalian predator would have to see through and to move through the vegetation, respectively. Visual obstruction was evaluated by using the method described by Robel et al. (1970). It corresponded to the mean height of the vegetation at a given site of 4-m radius measured from 0.5 m off the ground. Visual obstruction was also measured at each duck nest when first found. An index of physical obstruction was an estimate of the resistance to movement posed by the structure of the vegetation. We obtained this index by measuring the force necessary to drag a 0.4-kg soccer ball on the surface, through the vegetation. We pulled a ball with a 4-m string attached to a Pesola scale and determined the maximum force necessary to drag the ball at a speed of approximately 1 m/sec. Estimates for each site were the average of 80 measurements.

Assessing abundance of alternative food for predators

We obtained indices of small mammal and arthropod abundances at each site. These two prey categories constitute most, or an important part, of the diet of red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*), which are the most common nest predators in the region (Scott 1943, Verts 1967, Fritzell 1978, Greenwood 1981, 1982, 1986, Godin 1982, Kaufman 1982, Samuel and Nelson 1982, Sargeant 1982, Sargeant et al. 1986, 1993, Greenwood et al. 1985, Rosatte 1987, Sanderson 1987, Voigt 1987). Small mammal abundance was estimated using 20 medium-sized Sherman traps baited with rolled oats and peanut butter. Traps were located every 10 m along a line that ran across each patch, perpendicular and at least 50 m from an edge. Traps were checked every morning for three consecutive days. The total number of individual small mammals caught during the 60 trap-nights provided an abundance index for each site.

Arthropods were captured using a line of 20 pit-fall traps, without bait or preservation liquid (Sutherland 1996). A pit-fall trap was set every 10 m along the same line as the Sherman traps, equidistant between adjacent traps. Pit-fall traps were operated for 5 days. These traps selectively collect invertebrates that move above the ground and are more likely preyed upon by mammalian predators. We counted the number of arthropods > 5 mm collected in each trap, separating them by size into small (< 1 cm) and large (> 1 cm) and by taxa (Order or Family if possible). To account for differences in biomass, the smaller arthropods were weighted as 0.2 of the larger (i. e., five small were equivalent to one large). The number of arthropods collected in the 20 traps provided an index of abundance for the site.

Assessing predator abundance and species composition

Mammalian carnivores are the most abundant and the principal causes of nest failure in North Dakota (Duebbert and Kantrud 1974, Cowardin et al. 1985, Sargeant et al. 1993). At each site, we estimated the relative abundance of mammalian predators and the species richness of predators by using visitations to scent stations as described by Linhart and Knowlton (1975), refined by Roughton and Sweeny (1982) and used by Jiménez (1993) and Jiménez et al. (1996, see also Travaini et al. 1996). Local predator tracks were distinguished based on shape and size (Murie 1974, Halfpenny and Biesiot 1986, Sargeant et al. 1993). At each site, a line of six scent stations, spaced 250 m apart, was placed in the patch interior. If a straight line did not fit into a site, it was curved so that no station was closer than 50 m from an edge. Another similar line of scent stations was run along the edge of each patch. Both lines were operated simultaneously for two days/nights (Travaini et al. 1996). The predator abundance index for a site was the percentage of the 12 stations visited by predators. The species richness index was based on all the species recorded at these same scent stations combined with supplemental observations of avian and mammalian predators, their tracks, feces, or dens recorded within 1.6 km of a site, while conducting other surveys (Keith 1961). We combined local avian predators in four functional groups: (1) hawks, harriers, and falcons; (2) owls; (3) large-sized gulls; and (4) crows and magpies. Given that we spent similar amounts of time at all sites, data are comparable.

Variable selection and model building

Examining the relationship between nest success and the predictor variables and building a statistical model will help managers and scientists to understand the importance of the different variables on nest success and also to predict future responses in nest success given known levels of the independent variables (Neter and Wasserman 1974, Montgomery and Peck 1982, Hatcher and Stepanski 1994). One of our goals was to build separate models for the early and late seasons. Because 14 sites were used both years, a repeated-measures design was appropriate (Benington and Thayne 1994). For one of each season, we fit a repeated-measures model using PROC MIXED in SAS Release 6.12 (SAS Institute 1997). Nest success was the response variable, and year, patch size, nest density, predator abundance, predator richness, arthropod abundance, small mammal abundance, visual obstruction, and physical obstruction were predictor variables. Because the variance of the Mayfield estimator is inversely related to the number of exposure days (Greenwood 1986, Klett et al. 1988, Greenwood et al. 1995, 1998), we weighted all analyses by the number of exposure days to eliminate that bias (Freund and Littell 1991:80).

The analysis for early season showed no year effect ($F_{1,14} = 0.16$, $P = 0.693$). In contrast, the late-season model run did not converge to a solution after 25 iterations, probably due to lack of structure in the small data set. Hence, we built four separate models, one for each year and season. From this, it followed that if year was important, then differences in the models for the respective years should reflect that difference. Conversely, if the effect of year was not important, the models should be similar for both years, in which case only one model per season would suffice. Limited sample sizes precluded testing for interactions; only first-order models were analyzed (Neter and Wasserman 1974).

Given the small sample size (i.e., 15 sites), we attempted to reduce the number of predictor variables by eliminating redundancy in the data by using principal components analysis (Linhart and Zucchini 1986, Afifi and Clark 1990, Myers 1990:125). However, this was not successful, because multicollinearity among the predictors was low (Neter and Wasserman 1974, Montgomery and Peck 1982). The highest number of significant pairwise correlations among the predictors was detected for late 1998, when only 5 (17.9%) of the 36 combinations were significant (Tables 2-2 and 2-3). This is a conservative estimate because experimentwise error was not controlled in these tests.

Prior to running the four analyses, we examined the data for outliers (Fig. 2-1). We transformed the response variable to better meet the assumptions of normality and homoscedasticity and the predictor variables to improve the linear relationship with the response variable (Table 2-4, Neter and Wasserman 1974, Hines and O'Hara Hines 1987). Model fitting was performed using PROC REG in SAS (SAS Institute 1988). The strength of the relationship between nest success and each variable is indicated by its partial regression coefficient (Neter and Wasserman 1974, Sokal and Rohlf 1981:620), the direction of the trend by its sign (Myers 1990:98), and its relative importance by the standardized partial regression coefficient (Freund and Littell 1991, Hatcher and Stepanski 1994).

To choose among models we used the criterion of parsimony by combining statistical criteria and the simplest model that resulted in the best fit to the data (Neter and Wasserman 1974, Henderson and Velleman 1981, Montgomery and Peck 1982, Linhart and Zucchini 1986). We generated all possible regressions and examined the plots of the number of predictors against the adjusted R^2, Mallows C_p, and residual mean square (i. e., MSE). We selected those models that produced the largest adjusted R, the smallest C_p, and the smallest MSE, and that had the fewest number of predictors (Neter and Wasserman 1974, Montgomery and Peck 1982, Linhart and Zucchini 1986, Feund and Littell 1991, Brown and Rothery 1993, Draper and Smith 1998). The three diagnostic statistics are related and are therefore expected to produce convergent results (Draper and Smith 1998).

To select the "best" model, we chose a small set of candidate models based on the three statistical criteria. Each candidate model was scrutinized closely. One or more "best" models were then selected from among candidate models. Because of the small sample sizes relative to the numbers of parameters to be estimated, only models with three or fewer variables were selected for final candidate models (Hatcher and Sepanski 1994, Holiday et al. 1995). Two or more competing models were compared using the PRESS (predicted residual sum of squares) statistic. A smaller PRESS indicates a relatively better predictive model (Cook and Weisberg 1982, Montgomery and Peck 1982). PRESS also allowed us to detect influential data cases. As a jackknife procedure, PRESS served to validate the models (Holiday et al. 1995). The use of this statistic instead of other cross-validation techniques (Linhart and Zucchini 1986, Verbyla and Litvaitis 1989) is justified in this case because of the nature of the data. PRESS uses all the data, avoids data-splitting difficulties, and provides similar unbiased estimates compared to other more traditional methods (Holiday et al. 1995). Each candidate model was examined in detail using regression diagnostics by plotting the studentized residuals versus the predictors and the fitted values, and by plotting the partial residuals (Cook and Weisberg 1982, Montgomery and Peck 1982, Freund and Ltell 1991, Brown and Rothery 1993). One or more competing models were finally selected as the "best" models (Montgomery and Peck 1982, Myers 1990).

Unless otherwise indicated, tests were two-tailed and the significance level was $\alpha = 0.05$. For the model selection analysis, we used a critical α of 0.10. This more liberal decision rule will protect against leaving out a potentially important variable (i.e., committing a Type II error).

RESULTS

During the 2 years of study, 1,859 nests representing five dabbling duck species were found (Fig. 2-2). Of these nests, 843 and 826 either hatched or were destroyed by predators during 1997 and 1998, respectively, and were thus used in the analysis (Table 2-5). Numbers of nests used were 422 early and 413 late in 1997 and 421 early and 413 late in 1998.

Bivariate relationships

The data gathered and the estimators computed were highly variable among sites for the same seasons and years (Table 2-6, Figs. A-1 to A-8). On average, nest success was similar between seasons ($F_{1,53} = 0.08$, $P = 0.785$), but higher for 1998 than for 1997 ($F_{1,53} = 4.96$, $P = 0.030$). There was no interaction between season and year ($F_{1,53} = 1.97$, $P = 0.166$, Table 2-7). When estimated on the same sites, nest success in 1998 was independent from that in 1997 for the corresponding seasons (regression slopes were indistinguishable from zero; $P = 0.973$, $n = 15$ and $P = 0.333$, $n = 14$, for early and late season, respectively; Fig. 2-3).

The bivariate relationship between nest success and each of the predictors also showed considerable scatter and few strong associations (Fig. 2-1). Out of all 32 pairwise correlations, only 5 were significant and all of them occurred during 1998.

These results represented higher nest success with increases in: (a) nest density during late season of 1998 (slope = 0.217, t = 2.715, df = 14, P = 0.018); (b) arthropod abundance during both seasons of 1998 (slopes = 0.0015 and 0.0013, respectively, t's > 3.4, df = 14, P's < 0.005) and (c) small mammal abundance (slopes = 0.0234 and 0.0210, respectively, t's > 2.2, df = 14, P's < 0.05) during both seasons of 1998. Results of the tests are very liberal, because significance levels were not adjusted for multiple comparisons. Although nonsignificant, associations such as patch size, visual obstruction, arthropod and small mammal abundance during early season, nest density and predator abundance during late season, and physical obstruction during both seasons exhibited changes in the direction of the relationship (i.e., the sign of the slope) between consecutive years (Fig. 2-1, see also Tables 2-2 and 2-3).

It should be noted, however, that most of the significant associations were likely determined by only one or two influential points (Fig. 2-1). In fact, all the associations between nest success and single independent variables completely vanished when the variables were transformed to comply with the model assumptions (Tables 2-2 and 2-3). Inconsistencies in the direction of the relationship also occurred commonly between the pairwise combinations of the independent variables in the two years. This was true for 50.0% and 44.4% of the pairs during early and late seasons, respectively (Tables 2-2 and 2-3).

In summary, the data collected on the same sites were highly variable and appeared to be independent between two consecutive years. This was reflected in nest success and in the bivariate relationships between nest success and the eight independent variables measured both during early and late seasons. In addition, nest success showed no consistent relationship with any of the variables during the two years and the two seasons.

Full multivariate models

The full multiple regression models showed little consistency among themselves. The best models were those for the early seasons. However, the early season 1998 was the only significant model, and it explained 83% of the variation in the data (Table 2-8). The only variable with significant slope in the early 1997 model was physical obstruction (Table 2-9). This variable was also significant in the early 1998 model; however, although the magnitude of the slope for physical obstruction was similar for early 1997 and 1998 models (1.1631 and 0.9596, respectively), their signs were opposite, indicating different trends in both years. This means that nest success increased with increasing physical obstruction in early 1997 and decreased with increasing physical obstruction in early 1998. In addition to physical obstruction, predator richness, predator abundance, and patch size were also significant in the early 1998 model (Table 2-9). No variable was significant in either of the late models.

Although nonsignificant, physical obstruction in the late models also showed reversed signs between years, but now with opposite direction for the respective seasons within the same year. As indicated in the bivariate analyses, several other variables showed inconsistent trends for the same season in the two years (Table 2-9).

Final models

Two final models appeared reasonable for describing nest success during early season of 1997 (Table 2-10). The best two-variable model explained 42% of the variability in the data, whereas the best three-variable model explained 54%. Both models included physical obstruction and density of nests as the most important variables. The most parsimonious model would be the one that retained only two variables. According to this model, which is significant (Table 2-11), nest success was positively associated with physical obstruction and nest density (Table 2-12).

For the early season of 1998, the best model appeared to be the one that contained predator abundance as the only variable (Table 2-10). It performed well (Table 2-11) and explained 63% of the variance. Nest success was negatively associated with predator abundance (Table 2-12). Models with more variables become more complex, without explaining significantly more variability in the data. Further, the coefficients of the additional variables were indistinguishable from zero (t = -1.252 and 1.238, P = 0.235 and 0.239, respectively).

The late season 1997 model did not produce a reasonable solution. According to the variable selection criteria, the best model contained nest density and abundance of small mammals (Table 2-10). This model explained only 13.1% of the variance in the data and was nonsignificant (Table 2-11). The variable small mammal abundance was not significant (Table 2-12), but when that variable was removed, it rendered nest density nonsignificant (t = -1.221, P = 0.246). Nest success was negatively associated with nest density (Table 2-12), but only in the presence of small mammal abundance. The best three-variable model performed even worse.

For the late season of 1998, two final models appeared to be reasonable, and both were significant (Table 2-11). Two one-variable models retained arthropod abundance and small mammal abundance, which explained 39.7 and 39.4% of the variance, respectively (Table 2-10). In the former, nest success was positively associated with arthropod abundance (note that this variable was transformed by its inverse), and in the latter, it was positively associated with small mammal abundance (Table 2-12). The PRESS statistics indicate that the model containing arthropod abundance was slightly better than the one with small mammal abundance (282.59 and 300.92, respectively). The two-variable models improved the amount of variability explained compared to the simpler models (Table 2-10). However, in both of these models, the common variable, predator richness, was nonsignificant (t's < 1.7, P's > 012).

In summary, only three of the four season and year combinations produced reasonable models, all of which explained more than 41% of the variability in the data. Given that none of the "best" significant models retained the same variables, no common patterns were found between seasons and between years. Five out of the eight variables were kept in final models. Patch size, predator richness, and visual obstruction were not associated with nest success. Judging from the magnitude of the standard errors of the coefficients (Table 2-12), the predictive abilities of the models appear to be weak.

DISCUSSION

Individual variables

This is the first study that tested explicitly the effect of patch size on nest success in nesting waterfowl. We found no evidence of a relationship. Our data do not support the paradigm that nest success is correlated with patch size, which derived from predation studies in forested landscapes using artificial nests (Wilcove 1985, Møller 1988, Small and Hunter 1988, but see Nour et al. 1993, Huhta 1995). The evidence of this phenomenon for duck nests in grasslands is scarce and results are unclear. Although Ball et al. (1995) claimed high "productivity of ducks" on large patches, they provided no test that it was low in small patches and their justifications are speculative.

Our findings of no effect of patch size on nest success concur with Clark and Nudds' (1991) observations, their reanalysis of Duebbert and Lokemoen's (1976) data, and our own reanalysis of Sargeant and others' (1995:Table 1) data ($r_s = -0.309$, $n = 15$, $P = 0.264$). Given that the amount of edge decreases with patch size, these results are in line with the lack of edge effect found by Livezey (1980), Cowardin et al. (1985), Pasitschniak-Arts et al. (1998), and our own data (Jiménez et al. unpublished data). Thus, as implied by Andrén (1995), it appears that the forces that control nest predation in grassland patches differ from those in forested patches, at least in relation to patch size and edge effect.

It has been speculated that large habitat patches allow waterfowl nests to be spaced out and that this reduces nest predation (Sugden and Beyersbergen 1986, Higgins et al. 1992, Kantrud 1993, Ball et al. 1995, Greenwood et al. 1995, Larivière and Messier 1998). Our data support neither of these propositions. We found that nest density was uncorrelated to patch size ($r_s = -0.12$, $n = 60$, $P = 0.361$) and that nest density was uncorrelated with nest success ($r_s = 0.12$, $n = 59$, $P = 0.364$, Fig. 2-1). In turn, nest success was uncorrelated with patch size ($r_s = 0.05$, $n = 59$, $P = 0.680$, Fig. 2-1). The same conclusions can be drawn from Duebbert and Lokemoen's (1976) and Sargeant and others' (1995) data.

Apparently, predators do not respond to nests in a density-dependent manner as proposed by Tinbergen et al. (1967) and shown by Larivière and Messier (1998) using artificial nests (see Hill 1984 for natural nests). The main predator in our region, as in the latter study, was the skunk, and skunks can respond to nests in a density-dependent manner by developing an olfactory search image for finding nests up to about 25 m away (Nams 1997). Another important predator in our study, the red fox, can detect nests up to 30 m using olfaction (Sargeant pers. comm.). Our nests were at mean densities of < 1/ha, accumulated through the season, which rendered distances to nearest-neighbors far beyond the minimum density necessary to develop density-dependent responses by predators (Andrén 1991:Figure 1). The results of Larivière and Messier (1998) are not clear because they found a response only at intermediate densities (i.e., 10 nests/ha) and only late in the season. In addition, they deployed all nests at once, at densities ≥ 2.5 nests/ha, which, added to the unaccounted natural nests, would lead to unnaturally high nest densities. Hence, at least for the densities observed in our study, if predation on nests does not act density-dependently, then spacing-out would not be advantageous for ground-nesting waterfowl (Andrén 1991).

Although the hypothesis that alternative prey reduces predation on nests has not been demonstrated empirically (Crabtree and Wolfe 1988, Greenwood et al. 1998, King et al. unpublished data), many studies explain their findings involving alternative prey without providing any data (Keith 1961, Schranck 1972, Klett and Johnson 1982, Crabtree and Wolfe 1988, Klett et al. 1988, Johnson et al. 1989, Trevor 1989, Kantrud 1993, Greenwood et al. 1995, Huhta 1995, Pasitschniak-Arts and Messier 1995, Sovada et al. 1995). The few works on nest predation that actually measured abundance of alternative prey found contradictory results (Komarek 1937, Darrow 1945, Byers 1974, Weller 1979, Angelstam et al. 1984, Vickery et al. 1992, Ritchie et al. 1994). We separately quantified the abundances of both arthropods and small mammals. Our assessment of the relationship of alternative prey and nest success showed that the effect varies between years, seasons, and type of alternative prey. In the best case, the evidence is contrary to the assumed buffering effect of alternative prey on nest predation, and agrees with Komarek (1937), Vickery et al. (1992), and Ritchie et al. (1994) that abundant prey may actually attract predators, which in turn prey opportunistically on the nests.

The number of predatory species and the relative abundance of predators (measured as an activity index) appeared unrelated to nest success. It seems that a few species or low predator activity in a site produced an effect similar to more species or higher predator activity. Often, studies assume a negative correlation between predator abundance and nest success (Urban 1970, Klett et al. 1988, Sovada et al. 1995). Aside from Keith (1961), apparently no study has directly assessed the abundance of predators and its effect on nesting ducks, likely because of the difficulty of doing it (Trevor 1989). Keith (1961) found a tendency for lower nest success with increasing abundance of mammalian predators. DeLong et al. (1995) reported no relationship between predation on artificial ground-nests and predator abundance. Johnson et al. (1989) established species-specific correlations between nest predators and duck nest success, but did not provide data combining all species per site. Our results argue in favor of compensatory predation, as reflected by the lack of effect found with predator removal (Duebbert and Kantrud 1974, Parker 1984, Greenwood 1986, Clark et al. 1995, Sargeant et al. 1995) or mammalian exclusion studies (Beauchamp et al. 1996*b*). We concur with Sargeant et al. (1993) in recognizing the need to examine the effect of abundance and predator composition on nest success more closely.

The height of the vegetative cover and the index of physical obstruction at the sites was unrelated to nest success. Similar findings were reported by Crabtree et al. (1989), which was the only study we found that assessed obstruction to movement. It seems that when the primary predators are mammals, cover plays no role in protecting nests, as concluded by Clark and Nudds (1991). Further, patches of dense nesting cover apparently attract both predators and nesting hens, resulting in increased encounters between predators and nests and lower nest success (Schranck 1972, Sugden and Beyersbergen 1987, Crabtree et al. 1989, Reynolds et al. 1994). These results and observations call into question the widely held assumption that cover deters predators and the utility of the management practice (Duebbert 1969, Kirsch 1969, Schranck 1972, Weller 1979, Hines and Mitchell 1983).

The lack of patterns

Our evidence indicates that there is no constancy or pattern in the relationship between nest success, and habitat and predator-related variables that may affect duck nest vulnerability. Both the bivariate and the multivariate analyses point out that this is true for different years, and for different periods within the same breeding season. Our results of predation on upland waterfowl nests in this region were extremely variable. There was not even a correlation for nest success between consecutive years estimated on the same sites.

We found high variability in nest success and in all the confounding variables measured, among the different study sites for the same time period, and for the same sites in different periods. Nest predation was not only highly variable in space and time, but there was no repeated pattern. At the scale of space and time examined, no consistent relationship between nest success and any variable or group of variables was found. Hence, conclusions derived from studies conducted during one breeding season, or from research at a few sites, may be misleading.

We do not believe that our results reflect an artifact of the methods or of the sampling design used. In fact, by randomly selecting the study sites from almost the entire pool of sites available in a region of ca. 7,800 km^2, we included all the actual variability possible at that spatial scale. In addition to the spatial scale, and the variability observed among sites, we also detected temporal changes, even by using the minimum number of levels possible for intra-year and inter-year comparisons. We used the same techniques and repeated the exact protocol on the same study sites during similar time periods. Thus, even if the techniques, most of which are standard, were biased, this would not preclude our drawing conclusions from comparisons. What did limit our analysis was our relatively small number of independent sites. Despite this, we still believe that our results reflect a real pattern.

Are we missing the boat? Or, nest success cannot be predicted

The high inherent variability in all variables measured in the fragmented prairie was responsible for our inability to build even one predictive model. The poor predictive ability of the "best" models was likely a result of the nature of the data, and apparently not of the model or the variable selection process. We were not only unable to build a model to predict nest success of dabbling ducks in the PPR, but the more specific "best" models chosen, which represented a more limited set of conditions, performed poorly. It appears that, at least with the variables measured, the range of conditions observed, and the variability in the data, nest success cannot be predicted with confidence.

Violation of the model assumptions might have resulted in the observed lack of patterns. However, this seems unlikely, given the data screening process, the diagnostics performed, and the transformation of the data to better meet the assumptions. We did not test for interactions among variables, aside from the involvement of year effect. Higher-order effects of the predictor variables may have masked a clearer relationship with nest success. We could not perform these analyses, however, because of the limited sample size available and the several variables used.

There were four reasons why we evaluated the seven predictor variables and attempted to model them to predict nest success. First, all variables appeared related directly or indirectly to predation risk for ground nests. Second, these variables were previously studied in relation to nest success of ground nesting birds, generally with little consensus among studies. Third, the variables were able to be measured in the field, and with enough replication. Lastly, these variables are potentially subjected to management. There are numerous other variables that could have affected the results that we did not evaluate, such as delayed effects resulting from climatic patterns, species-specific differences among duck species, the landscape matrix around the study sites, etc. For instance, the absence of foxes from a site might be because a neighboring farmer had free-ranging dogs, or because the traffic of a nearby road killed them. Another reason may be the limited precision of our estimates or that too much error could have blurred any pattern. An alternative could be that given that so many variables influence nest success, with so many potential dependencies among variables, each one with high natural variability, nest success appears chaotic or unpredictable.

A landscape swamped with predators

Predation risk on ground nests is inherently high and regardless in which patch nests are placed, the likelihood of predation is high. Despite the efforts of managers to create habitats with dense nesting cover, predators were efficient in finding and destroying the nests. The role of vegetative cover was of little importance in protecting nests. In fact, good cover may have provided good habitat for other prey species, such as arthropods and small mammals, which may have attracted predators. In addition, the availability of prey for carnivore mammals appeared low in the landscape matrix of cultivated fields. In contrast, the agricultural fields provided little cover for the predators themselves, especially early in the season, and because of the farming operations, constituted a habitat of high risk for them. Hence, predators were attracted to habitat patches of dense nesting cover. We contend that, compared to the matrix of crop fields, patches of dense nesting cover provide year-round safe habitats for carnivores. It is in these patches that carnivores breed and fulfill their feeding requirements. Nesting hens are also attracted to the few same high-risk patches, which are, however, still better than cultivated fields.

The lack of consistency in the relationship of duck nest predation and nest density, patch size, abundance of two types of alternative prey, abundance and number of predator species, and the visual and physical obstruction of cover indicates that the landscape is swamped with predators. We hypothesize that there are no safe places for the ducks to nest, and no matter where a hen places a nest, escaping predation is a rare event. Predation on nests appeared unpredictable and incidental, and probably positively related to the abundance of alternative prey. Predators are not deterred by the dense nesting cover, and if vegetation structure poses any obstruction to the predators' movement and foraging efficiency, it does not prevent them finding most of the nests. Almost all of our sites had a rich community of generalist predators whose home ranges were at least as large as the patches themselves. It appeared that a few predators could completely search a patch for nests in a couple of nights. Radio-telemetry data, which we collected for another study (Jiménez unpublished data), support this hypothesis. I documented (nocturnal) movements of skunk females, one of the purportedly less mobile predators species/gender. Assuming that skunks could detect nests 25 m away, as experimentally determined, just one individual could potentially find 20-30% of the nests in an average-sized patch during one night (Fig. 4). Aside from other syntopic predator species, we usually observed more than one skunk per patch.

What strategy would a hen use for placing her nest in a landscape that has limited suitable cover and is swamped with predators? Probably nest in any spot, and play with the odds by providing no pattern or clue for predators. Nest predators and nesting ducks may play "hide and seek" in the landscape. Our data support this hypothesis.

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Table 2-1. Characteristics of the study sites used in North Dakota. Sites are ordered in a decreasing order of upland area.

Name	County	Managemt. status[1]	Year created	Total area (ha)	Upland area (ha)	Shape[2]	Wetlands[3]	Trees[4]
Nelson South	Nelson	CRP	1987	388.7	267.2	2	2	1
Edwards	Cavalier	WPA	1972	251.0	206.0	1	3	1
Mellin	Ramsey	WPA	1972	226.7	177.3	1	3	1
Stinkeoway	Cavalier	WPA	1972	259.1	161.9	1	3	1
Nelson North	Nelson	CRP	1987	259.1	129.6	1	2	1
Thorson	Cavalier	WPA	1972	129.6	96.9	2	3	1
Gette	Ramsey	WPA	1972	107.3	65.4	2	2	1
Hall	Ramsey	WPA	1972	64.8	45.0	1	3	1
Pung	Cavalier	WPA	1962	57.7	43.7	1	2	1
Storlie	Cavalier	WDA	1987	64.8	40.3	1	3	0
Eidness	Ramsey	WPA	1977	64.8	35.3	2	2	1
Howes	Ramsey	WPA	1973	40.5	28.3	1	2	1
Wengler West	Cavalier	WPA	1972	32.4	26.3	2	2	0
Pollestad	Cavalier	WPA	1967	16.1	10.2	1	2	1
Seitz	Ramsey	WPA	1967	25.9	10.0	3	1	2
Babcock	Ramsey	WPA	1967	13.2	6.5	3	3	1

[1] CRP = private conservation reserve program land; WDA = U. S. Fish & Wildlife Service wildlife development area; WPA = USFWS waterfowl production area.

[2] 1 = compact; 2 = elongated; 3 = most edge.

[3] 1 = one large; 2 = large + small; 3 = many small.

[4] 0 = absent; 1 = present; 2 = nearby.

Table 2-[illegible]. Spearman correlation coefficients matrix of the transformed variables during early season in 1997 (above the diagonal) and in 1998 (below the diagonal). Correlation coefficients are shown in the first line and the significance level in the second line. Significant coefficients at $\alpha = 0.05$ are shown in bold and those pairs that change sign between years are underlined. Sample sizes are 15. Experimentwise type I error rate due to the multiple pairwise comparisons was not controlled. Abbreviations as in Table 2-4.

	SQMAYFI	SQDENSI	LNUPLAN	SQPREAB	PREDSPP	LNARTHR	LNSMALL	LNVISUA	LNPHYSI
SQMAYFI	-	0.282 0.308	-0.004 0.990	-0.343 0.211	-0.060 0.833	0.096 0.733	-0.428 0.112	0.286 0.302	0.374 0.169
SQDENSI	0.236 0.676	-	0.311 0.260	0.074 0.792	0.127 0.652	-0.200 0.475	0.085 0.763	0.375 0.168	-0.088 0.756
LNUPLAN	0.236 0.990	-0.021 0.940	-	0.205 0.464	0.064 0.822	0.150 0.594	-0.179 0.522	0.054 0.850	0.018 0.950
SQPREAB	-0.259 0.351	-0.294 0.287	0.147 0.601	-	0.110 0.696	-0.013 0.964	0.477 0.072	-0.265 0.340	-0.136 0.628
PREDSPP	-0.188 0.502	-0.211 0.450	0.246 0.377	0.265 0.340	-	0.135 0.633	0.119 0.673	-0.421 0.118	0.279 0.313
LNARTHR	-0.136 0.630	0.464 0.081	-0.104 0.713	-0.289 0.297	-0.073 0.796	-	0.011 0.969	0.161 0.567	0.331 0.228
LNSMALL	0.178 0.526	**0.577** **0.024**	-0.433 0.107	-0.433 0.107	**-0.541** **0.037**	0.401 0.139	-	-0.219 0.432	-0.015 0.957
LNVISUA	-0.325 0.237	-0.150 0.594	0.150 0.594	-0.064 0.820	-0.296 0.284	-0.004 0.990	0.241 0.387	-	-0.202 0.470
LNPHYSI	-0.207 0.459	-0.189 0.499	**0.564** **0.028**	-0.110 0.695	-0.227 0.417	-0.171 0.541	-0.203 0.468	0.414 0.125	-

Table 2-3. Spearman correlation coefficients matrix of the transformed variables during late season in 1997 (above the diagonal) and in 1998 (below the diagonal). Correlation coefficients are shown in the first line and their significant level in the second. Significant coefficients at $\alpha = 0.05$ are shown in bold and those pairs that change sign between years are underlined. Sample sizes are 15, except for SQMAYFI during 1997, which is 14. Experimentwise type I error rate due to the multiple pairwise comparisons was not controlled. Abbreviations as in Table 2-4.

	SQMAYFI	LNDENSI	LNUPLAN	SQPREAB	PREDSPP	ARTHR_1	ASSMALL	SQVISUA	LNPHYSI
SQMAYFI	-	-0.117	0.090	0.193	-0.027	-0.169	0.449	0.358	0.108
		0.692	0.759	0.508	0.926	0.563	0.107	0.209	0.714
LNDENSI	0.250	-	-0.157	0.354	0.220	0.243	0.214	0.046	-0.080
	0.369		0.576	0.196	0.430	0.383	0.444	0.870	0.776
LNUPLAN	-0.086	**-0.561**	-	-0.240	0.196	0.193	-0.476	0.443	0.272
	0.761	**0.030**		0.389	0.483	0.491	0.073	0.098	0.327
SQPREAB	0.220	-0.279	0.120	-	0.468	-0.033	0.447	0.365	0.187
	0.432	0.315	0.670		0.078	0.907	0.095	0.181	0.504
PREDSPP	-0.207	-0.223	0.205	0.157	-	0.231	0.224	**0.635**	0.430
	0.460	0.424	0.464	0.576		0.407	0.423	**0.011**	0.110
ARTHR_1	-0.168	-0.339	-0.007	0.373	0.513	-	-0.162	-0.032	-0.182
	0.550	0.216	0.980	0.172	0.052		0.565	0.910	0.516
ASSMALL	0.451	0.494	**-0.533**	-0.079	-0.446	-0.382	-	0.173	0.208
	0.092	0.061	**0.041**	0.780	0.096	0.160		0.539	0.458
SQVISUA	0.136	0.132	0.211	-0.181	-0.371	**-0.582**	0.040	-	**0.717**
	0.630	0.639	0.451	0.519	0.174	**0.023**	0.889		**0.003**
LNPHYSI	-0.047	0.126	0.354	-0.338	-0.302	**-0.628**	0.067	**0.803**	-
	0.869	0.655	0.196	0.217	0.274	**0.012**	0.813	**0.001**	

Table 2-4. Acronyms and transformations of the variables used in modeling. See text for more details.

Variable	Unit of measurement	Transformation	Acronym
Nest success	% (Mayfield)	Square root	SQMAYFI
Nest density	Nests/ha	Log_e (x+0.5)	LNDENSI
		Square root	SQDENSI
Upland area (= patch size)	ha	Log_e	LNUPLAN
Predator abundance	% scent stations visited	Square root	SQPREAB
Predator richness	Species detected	Not transformed	PREDSPP
Arthropod abundance	Numbers trapped	Inverse	ARTHR_1
		Log_e	LNARTHR
Small mammal abundance	Individuals trapped	Arcsine square root	ASSMALL
		Log_e(x+1)	LNSMALL
Visual obstruction	dm (Robel)	Log_e	LNVISUA
		Square root	SQVISUA
Physical obstruction	kg force	Log_e(x+0.5)	LNPHYSI

Table 2-5. Number of dabbling duck nests, by year, season, species, and fate, found on 16 sites in North Dakota.

		Early season							Late season							
Year	Fate	BW[1]	GD	GW	ML	PT	SV	STOT	BW	GD	GW	ML	PT	SV	STOT	Total
1997	Hatched	80	23	6	19	21	17	166	43	28	6	13	19	17	126	292
	Depredated	143	27	9	34	19	24	256	97	64	5	66	32	31	295	551
	Abandoned	20	1	1	11	5	3	41	11	2	1	9	2	5	30	71
	Unknown	13	2	2	3	3	2	25	9	7	0	0	3	1	20	45
Subtotal		256	53	18	67	48	46	488	160	101	12	88	56	54	471	959
1998	Hatched	113	21	6	28	5	17	190	90	48	3	26	11	15	193	383
	Depredated	129	28	5	39	5	17	223	118	48	2	27	6	19	220	443
	Abandoned	11	2	0	3	0	1	17	10	8	2	6	1	2	29	46
	Unknown	9	2	0	3	1	3	18	4	6	1	2	2	1	16	34
Subtotal		262	53	11	73	11	38	448	222	110	8	61	20	37	458	906
Total		518	106	29	140	59	84	936	382	211	20	149	76	91	929	1865

[1] BW = Blue-winged teal *Anas discors*, GD = Gadwall *A. strepera*, GW = Green-winged teal *A. crecca*, ML = Mallard *A. platyrhynchos*, PT = Pintail *A. acuta*, SV = Shoveler *A. clypeata*, STOT = Subtotal.

Table 2-6. Statistics of the variables used. Shown are means ± 1 SE (first and second lines, respectively).

Year	Season	Nest success (Mayfield)	Density of nests (nests/ha)	Patch size (ha)	Predator abundance (% visit. to scent stat.)	Predator richness (species detected)	Abundance of insects	Abundance of small mammal	Visual obstruction (Robel estimate in dm)	Physical obstruction (kg force)
1997	Early	0.187	0.946	88.14	27.78	4.33	68.19	2.73	4.32	1.091
		0.038	0.130	21.05	3.79	0.36	13.05	0.61	0.23	0.040
1997	Late	0.159	0.971	88.14	27.78	4.13	93.16	5.80	5.84	1.240
		0.030	0.147	21.05	4.65	0.34	32.62	1.11	0.31	0.038
1998	Early	0.186	0.972	87.90	21.11	4.40	62.32	5.40	4.57	0.921
		0.047	0.134	21.11	4.29	0.25	21.74	1.25	0.27	0.041
1998	Late	0.239	0.989	87.90	20.00	4.47	70.57	9.73	6.99	1.182
		0.052	0.139	21.11	2.55	0.31	27.90	1.32	0.44	0.063

Table 2-7. Dabbling duck nest success in North Dakota by year and season (mean ± 1SE (*n*)). Computed statistics were weighted by exposure days.

Season	1997	1998	Total
Early	0.238±0.041 (15)	0.293±0.060 (15)	0.265±0.036 (30)
Late	0.177±0.031 (14)	0.407±0.070 (15)	0.298±0.044 (29)
Total	0.207±0.026 (29)	0.354±0.047 (30)	-

Table 2-8. ANOVA information of fitted full multiple regression models by year and season. Nest success of dabbling ducks was modeled as a function of 8 independent variables. During each period, data were estimated on 15 sites in North Dakota.

Season	Year	R^2	R^2_{adj}	MSE	df	F	P
Early	1997	0.8155	0.5695	4.422	8,6	3.315	0.081
Early	1998	0.9275	0.8307	2.511	8,6	9.590	0.007
Late	1997	0.5397	-0.1967	8.642	8,5	0.733	0.669
Late	1998	0.6745	0.2406	19.087	8,6	1.554	0.304

Table 2-9. Parameter estimates of full multiple regression models by year and season. Nest success of dabbling ducks was modeled as a function of 8 independent variables. During each period, data were estimated on 15 sites in North Dakota. Variable abbreviations as in Table 2-4.

Season	Year	Variable	Slope	SE	*t*	*P*	Standardized slope
Early	1997	INTERCEPT	0.4305	0.0432	9.974	<0.001	0.0000
		SQDENSI	0.2971	0.1465	2.028	0.089	0.4377
		LNUPLAN	-0.0852	0.0511	-1.667	0.147	-0.4168
		SQPREAB	0.0685	0.0401	1.706	0.139	0.5033
		PREDSPP	-0.0133	0.0370	-0.360	0.731	-0.1056
		LNARTHR	0.0034	0.0703	0.049	0.963	0.0140
		LNSMALL	-0.1428	0.0641	-2.229	0.067	-0.5964
		LNVISUA	0.0366	0.3260	0.112	0.914	0.0309
		LNPHYSI	1.1631	0.4133	2.814	0.031	0.6688
Early	1998	INTERCEPT	0.3996	0.0321	12.433	<0.001	0.0000
		SQDENSI	-0.1121	0.1613	-0.695	0.513	-0.1155
		LNUPLAN	0.1293	0.0390	3.320	0.016	0.5797
		SQPREAB	-0.0385	0.0186	-2.077	0.083	-0.4131
		PREDSPP	-0.1197	0.0311	-3.848	0.009	-0.6324
		LNARTHR	-0.0059	0.0371	-0.159	0.879	-0.0323
		LNSMALL	0.0234	0.0595	0.393	0.708	0.1074
		LNVISUA	-0.2722	0.1967	-1.384	0.216	-0.2333
		LNPHYSI	-0.9596	0.3829	-2.506	0.046	-0.3683
Late	1997	INTERCEPT	0.3839	0.0639	6.007	0.008	0.0000
		LNDENSI	-0.2442	0.1843	-1.325	0.242	-0.6831
		LNUPLAN	0.0595	0.0844	0.705	0.512	0.3541
		SQPREAB	-0.0198	0.0383	-0.516	0.628	-0.2457
		PREDSPP	-0.0615	0.0540	-1.139	0.306	-0.5697
		ARTHR_1	0.4341	2.6650	0.163	0.877	0.0623
		ASSMALL	1.0884	0.5934	1.834	0.126	1.0642
		SQVISUA	0.5957	0.5174	1.151	0.302	0.8353
		LNPHYSI	-1.0061	0.7936	-1.268	0.261	-0.7911
Late	1998	INTERCEPT	0.4583	0.0749	6.122	0.001	0.0000
		LNDENSI	0.0654	0.3732	0.175	0.867	0.1083
		LNUPLAN	0.1086	0.1030	1.055	0.332	0.3607
		SQPREAB	-0.0184	0.0508	-0.363	0.729	-0.1534
		PREDSPP	-0.1200	0.1024	-1.172	0.286	-0.4968
		ARTHR_1	3.8111	8.8121	0.432	0.681	0.2373
		ASSMALL	1.0983	0.9775	1.124	0.304	0.5247
		SQVISUA	-0.2948	0.4426	-0.666	0.530	-0.3371
		LNPHYSI	0.4447	0.6241	0.713	0.503	0.4172

Table 2-10. Partial results of all possible regression models for early and late seasons of 1997 and 1998. Only the two best candidate models with ≤ 3 variables are shown. The response variable was nest success (i.e., SQMAYFI). Sample size was 15 in all of them but for late 1997, which was 14. Variable abbreviations as in Table 2-4. Asterisks indicate the "best" models chosen.

R^2	R^2_{adj}	C_p	MSE	Variables in model
Early 1997				
0.3250	0.2732	10.9465	7.4658	LNPHYSI
0.2107	0.1500	14.6670	8.7315	LNUPLAN
0.5003	0.4170	7.2495	5.9884	LNPHYSI SQDENSI*
0.4162	0.3189	9.9823	6.9956	LNPHYSI LNPATCH
0.6368	0.5377	4.8102	4.7481	LNPHYSI SQDENSI PREDSPP
0.5787	0.4638	6.7006	5.5081	LNPHYSI SQDENSI LNSMALL
Early 1998				
0.6565	0.6301	17.4110	5.4877	SQPREAB*
0.4339	0.3904	35.8234	9.0441	LNARTHR
0.6962	0.6456	16.1295	5.2584	SQPREAB PREDSPP
0.6954	0.6447	16.1935	5.2718	SQPREAB LNUPLAN
0.8137	0.7629	8.4111	3.5179	LNUPLAN PREDSPP LNPHYSI
0.7736	0.7118	11.7295	4.2754	LNUPLAN PREDSPP SQPREAB
Late 1997				
0.1104	0.0363	-0.3362	6.9592	LNDENSI
0.0655	-0.0124	0.1517	7.3106	PREDSPP
0.2645	0.1308	-0.0098	6.2771	LNDENSI ASSMALL*
0.1521	-0.0020	1.2107	7.2359	LNDENSI PREDSPP
0.3442	0.1472	1.1244	6.1566	LNDENSI ASSMALL PREDSPP
0.3225	0.1192	1.3602	6.3604	LNDENSI ASSMALL LNPHYSI
Late 1998				
0.4400	0.3970	-0.6769	15.1572	ARTHR_1*
0.4368	0.3935	-0.6173	15.2440	ASSMALL*
0.5428	0.4666	-0.5719	13.4061	PREDSPP ASSMALL
0.5309	0.4528	-0.3526	13.7553	PREDSPP LNDENSI
0.5952	0.4848	0.4625	12.9492	ASSMALL LNPATCH PREDSPP
0.5895	0.4776	0.5670	13.1304	ASSMALL LNPATCH LNDENSI

Table 2-11. ANOVA information of best selected models for early and late seasons of 1997 and 1998.

Season	Year	R^2	R^2_{adj}	MSE	df	F	P
Early	1997	0.5003	0.4170	5.98	2,12	6.007	0.016
Early	1998	0.6565	0.6301	5.49	1,13	24.849	<0.001
Late	1997	0.2645	0.1308	6.28	2,11	1.978	0.185
A Late	1998	0.4401	0.3970	15.16	1,13	10.216	0.007
B Late	1998	0.4368	0.3935	15.24	1,13	10.083	0.007

Table 2-12. Parameter estimates of best selected models for early and late seasons of 1997 and 1998. Variable abbreviations as in Table 2-4.

Season	Year	Variable	Slope	SE	*t*	*P*	Standardized slope
Early	1997	INTERCEPT	0.4071	0.0416	9.780	<0.001	0.0000
		SQDENSI	0.2941	0.1434	2.051	0.063	0.4333
		LNPHYSI	1.1863	0.3674	3.229	0.007	0.6821
Early	1998	INTERCEPT	0.4623	0.0339	13.621	<0.001	0.0000
		SQPREAB	-0.0756	0.0152	-4.985	<0.001	-0.8103
Late	1997	INTERCEPT	0.4257	0.0387	11.004	<0.001	0.0000
		LNDENSI	-0.2434	0.1236	-1.969	0.075	-0.6811
		ASSMALL	0.5370	0.3538	1.518	0.157	0.5251
Late	1998						
A		INTERCEPT	0.4963	0.0586	8.470	<0.001	0.0000
		ARTHR_1	-10.6532	3.3329	-3.196	0.007	-0.6634
B		INTERCEPT	0.5281	0.0546	9.681	<0.001	0.0000
		ASSMALL	1.3836	0.4357	3.175	0.007	0.6609

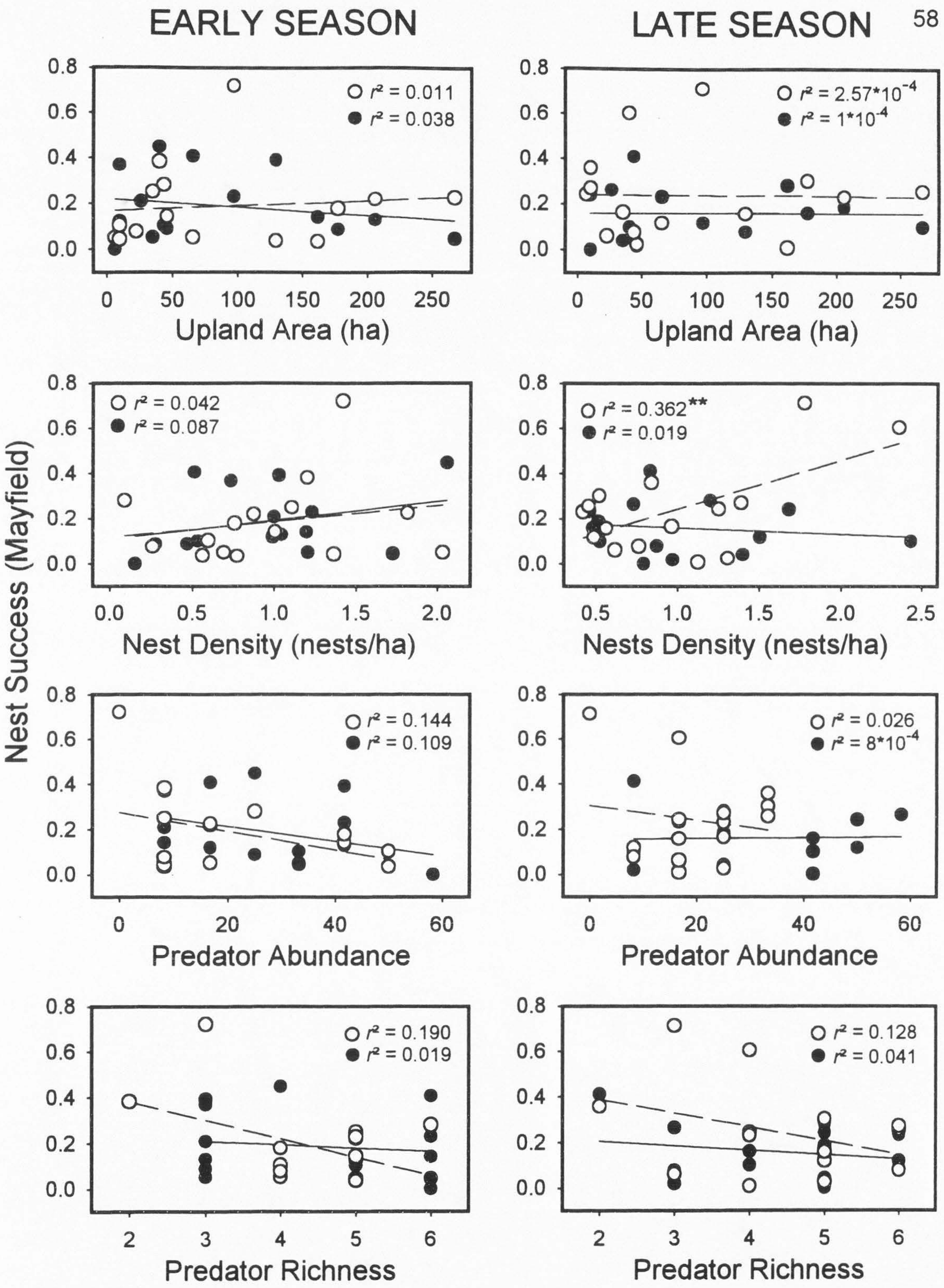

Fig. 2-1. Relationship of duck nest success and each predictor variable measured during early and late seasons of 1997 (filled circles) and 1998 (open circles) in North Dakota. Significant slopes are shown as *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

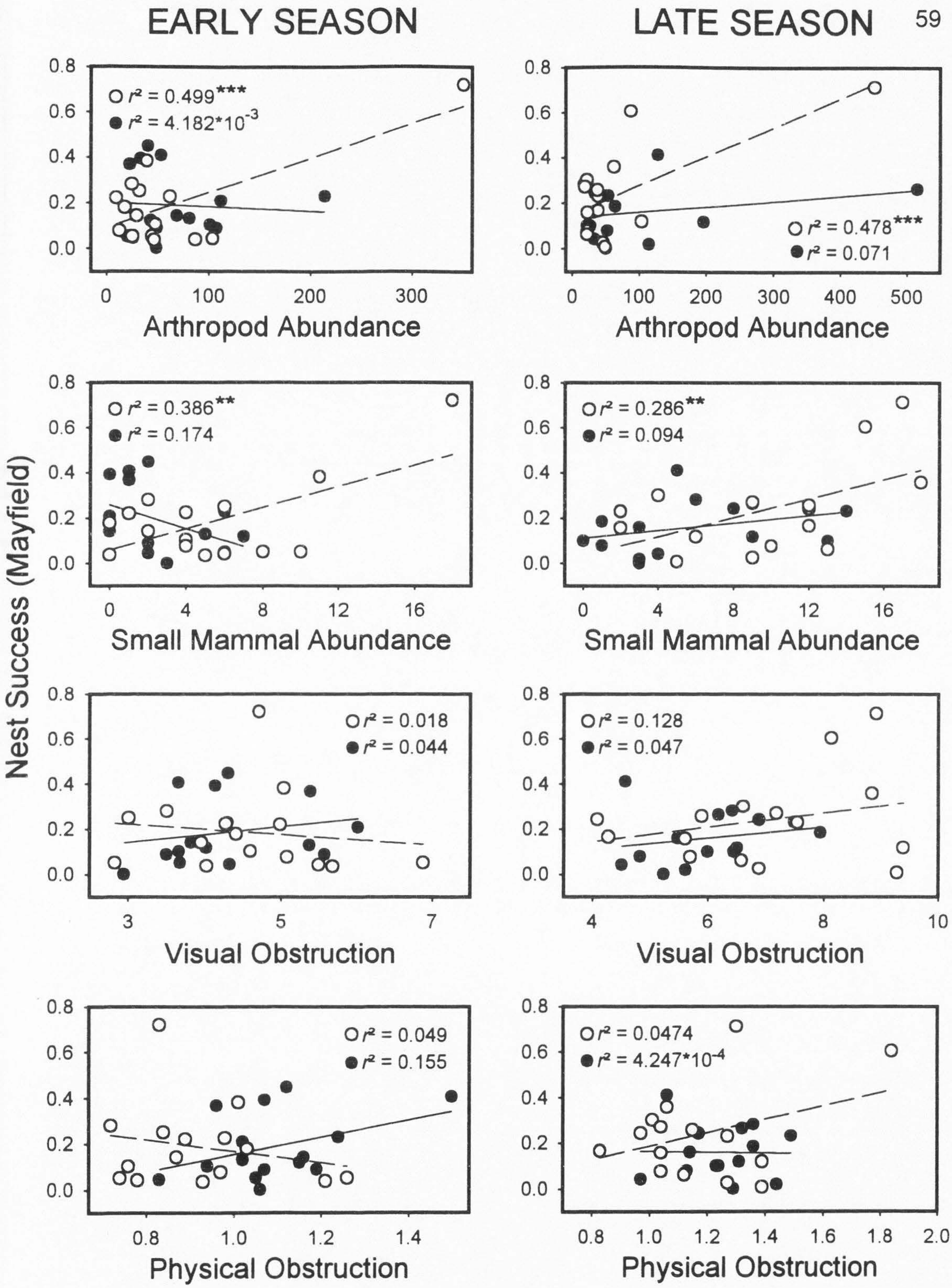

Fig. 2-1. (Continued).

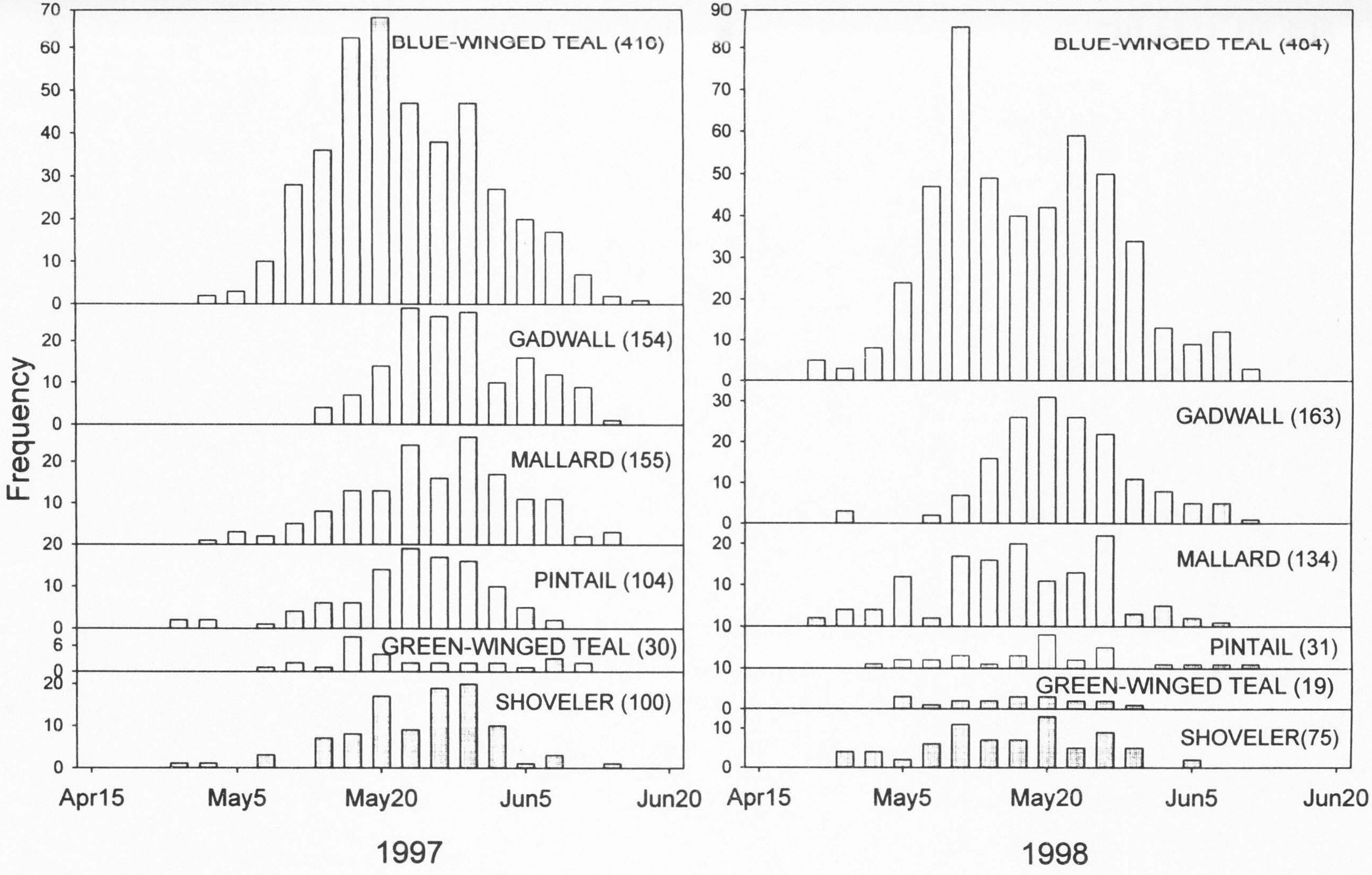

Fig. 2-2. Nest initiation dates of dabbling ducks in North Dakota (n).

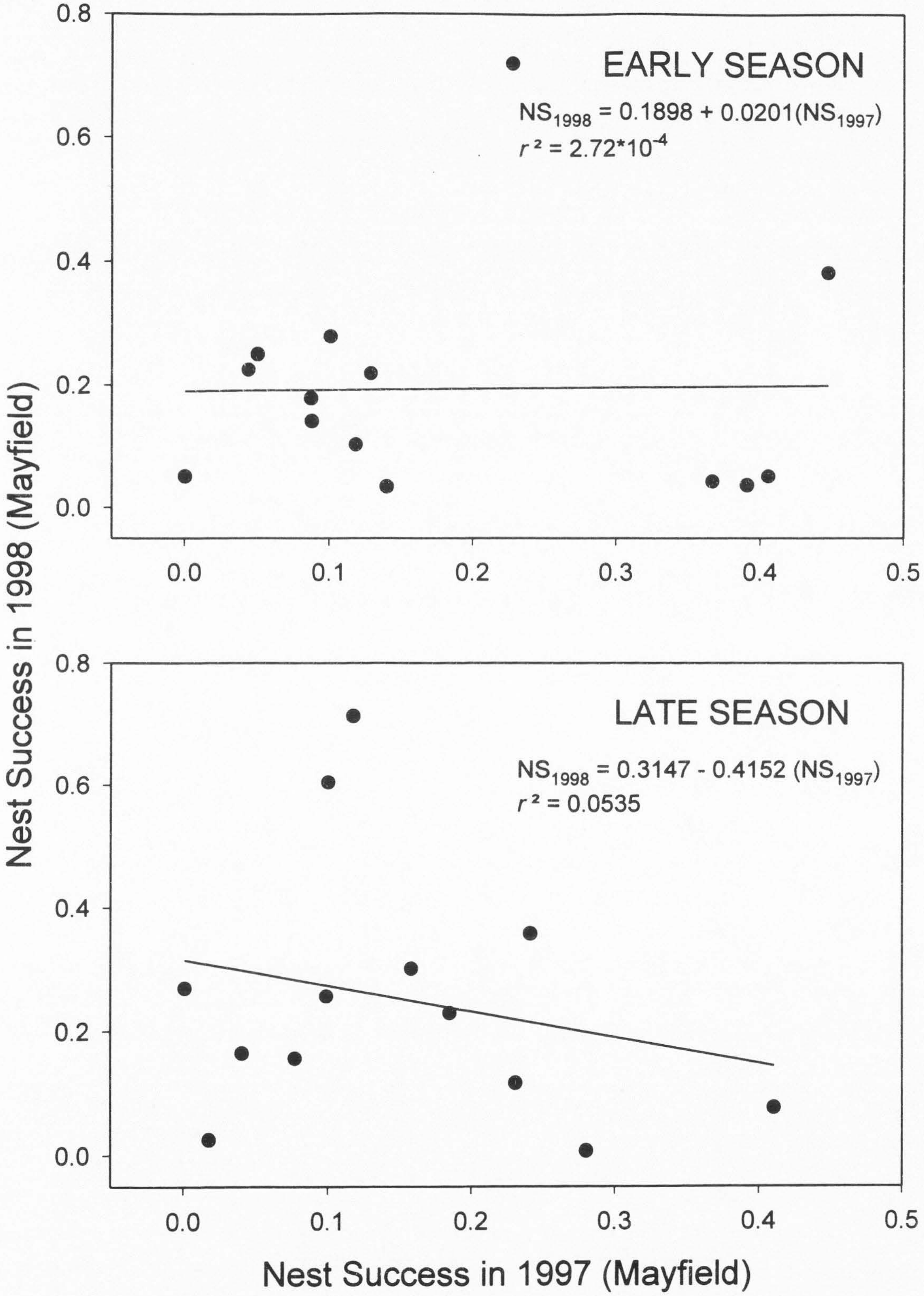

Fig. 2-3. Relationship of duck nest success estimated on the same sites in consecutive years during the same season.

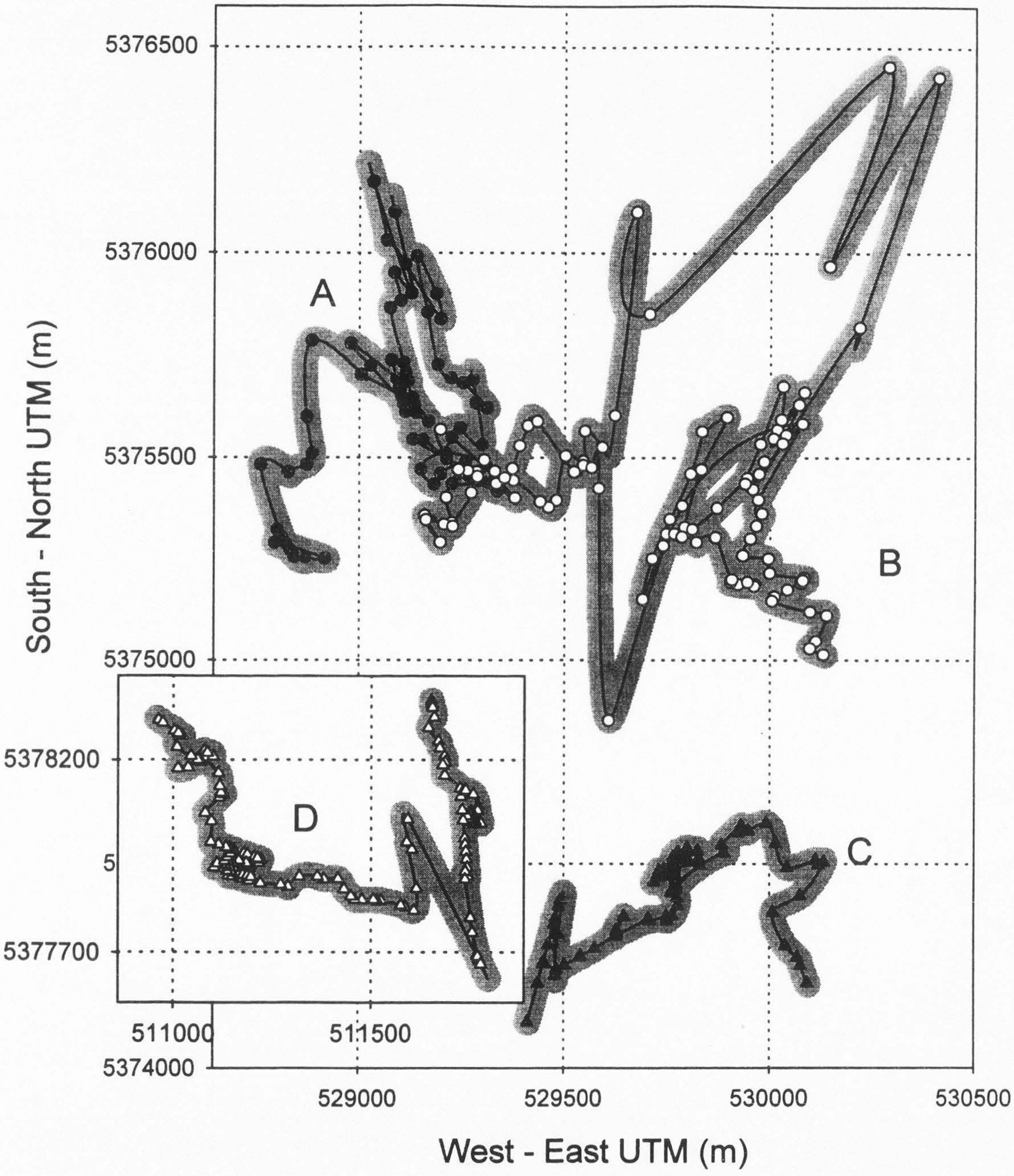

Fig. 2-4. Nightly movement pathways of 4 adult female striped skunks in North Dakota estimated through sequential radiolocations. Skunks A, B, and C were tracked on 25/26 August 1997 on Thorson every 4 min, whereas D was tracked on 27/28 August 1997 on Stinkeoway every 2 min. The buffer area in grey indicates the potential area scanned by each individual.

CHAPTER 3

EFFECTS OF ENVIRONMENTAL VARIABLES ON PRAIRIE DUCK NEST SUCCESS: A MULTIVARIATE APPROACH AT THE NEST LEVEL[1]

The fate of duck nests has been 1 of the most widely evaluated parameters in studies of waterfowl ecology (Johnson et al. 1992, Sargeant and Raveling 1992). Studies on upland breeding waterfowl in the Prairie Pothole Region (PPR) of North America almost invariably have found that predation on nests is very intense and, consequently, nest success is generally low (Beauchamp et al. 1996 and references therein). Beauchamp et al. (1996) have shown that nest success for 5 dabbling duck species has steadily declined during the last 4 decades, including gadwall (*Anas strepera*), blue-winged teal (*A. discors*), northern shoveler (*A. clypeata*), mallard (*A. platyrhynchos*), and northern pintail (*A. acuta*). In fact, the low nest success experienced by breeding ducks is an important factor limiting recruitment (Cowardin and Johnson 1979, Cowardin et al. 1985, Higgins et al. 1992) and makes populations nonsustainable (Greenwood et al. 1987, 1995, Klett et al. 1988). Not surprisingly, then, 3 of these duck species (blue-winged teal, mallard, and northern pintail) have also declined during that time span (Greenwood et al. 1995). The forecast is for continued population declines if current conditions persist (Cowardin et al. 1985, Johnson et al. 1985, Klett et al. 1988, Fleskes and Klaas 1991).

Several researchers have hypothesized that low nest success is due to increased predation levels resulting from the combination of an abundant and diverse

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[1] Coauthored by Jaime E. Jiménez, Michael R. Conover, Terry A. Messmer, and Raymond D. Dueser.

community of generalist predators living in the highly fragmented landscape where ducks breed. The PPR is considered a prime nesting ground for several waterfowl species. Since the mid-1800s, this ecosystem has been transformed from a grassland and parkland wilderness to an intensively cultivated farmland (Sargeant and Raveling 1992). What was once considered North America's duck factory, producing 50% of the ducks of the continent in an area only 10% of its size (Smith et al. 1964), is now considered the breadbasket of the world (Jones et al. 1985). Over 80% of the land is intensively cultivated (Higgins 1977, Sugden and Beyersbergen 1984, Reynolds et al. 1994). Ninety percent of the wetlands have been drained (Sargeant and Raveling 1992) and only about 1% of the native grassland remains (Samson and Knopf 1994). Concurrently, a diverse community of generalist egg predators has increased in numbers and expanded their ranges by benefitting from the human-related changes (Sargeant et al. 1993). In this landscape, upland-breeding ducks are forced to nest in a few scattered and isolated patches of idle fields near wetlands in a sea of agricultural lands (Sugden and Beyersbergen 1986, Trevor 1989, Clark and Nudds 1991, Higgins et al. 1992, Clark and Diamond 1993, Kantrud 1993, Larivière and Messier 1998). Because these habitat patches also attract carnivores that forage, rest, and den there, the spatially concentrated nests are easily found and preyed upon by predators (Sargeant and Arnold 1984). In fact, dabbling duck nest success decreases as the proportion of agricultural fields in the landscape increases (Greenwood et al. 1987, 1995). Andrén et al. (1985) have described the same pattern in Europe.

Although predation on ground-nesting birds has been much studied, our understanding of the mechanisms, the factors that affect nest vulnerability, and the relative importance of these factors is far from clear. Many variables related to predation risk have been identified (see reviews by Sargeant & Raveling 1992, Johnson et al.

1992), but no clear pattern of cause-and-effect has emerged and many of the results are conflicting results (Clark and Nudds 1991). It seems that the process of predation is more complex than originally thought and that many variables simultaneously affect the risk of predation for a nest.

We use a multivariate approach at the spatial scale of the nest and its neighborhood (Addicott et al. 1987) to examine the effects of several risk variables that have been observed elsewhere. We address the question of what makes certain nests of upland-breeding ducks, but not others, vulnerable to predation by determining which variables influence the risk of nest predation. We approach this question by building a mutiple logistic model of the likelihood of a nest being destroyed by a predator. The strength of this analysis is that it examines the influence of each variable after the effects of the other variables are statistically accounted for. We use data collected durng 2 years on 16 sites in the PPR of the United States. The risk variables used include components of time (nest initiation date and year), space (distance to edge and to water), cover type (proportion of forbs), vegetation concealment (visual obstruction), habitat heterogeneity (cover variability), predator abundance, presence/absence of specific predator species at the sites, and the duck species themselves. This modeling process should shed light on the variables that influence nest predation, enabling others to generate hypotheses that can be tested experimentally to improve our understanding of the mortality factors faced by nesting dabbling ducks.

BACKGROUND INFORMATION

A brief review is sufficient to show the complexity of predation on ground nests. Different variables influence the fate of nests of upland-nesting ducks and other ground-nesting game birds, and the observed effects often are inconsistent among studies within the same group of birds. There appears to be a lack of pattern. Sometimes interactions among variables were expected or were apparent (Wootton 1994), but were not evaluated.

Most studies of ground-nesting birds have found that nest success is positively correlated with vegetative cover (measured as plant concealment, density, height, and/or type) (Chesness et al. 1968, Duebbert 1969, Jarvis and Harris 1971, Schranck 1972, Hershey 1976, Keppie and Herzog 1978, Kirsch et al. 1978, Livezey 1981*a*, Hines and Mitchell 1983, Sugden and Beyersbergen 1986, 1987, Crabtree et al. 1989, Higgins et al. 1992, Mankin and Warner 1992, Riley et al. 1992, Gregg et al. 1994, DeLong et al. 1995, Pasitschniak-Arts and Messier 1995, Gilbert et al. 1996, Clawson and Rotella 1998). Other studies, however, have found no relationship (Kalmbach 1938, Hammond 1940, Glover 1956, Keith 1961, Urban 1970, Dwernychuk and Boag 1972, Byers 1974, Klimstra and Roseberry 1975, Bowman and Harris 1980, Erikstad et al. 1982, Fleskes and Klaas 1991, Kantrud 1993, Schieck and Hannon 1993, Clark and Wobeser 1997, Guyn and Clark 1997, Larivière and Messier 1998) or an inverse relationship between nest success and cover (Martz 1967, Higgins et al. 1992, Ritchie et al. 1994). Apparently, the effectiveness of cover in protecting nests depends on the type of predator (Clark and Nudds 1991). Nest concealment is generally more important against visually oriented predators who feed during the day, such as corvids and coyotes (*Canis latrans*), than against olfactory-oriented predators, such as most medium-sized mammals that feed under low light conditions (Dwernychuk and Boag 1972, Clark and Nudds 1991, Clark et al. 1995, Guyn and Clark 1997).

The structural heterogeneity of the habitat provided by the vegetation and landscape features can also influence nest fate. Bowman and Harris (1980) found experimentally that increased habitat structure, measured as spatial complexity, decreased the foraging efficiency of a predator searching for ground-nests. Field observations of Crabtree et al. (1989) and Mankin and Warner (1992) pointed in the same direction. However, Zimmerman (1984) found higher nest predation by snakes in more heterogeneous habitats. Dense and structurally heterogeneous cover may either deter predators from entering a patch or reduce hunting efficiency (Milonsky 1958, Schranck 1972, Hershey 1976, Hines and Mitchell 1983, Sugden and Beyersbergen 1987, Crabtree et al. 1989, Clawson and Rotella 1998). In addition, cover is thought to interfere with the dispersal of the scent of the incubating hen (Duebbert 1969, Duebbert and Lokemoen 1976). The association of increased nest success with vegetation concealment and spatial complexity led early researchers to propose the creation and maintenance of fields with dense nesting cover to improve recruitment of upland-nesting ducks (Duebbert 1969, Kirsch 1969, Duebbert and Lokemoen 1976, Higgins 1977, Kirsch et al. 1978, Cowardin and Johnson 1979, Weller 1979).

The location of a nest in relation to an edge or a wetland may also affect its vulnerability to predation. Well-known predators of nests or incubating hens, such as the raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and mink (*Mustela vison*), are attracted to and feed in meadows and wetland marshes (Keith 1961, Bailey 1968, Cowan 1973, Hershey 1976, Fritzell 1978, Greenwood 1982, Arnold and Fritzell 1987). Nest predators may concentrate on edges or ecotones or use them as travel lanes (Bider 1968, Schranck 1972, Hershey 1976, Fritzell 1978, Gates and Gysel 1978, Horkel et al. 1978, Ratti and Reese 1988). Avid duck nest predators such as skunks, red foxes (*Vulpes vulpes*), and American crows (*Corvus brachyrhynchos*) have been documented to use habitat edges for breeding or travel (Jacobson 1969, Moe 1974, Sargeant et al. 1987, 1993). However, the evidence of the relationship between the location of a nest relative to edges or wetlands and its fate is equivocal. Depredation may be higher on nests located closer to water (Keith 1961, Page and Cassel 1971, Livezey 1981*b*, Hill 1984, Losito et al. 1995) or further from water (Martz 1967). Often there is no apparent relationship (Labisky 1957, Duebbert and Lokemoen 1976, Pasitschniak-Arts and Messier 1995, Pasitschniak-Arts et al. 1998).

A positive correlation between nest success and distance to an edge -- the dogma of edge effect (Paton 1994) -- has been described for ground-nesting game birds only by Keppie and Herzog (1978), who observed higher nest success farther from trails through a forest. Most studies have found either no distance effect (Labisky 1957, Duebbert and Lokemoen 1976, Livezey 1980, Yahner and Wright 1985, Cowardin et al. 1985, Trevor 1989, Mankin and Warner 1992, Clawson and Rotella 1998, Pasitschniak-Arts et al. 1998) or a negative effect (Martz 1967, Boag et al. 1984, Small and Hunter 1988, Storch 1991, Yahner and Mahan 1996).

Predation risk and nest success can vary among years, likely in relation to climate. Wet years can result in lush cover that conceals nests against predators (Trevor 1989). Additionally, abundant plant food may trigger increases of alternative prey (Johnson et al. 1989), which reduces predation on nests. However, prey concentrations can attract predators and thus cancel any value of dense cover, rendering higher predation rates on nests (Byers 1974, Klimstra and Roseberry 1975, Ritchie et al. 1994). Abundant prey can also build up predator populations that increase predation during the next season, especially with low cover or low alternative prey (Komarek 1937, Marcström et al. 1988, Ebbinge 1989). During drought years, ducks concentrate their nests closer to wetlands (Stewart and Kantrud 1973, Greenwood et al. 1995) and so may increase their risk of predation (Higgins 1977, Krapu et al. 1983, Johnson et al. 1989, Trevor 1989). Alternatively, Klett and Johnson (1982) found higher nest success in a drought year, likely due to lower predation by fox. Changes in predator demography through reproduction or mortality caused by diseases, such as rabies in skunk (Greenwood et al. 1997), distemper in raccoon (Sanderson 1987), and sarcoptic mange in red foxes (Trainer and Halle 1969), can also produce marked variation in predation levels within short time spans, and likely affect nest fate.

Temporal variation in predation risk can occur during the year, as the nesting season progresses. Late in the breeding season nest success may increase (Kalmbach 1938, Chesness et al. 1968, Duebbert and Lokemoen 1976, Cowardin et al. 1985, Sugden and Beyersbergen 1986, Klett et al. 1988, Mankin and Warner 1992, Greenwood et al. 1995, Clawson and Rotella 1998), remain unchanged (Klett and Johnson 1982, Fleskes and Klaas 1991, DeLong et al. 1995, Pasitschniak-Arts and Messier 1996) or decline (Keith 1961, Klimstra and Roseberry 1975, Horkel et al. 1978, Pasitschniak-Arts and Messier 1995, Larivière and Messier 1998). Seasonal changes in predation risk have been attributed to changes in vegetative cover (Martz 1967, Mankin and Warner 1992, Greenwood et al. 1995, Clawson and Rotella 1998), availability of alternative prey (Sargeant 1972, Schranck 1972, Klett and Johnson 1982, Pasitschniak-Arts and Messier 1995), and predator abundance and behavior (Kalmbach 1938, Keith 1961, Horkel et al. 1978, Crabtree and Wolfe 1988, Johnson et al. 1989, Trevor 1989).

Individual predators can have important effects on nest survival, but this has been difficult to evaluate (Johnson et al. 1989, Higgins et al. 1992). Selective removal experiments of nest predators have not resulted in increased nest success, apparently due to compensation by other predators (Kalmbach 1938, Parker 1984, Greenwood 1986, Clark et al. 1995). Few studies on sites with different predator species or abundances have demonstrated the species-specific role of predators (Johnson et al. 1992). Sovada et al. (1995) and Greenwood et al. (1998) reported higher nest success in sites with coyotes than in sites with red foxes, everything else being equal. Fleskes and Klaas (1991) also found lower nest success in habitats with foxes, than without them. As a result, management to increase coyote populations at the expense of foxes has been proposed (Klett et al. 1988, Sovada et al. 1995). Kalmbach (1938) documented the importance of crows as nest predators in Canada and of skunks in North Dakota. Johnson et al. (1989) documented lower nest success on sites having higher activity of fox, skunk, and raccoon.

STUDY AREAS

We studied nest fates of upland-nesting ducks and measured environmental variables on 15 sites during the waterfowl breeding seasons of 1997 and 1998. Study sites were located in an area of about 100 km in diameter north and east of Devils Lake in North Dakota, in the Drift Plain biogeographical province of the PPR (Stewart and Kantrud 1973). The region exhibited a high density of breeding waterfowl and abundant potential terrestrial predators (R. Reynolds and B. Holien pers. comm., J. Jiménez pers. obs., Garrettson et al. 1996). The primary use of the region is for production of small grains and sunflowers (Cowardin et al. 1985). Precipitation averages 43.3 cm/year (at Edmore, N.D.), but is highly variable among years (Krapu et al. 1983). Most rain falls during spring and summer (Kantrud et al. 1989). Average minimum, mean, and maximum temperatures are -3.6, 2.9, and 9.5°C, respectively (at Edmore, N.D., Utah Climate Center).

To select the study sites, we considered all the sites in Ramsey, Cavalier, and part of Nelson Counties, that had dense nesting cover available during the breeding season of 1997. Dense nesting cover is considered the best available duck nesting habitat and the 1 that most closely resembles the original prairie vegetation (Klett et al. 1988, Higgins et al. 1992). Sites were not subjected to plowing, tilling, grazing, or predator control during at least the 2 years prior to this study. Areas enrolled in the Conservation Reserve Program (CRP) and U.S. Fish and Wildlife Service Waterfowl Production Areas (WPA) and Wildlife Development Areas (WDA) met these requirements. Other criteria for site selection included sites with abundant seasonal and temporary wetlands (Kantrud and Stewart 1977) that were relatively compact in shape. Sites with large wetlands were discarded. We stratified the remaining available sites by the amount of upland area in small, medium, and large-sized patches. From each group we randomly selected 5 sites. To gain independence among sites, selected sites were located at least 5 km apart. For comparative purposes we used all but 1 of the same sites in 1998. Because 1 site was mowed in autumn 1997, it was replaced by another with similar characteristics. These sites encompassed the whole range of variability available in the area. Site characteristics are shown in Table 3-1.

METHODS

Estimating Waterfowl Nest Fates

Nest fate was determined for all duck nests found. On large sites, 4 blocks of 16 ha each were searched for nests. On sites smaller than 64 ha of upland area, the entire site was surveyed. We employed the method described by Klett et al. (1986) for locating nests Nest locations were marked with a flagged bamboo stake 4 m from the nest, and the position was recorded with a hand-held GPS unit with differential correction. Hatching date was estimated as explained in Weller (1956) and Klett et al. (1986). Nest fate (FATE) was determined as reported by Klett et al. (1986), as abandoned, successful, or depredated (Cowardin et al. 1985). Abandoned nests or nests with unknown fate were not used in the analyses. In most cases, the predator species which destroyed a nest could not be determined, because the evidence left by predators is inconclusive (Sargeant et al. 1998).

Nest searching was conducted 3 times between early-May and late-July (Miller and Johnson 1978, Sargeant et al. 1984, Higgins et al. 1992, Greenwood et al. 1995). To determine the fate, nests with known locations were visited during and between searches, and 7-15 days after the last search.

Variables Measured at the Nest and Its Surroundings

When a nest was first found, the duck SPECIES (SP1-SP2, see Table 3-2 for variable abbreviations) was determined based on the flushed hen and the nest characteristics (Klett et al. 1986). The incubation stage of the nest was determined by estimating the development of the embryo in the eggs (Weller 1956). Using this information and the number of eggs in the clutch, the initiation date of each nest was estimated (Klett et al. 1986). For analytical purposes, that date (INITIAT) was transformed to the number of days since January 1 of the year. Laying initiation date has been found to be related to nest survival in dabbling ducks (Keith 1961, Cowardin et al. 1985). Year (YEAR) was coded 0 for 1997 and 1 for 1998. The amount of horizontal visual obstruction of the vegetation around the nest was measured (in dm) in the 4 cardinal directions using the method described by Robel et al. (1970). Visual obstruction (VISUAL), measured as the average maximum vegetation height around a nest, was an index of horizontal visibility. The coefficient of variation of visual obstruction (CVVISUAL) was a measure of heterogeneity of the cover in the immediate vicinity of the nest (Joern and Jackson 1983). The type of cover around the nest was assessed as the proportion of forbs (out of forbs+grasses, PFORBS) in a circle of 1 m diameter centered on the nest. This variable was measured only on nests found during 1998. The distance (in m) from the nest to the nearest wetland or water body (DISTWAT, Pasitschniak-Arts et al.

1998) and to the nearest edge (DISTEDG) was visually estimated. An edge was defined as any change or discontinuity in cover structure (Paton 1994), such as a grassland/cropland or a grassland/plowed field interface or the presence of a shelterbelt, a fence, or a road. Given that most edges in the PPR are human-made, they are abrupt and easily recognized. Edges and marshes around water bodies have been considered sources of predators. From tests of our ability to estimate distances, we realized that our estimates were less precise at farther distances, but still remained within 12-20% of the true values. We believe this did not affect the analysis substantially.

Because we could not obtain an index of predator risk at each nest, we estimated risk indices for each site. We obtained these estimates early and late in the season during each year to account for potential temporal changes. We estimated the abundance of predators and the presence/absence of the 5 most common mammalian carnivores (Sargeant et al. 1993) based on visitations to scent-station lines (Linhart and Knowlton 1975). A scent station was a 1-m-diameter circle of cleared ground with sifted soil on top and a scented fatty acid tablet in the center. A scent station line consisted of 6 stations 250 m apart. One line of scent stations was laid out in the center and another along the edge of each site. Lines were operated for 2 consecutive nights and checked during the morning (Roughton and Sweeny 1982). The percent of stations visited by 1 or more predators provided an estimate of relative predator abundance (PREDABU). Through the species-specific record of tracks found on the scent stations (Sargeant et al. 1993, Sovada et al. 1995), we could determine which species of predator(s) was(were) present at each site. We supplemented this information with tracks observed around wetlands, on roads, and with direct observations of feces, dens, or animals within 1.6 km of the site (Johnson et al. 1989). In this way, we determined the presence/absence of red fox (FOX), striped skunk (SKUNK), raccoon (RACCOON), badger (*Taxidea taxus*, BADGER), and mink (MINK) at each site during each season and year. Each of these variables was coded 1 for presence and 0 for absence of the predator species. Inclusion of these carnivore predators into the model is justified given that they are the most important nest predators in the region (Sargeant et al. 1993, 1998). The predator indices are conservative because they indicate positive predator presence only during relatively short time periods and over limited portions of each site.

In summary, at each nest in this study we examined 3 variables related to the cover component, concealment (VISUAL), heterogeneity (CVVISUAL), and type of cover (PFORBS); 2 spatial components related to potential sources of predators (DISTEDG and DISTWAT); 2 temporally-related variables (INITIAT and YEAR); and 1 variable representing the duck species themselves (SPECIES). In addition, at the site level, we studied 6 variables representing predation risk: relative abundance (PREDABU) and identity of predator species present (FOX, SKUNK, RACCOON, BADGER, and MINK). A list of the response variables, their acronyms, and measurements units are shown in Table 3-2.

Model Building and Model Selection

We examined risk factors that may determine the probability of nest predation by assessing associations of the binary response variable FATE to the explanatory variables INITIAT, DISTWAT, DISTEDG, VISUAL, CVVISUAL, PFORBS, PREDABU, SPECIES, FOX, SKUNK, BADGER, and MINK using multiple logistic regression (Collett 1991, Stokes et al. 1995). One advantage of this multivariate technique over multiple bivariate models is that it statistically adjusts the estimated effects of each variable for differences of, and associations among, the other explanatory variables. We chose the "best" model as described by Hosmer and Lemeshow (1989) and Collett (1991). The model selection process is intended to find a model that is both parsimonious and biologically reasonable (Hosmer and Lemeshow 1989).

Variables were selected for the model based on likelihood ratio tests comparing the fit of nested models (Hosmer and Lemeshow 1989, Collett 1991, Hamilton 1992). The significance of a variable was based on the ΔG^2 statistic. This statistic represents the difference in the log likelihood ratios between the models, which is distributed χ^2 with Δdf degrees of freedom. In the final model, the sign of a parameter estimate indicates the trend of the association of a variable and the probability of a predation event; the Wald test assesses significance of the relationship between a variable and FATE, keeping all other variables constant; and the standardized parameter estimate indicates the absolute importance of a variable in the model. The odds ratio of a variable (computed as: $e^{\text{parameter estimate}}$) reflects the relative risk of a nest to a certain event and describes the strength of an effect (Afifi and Clark 1990, Hamilton 1992). As a measure of association between a variable and FATE, the odds ratio represents the likelihood of a nest being depredated when the variable takes a value of 1 rather than a value of 0, for binary variables, or for a unit increment, for continuous variables (Hosmer and Lemeshow 1989, Stokes et al. 1995). Odds ratios as reported in outputs are not interpretable when the variable is involved in an interaction, and they were therefore computed separately (SAS Institute 1995) according to Hosmer and Lemeshow (1989:14). The -2 log likelihood statistic indicates the model's overall significance, and the Pearson χ^2 and the Hosmer and Lemeshow test assess the adequacy of the model fit (Collett 1991, Hamilton 1992, Stokes et al. 1995). The predictive ability of the model was evaluated by generating an unbiased classification table by jackknifing the data and examining the area under the receiver operating characteristic curve (ROC; Affifi and Clark 1990, SAS Institute 1995). The classification table and the ROC are based on the relative cost of misclassification. Curve area values are represented by the *c* statistic, which ranges from 0 to 1 (SAS Institute 1995, 1997). Values closer to 1 imply higher predictive ability.

Continuous variables were tested to fit a linear logit model using the Hosmer and Lemeshow test (Hosmer and Lemeshow 1989, SAS Institute 1997). Variables that did not fit that distribution were transformed for a better fit. Binary variables were coded 1 or 0 representing an event (i.e., predation) and a non-event (i.e., hatch) for FATE, presence or absence for FOX, SKUNK, RACCOON, BADGER, and MINK, and 1998 and 1997 for YEAR, respectively. For the nominal variable SPECIES, we coded 5 dummy variables (representing 6 duck species, blue-winged teal being the reference group; Collett 1991). Accordingly, the association of FATE with SPECIES is based on a likelihood ratio test comparing the fits of a model with SPECIES (i.e., the set of 5 design variables) to that model without SPECIES (Hosmer and Lemeshow 1989, Collett 1991).

Before model building, we examined the explanatory variables in detail. For continuous variables, we assessed the linearity assumption and compared the means between successful and failed nests using *t*-tests. For PFORBS, whose distribution departed from normality, we used the Wilcoxon 2-sample test (Hollander and Wolfe 1973). Categorical explanatory variables were examined for cells with 0 values and differences in the proportions of hatched and depredated nests were tested with χ^2 tests (Stokes et al. 1995).

The next steps were sequentially followed to obtain the final logistic regression model. We tested the significance of PFORBS in the model using the 1998 data set only. Given that this variable was not significant, we fitted 1 model for each year with all explanatory variables (except PFORBS). We compared parameter estimates between years, looking for changes in sign or magnitude. Then, we pooled the 2 data sets and fit a model including YEAR as a variable and the interactions with YEAR of the variables that differed sign in the previous models. In an iterative process, examining the least significant variable at a time, we retained all significant main effects and interactions as well as the nonsignificant main effects involved in interactions (Collett 1991). This gave rise to the "best" model. We assessed the significance of the duck species by testing pairs of duck species with multiple *t*-tests obtained by sequentially changing the reference group and rerunning the logistic model. These tests provide unadjusted *P*-values.

We did the computations with PROC LOGISTIC in SAS Release 6.12 (SAS Institute 1997), using the DESCENDING option to model predation events (Stokes et al. 1995, SAS 1997). We also used PROC GLM, NPAR1WAY, and TTEST (SAS Institute 1988). Our critical significant level was set at $\alpha = 0.05$.

RESULTS

Eight hundred forty-three nests in 1997 and 826 nests in 1998 were characterized as hatched or destroyed by predators. Overall, 59.6% of these nests were depredated. Another 196 nests were either abandoned, or run over, or their fate could not be determined; these nests were not used in the analysis. Nests of 6 duck species were found: blue-winged teal (48.7%), gadwall (17.2%), mallard (15.1%), northern shoveler (9.4%), northern pintail (7.1%), and green-winged teal (*A. crecca*, 2.5%).

Single Variable Analysis

Bivariate analyses of continuous variables indicated that nests were more likely to be depredated if started later in the season, were closer to water, were on sites with higher abundance of predators, and were located in spots with more grass than forbs (Table 3-3, Fig. 3-1). DISTEDG, VISUAL, and CVVISUAL were similar for depredated and hatched nests (Table 3-3). Separate analysis of categorical variables indicated that the proportion of depredated nests varied by duck species, decreasing in order: mallard > blue-winged teal > gadwall > shoveler > pintail > green-winged teal (Table 3-4). However, only mallard differed statistically from green-winged teal (χ^2 = 3.918, df = 1, P = 0.048). Nests on sites with foxes or with badgers were depredated at higher rates than those on sites without these predators. In contrast, nests on sites with skunk, raccoon, or mink were no more likely to be destroyed than those without them. A higher proportion of nests was depredated during 1997 than 1998 (Table 3-4).

Model Building

The only variable that failed to meet the linearity assumption of logistic regression was INITIAT. Transformation did not improve the fit. Because the departure was due to only a few observations and was therefore considered unimportant, INITIAT was included in the model selection process. PFORBS, when included with all other variables as main effects, did not contribute to the model (ΔG^2 = 0.31, df = 1, P = 0.578) and was discarded. We fit a separate model for each year with all remaining main effects. Slope estimates for DISTEDG, FOX, RACCOON, MINK, and 2 duck species changed signs between years, and so were candidates for interaction with YEAR (Table 3-5). We pooled data for both years and fit 1 model with all the main effects, including YEAR, and the interactions with YEAR. The interactions DISTEDG*YEAR and SPECIES*YEAR, and the main effects DISTEDG, CVVISUAL, SKUNK, and BADGER did not contribute to the model and were dropped.

Final Model

All the variables including interaction terms, retained in the final model, were statistically significant (Table 3-6). The data fit the model adequately, as reflected by the

Hosmer and Lemeshow goodness-of-fit test (χ^2 = 5.12, df = 8, P = 0.745) and Pearson chi-square (χ^2 = 1653.7, df = 1631, P = 0.432). Visual examination of the residual plots did not indicate extreme departures in the observations compared to their predicted values.

None of the retained continuous variables (INITIAT, DISTWAT, VISUAL, PREDABU) exhibited an interaction with YEAR. Hence, the observed relationships were consistent in both years of the study. The probability of predation increased as the breeding season progressed and with predator abundance; it decreased with increasing distance to water and with taller vegetation (Table 3-6). The odds of predation increased 1.18 times for every increase of 10 days and increases 1.18 times for every 10% increase in predator abundance. It decreases 1.36 times for every 100 m away from a wetland, and 1.13 times for every 10 cm increase of vegetation height (Table 3-7). Relationships are depicted graphically in Figs. 3-2, 3-3, and 3-4. Predicted probability of predation as a function of the variable throughout its observed range is computed keeping other continuous variables at their observed means and binary variables at 0 (i.e., no fox; no badger; no mink; blue-winged teal; 1997). Under these conditions, the probability of predation on a nest was almost always over 0.6.

Among duck species, the following trend of depredation risk was noted: mallard > gadwall > blue-winged teal > shoveler > pintail > green-winged teal (Tables 3-6 and 3-7, Fig 3-3). However, only mallard nests were preyed upon at a significantly higher rate than any of the other species (Wald χ^2's > 4.5, df = 1, P's < 0.035).

Predation risk was high in 1997 regardless of whether fox, mink, or raccoon were present or absent. Risk was low in 1998 in absence of predators, and increased when predators were present (Fig. 3-4). The odds of a nest being destroyed when foxes were present decreased 0.6 times in 1997 and increased 6.3 times in 1998 (Table 3-7).

Similar patterns were observed with raccoon and mink present (Table 3-7 and Fig. 3-4).

The predictive accuracy of the model is not high (Table 3-8). Using the unbiased classifcation procedure, the model correctly classified 66.5% of the nests. Misclassifications included 8.8% false positives (i.e., predicted predation when in fact was a hatched nest) and 24.6% false negatives (i.e., predicted a hatched nest when in fact was a depredated nest). Similarly, the ROC curve was not very steep, resulting in a *c* statistic of 0.706.

DISCUSSION

Single Variable Analysis

Our results confirmed previous findings of high inherent risk of predation on nests in the PPR (Beauchamp et al. 1996), and in our region, was dominated by a diverse and abundant carnivore community (Sargeant et al. 1993). Our single-variable analyses disagree in part with the results of other studies conducted in the region. We observed that the likelihood of nest predation increased as the season progressed, concurring with reports of Keith (1961) using natural duck nests and of Pasitschniak-Arts and Messier (1995) and Larivière and Messier (1998) using artificial nests. We also observed that neither the abundance nor the number of predator species changed through the breeding season (Jiménez et al. unpublished data). Hence, increased nest mortality through the season appeared unrelated to changes in predator abundance, unlike the report by Johnson et al. (1989). The observed trend was also contrary to the reports that predation decreases through the season as vegetative growth provides better nest concealment (Martz 1967, Greenwood et al. 1995). Indeed, visual and physical obstruction provided by the vegetation increased through the year on our sites (Jiménez et al. unpublished data). A more likely explanation is that predators were attracted to the study sites by the increase in the number of alternative prey, as proposed by Keith (1961) and Trevor (1989). In fact, our observations that the numbers of both small mammals and arthropods increased late in the season (Jiménez et al. unpublished data) support that hypothesis.

These results contradict the idea that alternative prey buffers predation on nests (Sargeant 1972, Crabtree and Wolfe 1988, Johnson et al. 1989, Trevor 1989, Greenwood et al. 1995). Predation on nest appeared incidental: predators were attracted by the abundant prey (nest densities did not increase through the season) and encountered duck nests by chance and ate the eggs (Sargeant 1972, Hershey 1976, Vickery et al. 1992).

Nests closer to wetlands suffered higher predation rates than those farther away. Similar results were found by Keith (1961), Page and Casell (1971), Hill (1984), Livezey (1991b), and Losito et al. (1995). This observation is consistent with the fact that predator species that forage in and near wetlands --including mink (Arnold and Fritzell 1987) and raccoons (Fritzell 1978, Greenwood 1982)-- were abundant after a series of wet years (Greenwood and Sovada 1996). In addition, radiotelemetry data of skunks (Jiménez, unpublished data and R. Clark pers. comm.) indicate that skunks concentrate their feeding activities in wetland meadows. Skunks were the most abundant carnivore on most sites. Conversely, red foxes, which typically forage in the upland (Martz 1967, Sargeant et al. 1993), were generally scarce, likely as a result of a mange outbreak as reported by local trappers (D. Jewison and B. Hollien, pers. comm.). The evidence indicates that predators concentrate their activities closer to wetlands and consequently, nests located closer to water are more vulnerable to predation.

In contrast, nest fate was unrelated to distance to an edge, as found in several waterfowl studies (Labisky 1957, Duebbert and Lokemoen 1976, Livezey 1980, Cowardin et al. 1995, Trevor 1989, Pasitschniak-Arts et al. 1998). Predators appeared not to concentrate their foraging activities along edges, where neither small mammal abundance nor the composition of the small mammal community differed from those in the upland vegetation (Jiménez et al. unpublished data). Vegetative structure and composition did not appear to be different closer to edges than in the patch interior. Thus, as pointed out by Andrén (1995) and Pasitschniak-Arts et al. (1998), mammals appeared to have no reason to increase their foraging close to edges. Additionally, we seldom observed carnivores using dirt roads, trails, or grassland/cropland interfaces as travel lanes. Instead, carnivores were observed to move mainly through dense vegetation. Our findings confirm the suspicion of Andrén (1995), Clawson and Rotella (1998), and Pasitschniak-Arts et al. (1998) that nest predation in open grasslands patches does not conform to the dogma of edge effects (Paton 1994).

Dabbling duck studies have documented high nest success and preferential nest location in forb patches (Duebbert 1969, Hines and Mitchell 1983, Higgins et al. 1992). However, no previous study has explicitly examined the effect of cover composition at the nest site. We found that nests surrounded by higher proportions of forbs (mainly alfalfa *Medicago sativa* and sweet clover *Melilotus* sp.) had higher survival than those with higher proportions of grasses. This indicates that forbs provide better protection from predators than grasses. The growth form of alfalfa, in dense clumps, may provide more structural heterogeneity around a nest, and thus decrease the foraging efficiency of carnivores (Schranck 1972, Hershey 1976, Bowman and Harris 1980). Differences in nest concealment or structural heterogeneity beyond a meter around the nest could not explain differential nest fate, given that visual obstruction or its variability measured 4 m from the nest did not influence nest fate. Additionally, because forb cover is not preferred by voles (Lysne 1991), the staple prey of most nest predators (Hershey 1976, Greenwood 1981, Sargeant et al. 1986, Larivière and Messier 1997), forb cover may not attract foraging predators.

Predation rates varied among duck species. Given that nest concealment did not determine nest fate, other species-specific characteristics of nest site selection, such as species differences in their propensity to nest near to a wetland, as documented by Pasitschniak-Arts et al. (1998), might explain the results. However, mallard nests, which suffered the highest predation rates (see also Klett et al. 1988), are located further from the water than the other duck species' (Sowls 1955, Labisky 1957, Page and Cassel 1972, Duebbert and Lokemoen 1976). Perhaps the larger body size and nest size of mallards or the behavior of the incubating hen mallards may play a role.

Even though predator abundance is often mentioned as a causal explanation of nest success (Gates and Gysel 1978, Klett et al. 1988, Sargeant and Raveling 1992, Sargeant et al. 1993, Sovada et al. 1995), few studies have quantified this relationship (Keith 1961, Urban 1970) because of the difficulty of estimating predator numbers (Johnson et al. 1992). Most of the evidence of predator abundance effects on nest success comes from predator removal studies, but these have yielded inconsistent results (Sowls 1955, Schranck 1972, Andrén et al. 1985, Greenwood 1986, Andrén 1995, Sargeant et al. 1995, Garretson et al. 1996). Predator abundance may not reflect predation pressure on nests (Bailey 1968). We found that nests hatched at a higher rate in patches where combined predator abundance was low than in patches where it was high. Because our predator abundance index might represent predator activity rather than predator abundance, our observations are consistent with Johnson and others' (1989) findings, that nest fate is related to predator activity. Hence, predator activity indices may better represent predation pressure on nests. We agree with Sargeant and others' (1993) encouragement to examine this relationship more closely.

The predator guild included several generalist predators and the compositions of the predator community varied among sites. We did not find Franklin ground squirrels (*Citellus franklini*) and coyotes (*Canis latrans*) in any of our 16 study sites, although Sargeant et al. (1993) documented them in the region. We did find that nest fate was related to the presence or absence of 2 of the predator species (i.e., red fox and badger) on a given site. However, it was somewhat surprising that nest fate was unrelated to the presence/absence of the skunk, which is considered 1 of the primary nest predators (Sargeant et al. 1993, 1998). This was probably because skunk was present on almost all sites, rendering the analysis insensitive.

Multivariate Approach

Not all results of the logistic regression are consistent with the bivariate analysis. The continuous variables retained in the model did not interact with year, which indicates that the patterns were consistent across the 2 years. As discussed above, the probability of predation on a nest increased through the breeding season, with increasing predator abundance, and with proximity to water. It was unrelated to the distance to an edge and to the heterogeneity of vegetation structure around a nest. However, the type of cover at the nest site, evaluated as the relative abundance of forbs, had no effect on nest vulnerability in the multivariate analysis. Likely, part of the variation of that variable was accounted for by another variable in the model. Conversely, visual obstruction was significant and positively correlated with nest survival in the multivariate model.

Thus, according to these results, a hen would benefit by nesting late in the season, in taller vegetation, away from a wetland, and in patches with low predator activity. The first 3 variables could theoretically be evaluated and controlled by a hen. In fact, these species-specific attributes describe nesting gadwalls (Jiménez unpublished data, Beauchamp et al. 1996). Gadwalls, which are not considered to be declining, had low nest predation levels in our study (see also Duebbert and Lokemoen 1976, Klett et al. 1988). Assessing the activity level of predators on the landscape by a hen appears to be a more difficult task. It is unknown whether a hen can evaluate and avoid areas rich in predators. The fact that nest locations are independent of distance to predator dens argues against that hypothesis (Trevor 1989). Although time of nest initiation could be controlled, nesting late in the season to reduce predation would compromise the benefits of nesting early, such as larger clutch size, favorable climatic conditions, and having the option of renesting if the nest is destroyed (Duebbert and Lokemoen 1976).

Of the categorical variables kept in the model, duck species was significant and unrelated to year. As in the bivariate analysis, mallard was the species with the highest nest predation probability. Under average conditions during 1997, less than 20% of the mallard nests hatched. Mallards also are a species that has declined throughout most of its range (Johnson and Shaffer 1987). Hatch probabilities for the other species, with figures < 30%, were not very encouraging.

The presence or absence of 3 of the 5 predators was associated with nest vulnerability and showed consistent and opposite trends according to the year. These relationships and the species involved differed substantially from the bivariate analyses and these results are difficult to interpret. The presence of fox, raccoon, or mink at a site increased the probability of predation on a nest during 1998, when predation level was low. During 1997, the presence of each predator at a site improved the survivorship of a nest. One way that this might have occurred is if these predators depress the effects of another predator species. However, unlike Johnson and others' (1989) findings, we did not detect any association among pairs of carnivores at the sites (all 15 pairwise combinations, unadjusted for experimentwise error, had all $\chi^2 < 2.2$ and $P > 0.14$), and therefore this hypothesis is unlikely. We are quite confident of our ability to assess the presence of each predator, but we are unable to prove that a predator species was absent.

The logistic model indicated that year was an important variable to consider when examining predation risk, especially in relation to predator species. This appeared to be a reflection of the high variability of predator species composition in the study sites even in consecutive years. Predator community composition was found to be highly dynamic between consecutive seasons and also among sites, in accordance with a previous study (Johnson et al. 1989). Unlike responses of vegetation to environmental factors, which appeared to be more stable and predictable over time (we did not test for interactions with season, but see Martz 1967:240), predator species can probably respond and adjust quickly to varying resource levels in the fragmented landscape. They can also show delayed numerical responses across years (Ebbinge 1989).

MANAGEMENT IMPLICATIONS

The multivariate analysis confirmed most of the bivariate patterns and helped us to understand the multiple effects and interactions of several variables. However, its predictive ability was found to be low, and therefore would have limited use as a tool to guide management efforts to improve nest success of dabbling ducks. The analysis pointed out the importance of the inter-year effect. Even working on the same sites, generalization could not be made from 1 year to another. Hence, conclusions derived from single-year studies may be misleading (Martin et al. 1996).

Based on our results, we would agree with earlier works in recommending the establishment and maintenance of dense nesting cover in the remaining patches managed for waterfowl production in the PPR. However, even in the best cover on our study sites, the likelihood of predation on nests by carnivorous mammals was high. Improving cover will not solve the problem of high predation rates on nests, but will help. In addition, we would suggest increasing the size of the managed patches in order to provide more breeding habitat. The combination of better habitat quality (denser cover) and quantity (larger patch size) would attract more breeding hens. These changes could also result in changes of the predator composition, favoring upland predators, such as favoring coyotes at the expense of foxes, as hypothesized by Sovada et al. (1995). Keeping wetlands spaced out, as suggested by our data that predation probability on nests decreases with distance to wetland, would compromise habitat quality for the broods. The only way to find out whether these suggestions improve upland-nesting duck recruitment is by conducting much awaited well-designed manipulative experiments (Clark and Nudds 1991, Clark and Diamond 1993, Johnson et al. 1994, Wootton 1994).

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Table 3-1. Characteristics of the study sites used in North Dakota. Sites are ordered in a decreasing order of upland area.

Name	County	Managemt. status[1]	Year created	Total area (ha)	Upland area (ha)	Shape[2]	Wetlands[3]	Trees[4]
Nelson South	Nelson	CRP	1987	388.7	267.2	2	2	1
Edwards	Cavalier	WPA	1972	251.0	206.0	1	3	1
Mellin	Ramsey	WPA	1972	226.7	177.3	1	3	1
Stinkeoway	Cavalier	WPA	1972	259.1	161.9	1	3	1
Nelson North	Nelson	CRP	1987	259.1	129.6	1	2	1
Thorson	Cavalier	WPA	1972	129.6	96.9	2	3	1
Gette	Ramsey	WPA	1972	107.3	65.4	2	2	1
Hall	Ramsey	WPA	1972	64.8	45.0	1	3	1
Pung	Cavalier	WPA	1962	57.7	43.7	1	2	1
Storlie	Cavalier	WDA	1987	64.8	40.3	1	3	0
Eidness	Ramsey	WPA	1977	64.8	35.3	2	2	1
Howes	Ramsey	WPA	1973	40.5	28.3	1	2	1
Wengler West	Cavalier	WPA	1972	32.4	26.3	2	2	0
Pollestad	Cavalier	WPA	1967	16.1	10.2	1	2	1
Seitz	Ramsey	WPA	1967	25.9	10.0	3	1	2
Babcock	Ramsey	WPA	1967	13.2	6.5	3	3	1

[1] CRP = private conservation reserve program land; WDA = U. S. Fish & Wildlife Service wildlife development area; WPA = USFWS waterfowl production area.

[2] 1 = compact; 2 = elongated; 3 = most edge.

[3] 1 = one large; 2 = large + small; 3 = many small.

[4] 0 = absent; 1 = present; 2 = nearby.

Table 3-2. Response variables used in the modeling process.

Variable	Measured as	Acronym
Estimated day laying start referred to January 1 of the year	days	INITIAT
Distance to the nearest edge	m	DISTEDG
Distance to the nearest wetland or water body	m	DISTWAT
Horizontal visual obstruction of the vegetation (mean value measured from 4 directions)	dm	VISUAL
Variability of horizontal cover (CV of 4 measures)	CV	CVVISUAL
Proportion of forbs (out of forb/grass) 0.5m around the nest	proportion	PFORBS
Predator abundance (visitation to scent stations)	%	PREDABU
Duck species (dummy variable)	N/A	SP1 to SP5
Presence or absence of a fox	+/-*	FOX
Presence or absence of a skunk	+/-	SKUNK
Presence or absence of a raccoon	+/-	RACCOON
Presence or absence of a badger	+/-	BADGER
Presence or absence of a mink	+/-	MINK
Year	year	YEAR

* +/- = presence/absence.

Table 3-3. Continuous variables for hatched and depredated nests of dabbling ducks found in North Dakota. Sample sizes, means, and standard errors are shown by nest fate. Results of *t*-tests are reported. Abbreviations as in Table 3-2.

	Hatched			Depredated					
Variable	*n*	Mean	SE	*n*	Mean	SE	*t*	df	*P*
INITIAT	675	150.11	0.57	994	153.27	0.48	-4.217	1667.0	<0.001
DISTEDG	668	194.85	5.35	989	201.80	4.40	-0.946	1653.0	0.344
DISTWAT	667	71.82	2.28	988	64.92	1.88	2.338	1653.0	0.020
VISUAL	672	4.76	0.06	987	4.67	0.05	1.262	1657.0	0.207
CVVISUAL	672	11.04	0.32	987	11.39	0.27	-0.840	1657.0	0.401
PREDABU	675	19.17	0.56	994	26.56	0.46	-10.195	1433.3	<0.001
PFORBS	380	0.36	0.02	441	0.25	0.01	5.142*	-	<0.001

* Z score of Wilcoxon 2-sample test with normal approximation

Table 3-4. Effects of categorical variables on nest fate. Shown are tests for homogeneity of proportion of depredated nests for each variable.

Variables	χ^2	df	P	Depredated	Total nests
DUCK SPECIES	8.61	5	0.126		
Green-winged teal				0.500	42
Mallard				0.659	252
Gadwall				0.582	287
Pintail				0.525	118
Shoveler				0.580	157
Blue-winged teal				0.599	813
FOX	73.43	1	0.001		
Present				0.660	1202
Absent				0.430	467
SKUNK	0.001	1	0.970		
Present				0.596	1573
Absent				0.594	96
RACCOON	0.38	1	0.536		
Present				0.603	814
Absent				0.588	855

Table 3-4 (Continued).

Variables	χ^2	df	P	Depredated	Total nests
BADGER	6.34	1	0.012		
Present				0.630	727
Absent				0.569	942
MINK	1.63	1	0.202		
Present				0.615	649
Absent				0.583	1020
YEAR	23.83	1	0.001		
1997				0.654	843
1998				0.536	826
TOTAL NESTS				0.596	1669

Table 3-5. Logistic regression models for variables measured during 1997 (-2 log likelihood χ^2 = 1021.6, df = 820, P < 0.001) and 1998 (χ^2 = 956.7, df = 798, P < 0.001). Except duck species, all parameter estimates had 1 df. *P*-values of variables with α < 0.05 are shown in boldface, and slopes that changed sign between years are underlined. Abbreviations as in Table 3-2.

	1997				1998			
Variable	Slope	SE	Wald χ^2	*P*-value	Slope	SE	Wald χ^2	*P*-value
INTERCEPT	-2.687	1.218	4.870	0.027	-1.994	0.949	4.416	0.036
INITIAT	0.030	0.007	17.695	**<0.001**	0.008	0.006	1.711	0.191
DISTEDG	-0.001	0.001	0.666	0.415	0.001	0.001	1.620	0.203
DISTWAT	-0.003	0.001	4.604	**0.032**	-0.003	0.001	4.387	**0.036**
VISUAL	-0.125	0.078	2.556	0.110	-0.150	0.063	5.591	**0.018**
CVVISUAL	0.015	0.010	2.230	0.135	0.006	0.010	0.370	0.543
PREDABU	0.016	0.006	6.349	**0.012**	0.023	0.007	10.003	**0.002**
FOX	-0.525	0.300	3.071	0.080	1.683	0.241	48.881	**<0.001**
SKUNK	-0.472	0.499	0.898	0.343	-0.281	0.355	0.626	0.429
RACCOON	-0.286	0.219	1.712	0.191	1.193	0.225	28.058	**<0.001**
BADGER	0.231	0.202	1.312	0.252	0.058	0.171	0.115	0.735
MINK	-0.161	0.206	0.605	0.437	0.359	0.230	2.423	0.120
DUCK SPECIES	ΔG^2 = 16.05		Δdf = 5	*P* **<0.001**	ΔG^2 = 41.06		Δdf = 5	*P* **<0.001**
GREEN-W.TEAL	-0.531	0.425	1.558	0.212	-0.256	0.610	0.177	0.674
MALLARD	0.590	0.262	5.072	**0.024**	0.560	0.253	4.891	**0.027**
GADWALL	0.010	0.242	0.002	0.969	0.340	0.240	2.007	0.157
PINTAIL	-0.288	0.253	1.293	0.256	0.250	0.450	0.308	0.579
SHOVELER	-0.236	0.255	0.859	0.354	0.206	0.292	0.494	0.482

Table 3-6. Final logistic regression model with statistics (-2 log likelihood χ^2 = 1997.88, df = 1635, $P < 0.001$). Except for duck species, df are 1. Abbreviations as in Table 3-2.

Variable	Slope	SE	Wald χ^2	P-value	$\text{Slope}_{\text{std}}$
INTERCEPT	-0.977	0.687	2.021	0.155	-
INITIAT	0.017	0.004	14.862	0.001	0.140
DISTWAT	-0.003	0.001	10.846	0.001	-0.101
VISUAL	-0.123	0.047	6.990	0.008	-0.098
PREDABU	0.016	0.004	13.367	0.001	0.134
FOX	-0.505	0.274	3.391	0.066	-0.125
RACCON	-0.249	0.192	1.687	0.194	-0.069
MINK	-0.269	0.195	1.915	0.167	-0.073
YEAR	-2.378	0.346	47.157	0.001	-0.656
FOX*YEAR	2.346	0.349	45.125	0.001	0.584
RACCON*YEAR	1.423	0.297	22.983	0.001	0.260
MINK*YEAR	0.577	0.287	4.047	0.044	0.097
DUCK SPECIES	$\Delta G^2 = 16.30$	$\Delta df = 5$	$P = 0.006$		
GREEN-W. TEAL	-0.402	0.343	1.372	0.241	-0.034
MALLARD	0.592	0.179	10.960	0.001	0.117
GADWALL	0.169	0.168	1.023	0.312	0.035
PINTAIL	-0.156	0.217	0.520	0.471	-0.022
SHOVELER	-0.052	0.191	0.074	0.786	-0.008

Table 3-7. Odds ratios of variables in the final model. Odds ratios for INITIAT and PREDABU are for changes in 10 units of the variables and those for DISTWAT for changes in 100 m. Abbreviations as in Table 3-2.

	Odds ratio (95% CI)					Odds
Variable	Lower	Center	Upper	Variable		Ratio
INITIAT	1.087	1.184	1.290	FOX*YEAR	1997	0.603
DISTWAT	0.608	0.733	0.881		1998	6.301
VISUAL	0.807	0.884	0.969	RACCON*YEAR	1997	0.780
PREDABU	1.079	1.177	1.285		1998	3.235
GREEN-W. TEAL	0.341	0.669	1.321	MINK*YEAR	1997	0.764
MALLARD	1.277	1.807	2.575		1998	1.360
GADWALL	0.854	1.185	1.648			
PINTAIL	0.560	0.855	1.311			
SHOVELER	0.654	0.949	1.385			

Table 3-8. Classification table indicating the predictive ability of the model. The probability level of 0.5 was used as a cutoff point. 66.5% of the observations were correctly classified.

	Predicted		
Observed	Hatched	Depredated	Total
Hatched	260	146	688
Depredated	407	839	964
Total	667	985	1652

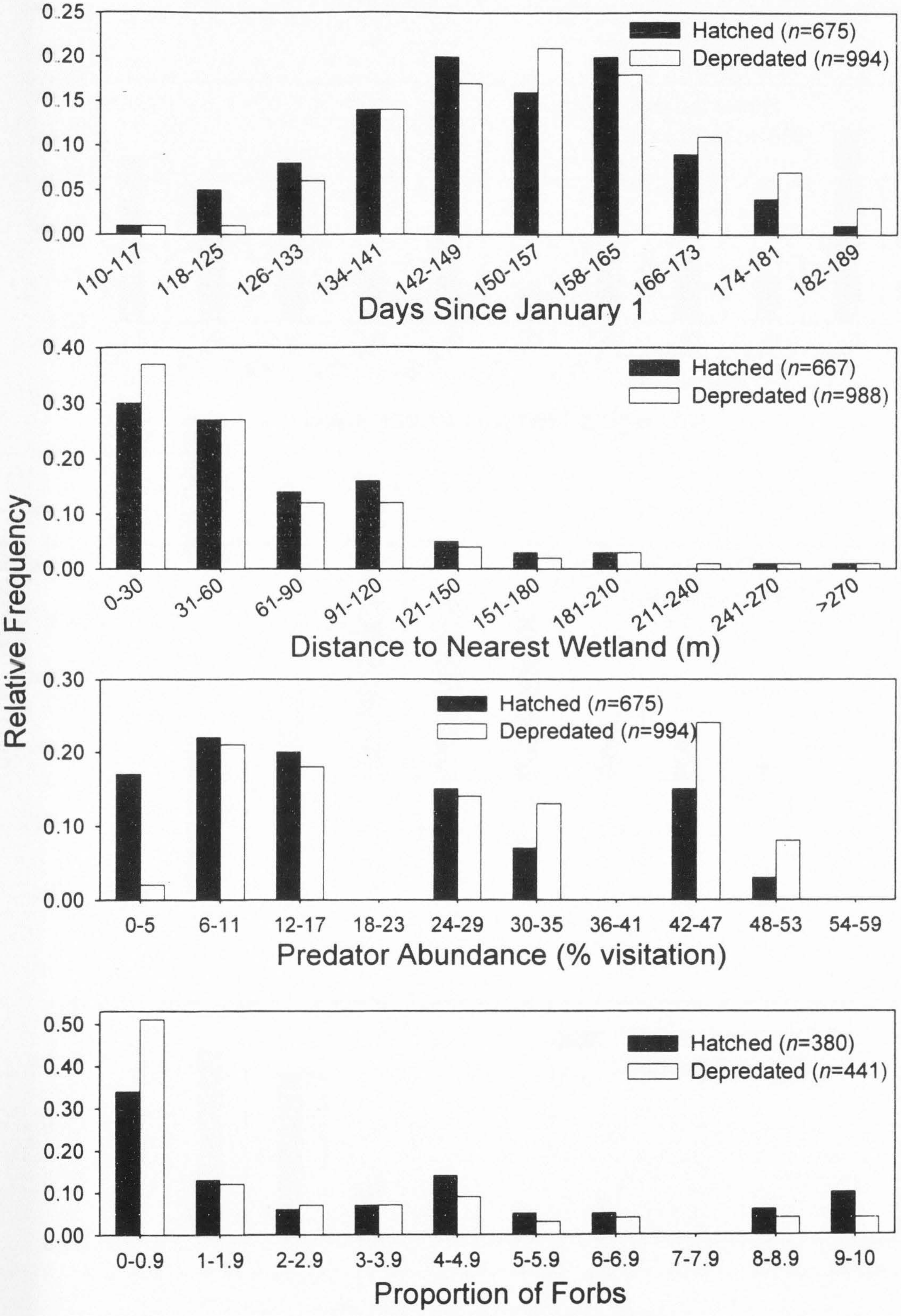

Fig. 3-1. Frequency distribution of hatched and depredated duck nests in relation to continuous variables measured at 16 sites in North Dakota. Means in the first 4 plots are significantly different.

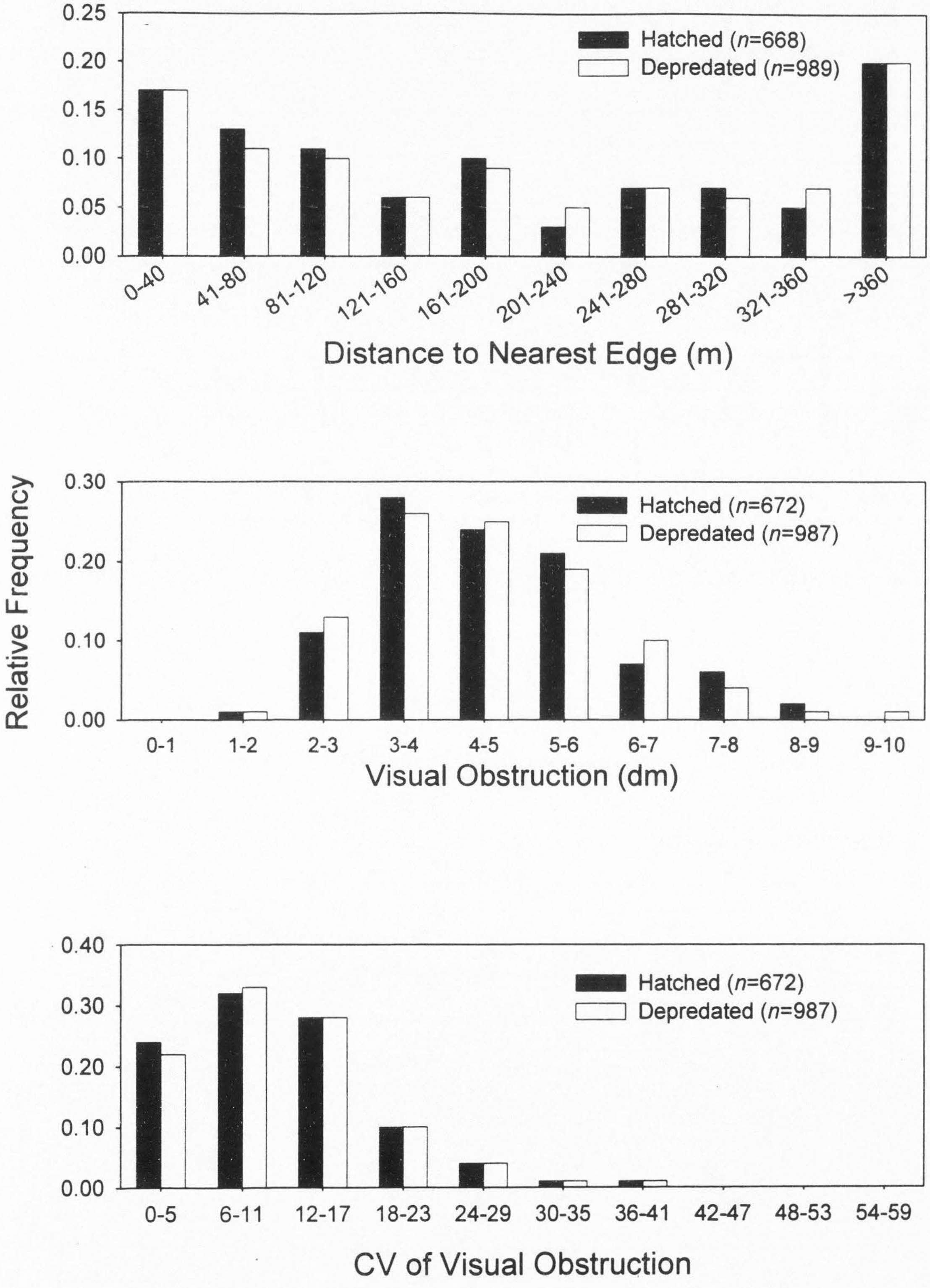

Fig. 3-1. (Continued).

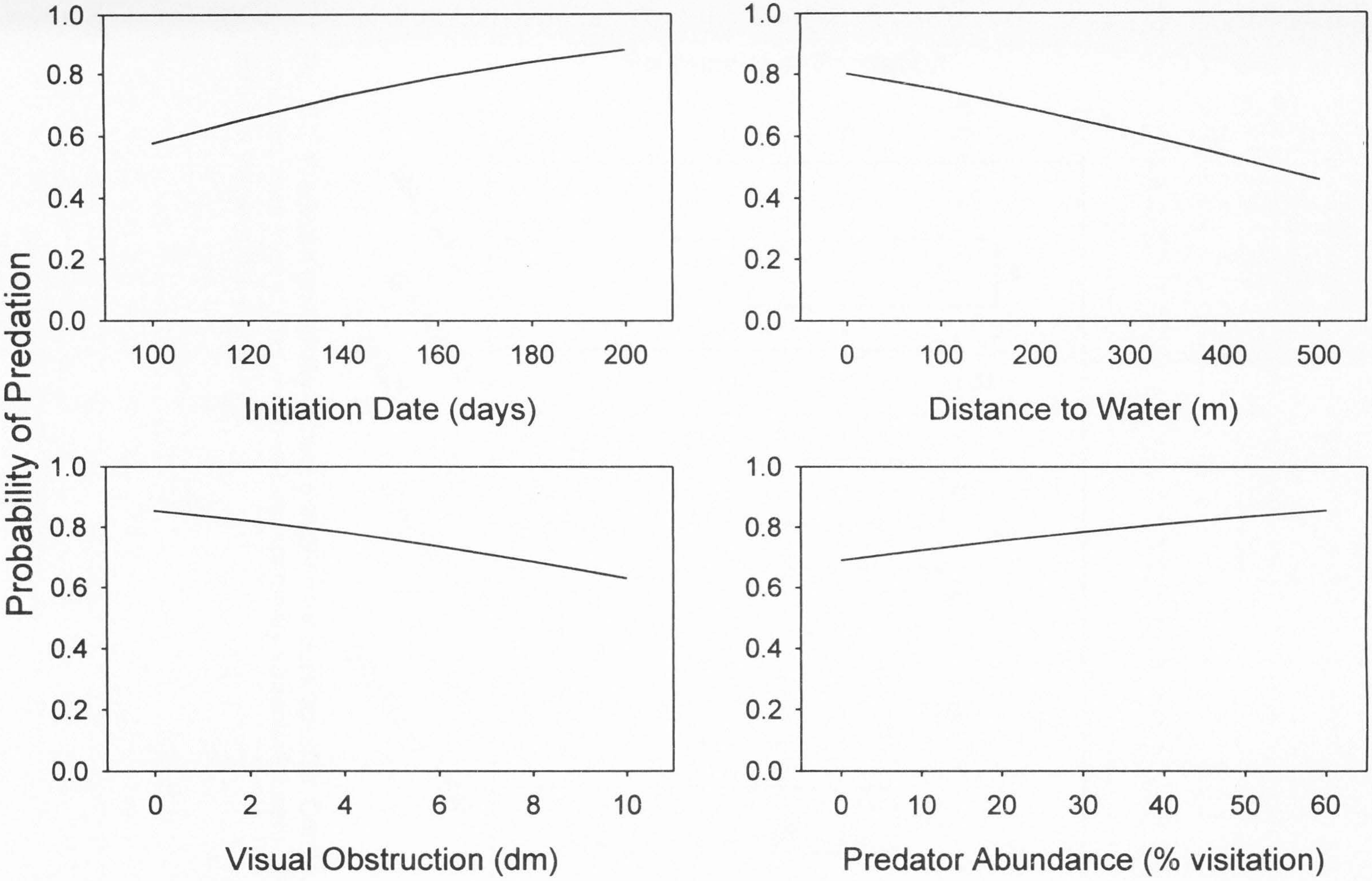

Fig. 3-2. Predicted probability of blue-winged teal nest predation across the observed range of continuous variables. For each variable, the line was obtained while maintaining other continuous variables at their mean values and the binary variables at zero.

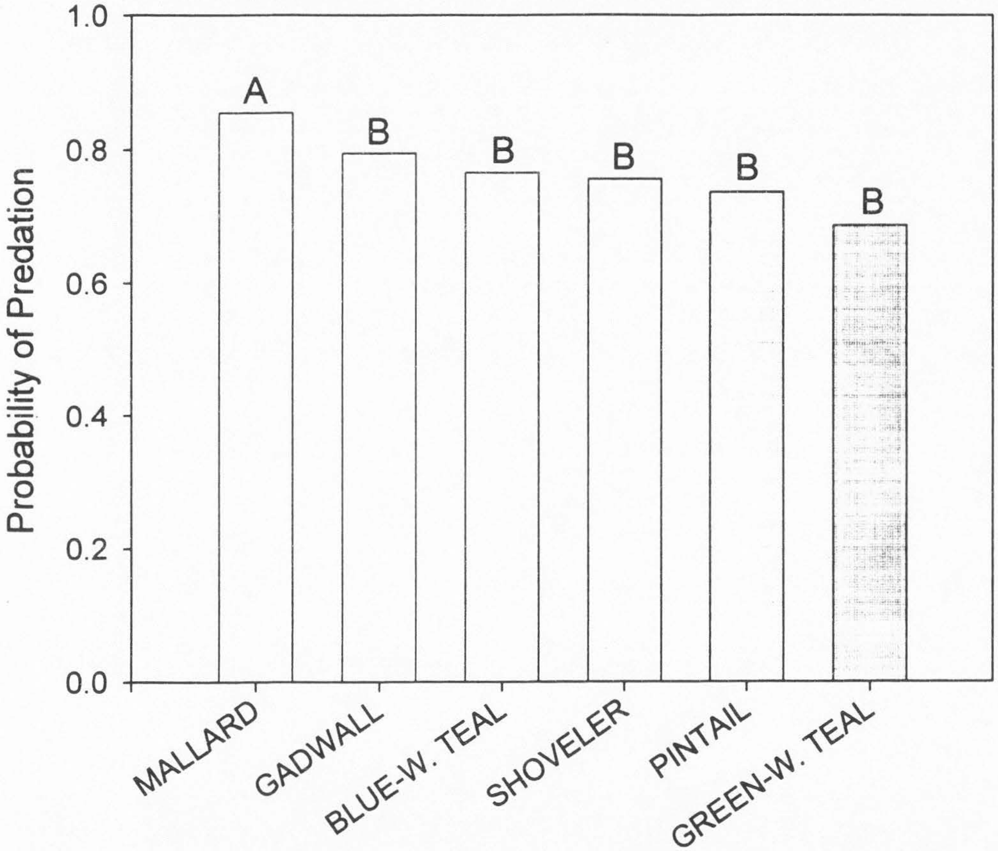

Fig. 3-3. Predicted probability of nest predation for duck species. Continuous variables were kept at their mean values and binary variables at zero. Bars with different letters differ at $\alpha = 0.05$.

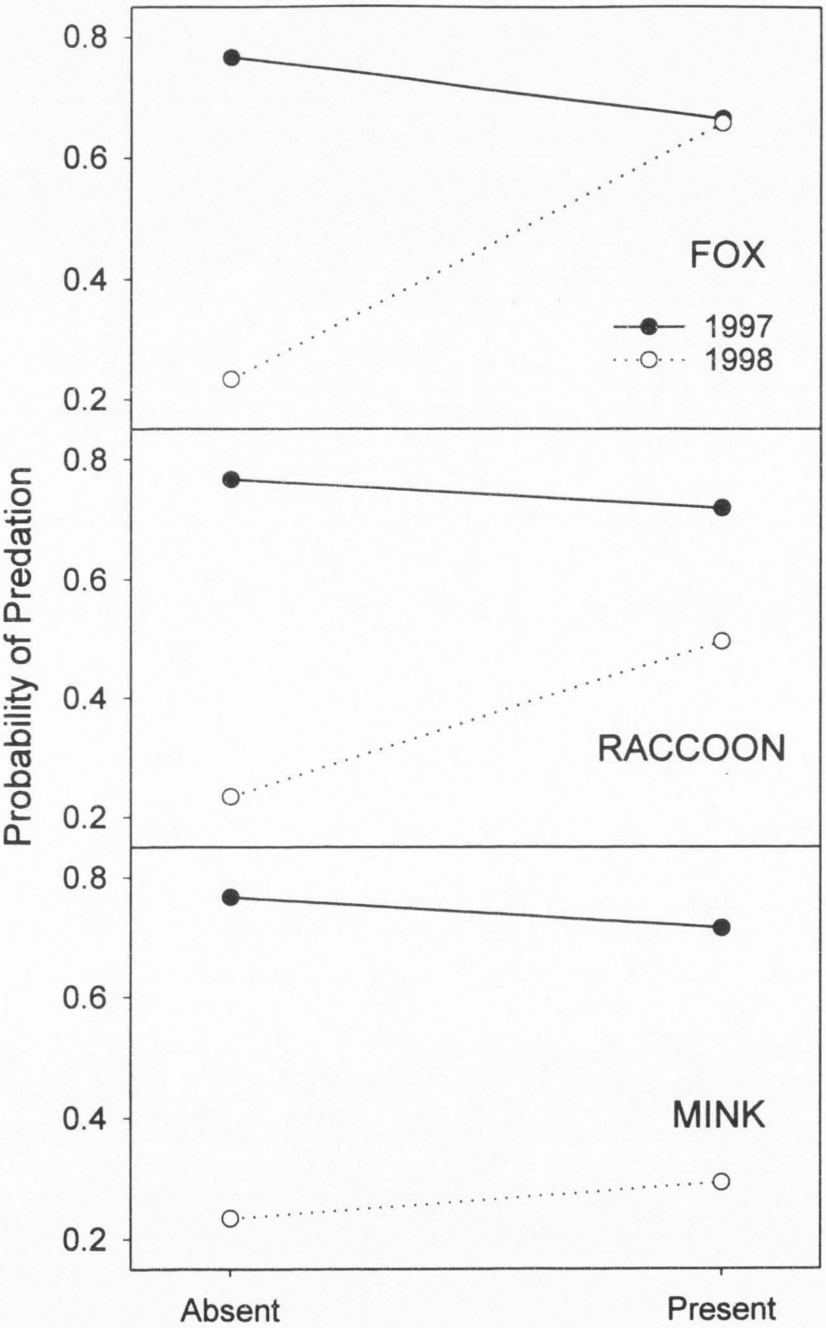

Fig. 3-4. Predicted probability of blue-winged teal nest predation for predator species and year. Continuous variables were kept at their mean values. All interactions are significant.

CHAPTER 4

ANALYSIS OF NONLETHAL METHODS TO REDUCE PREDATION ON GROUND-NESTING BIRDS AND THEIR NESTS [1]

High predation rates on ground-nesting birds and their eggs are a serious problem in many parts of North America. There is concern that predation rates have increased due to a decrease in nesting habitat quality and quantity (Cowardin et al. 1985, Wilcove 1985, Sargeant et al. 1993, Greenwood et al. 1995). In North America, the most serious nest predators are habitat and diet generalists which have thrived in human-modified environments (Sargeant 1982, Harris and Saunders 1993). Examples include the American crow (*Corvus brachyrhynchus*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*).

Increased nest predation contributing to reduced avian recruitment can limit population growth and make affected populations nonsustainable (Cowardin et al. 1985). In extreme cases, predation on breeding birds has resulted in extirpation of local populations, as documented by (Bailey 1993) for Aleutian islands, where arctic fox (*Alopex lagopus*) and red fox are the main predators. More subtle effects are long-term population declines, such as those experienced by dabbling duck populations nesting in the Prairie Pothole region (Cowardin et al. 1985, Greenwood et al. 1995, Beauchamp et al. 1996*a*). In this region, low nest success as a consequence of intense predation on eggs has resulted in a recruitment rate well below that needed to sustain dabbling duck populations (U.S. Fish and Wildlife Service 1986, Klett et al. 1988, Johnson et al. 1989, Clark and Nudds 1991, Sargeant et al. 1993, Greenwood et al. 1995, Beauchamp et al. 1996*a*, 1996*b*).

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[1] Coauthored by Jaime E. Jiménez and Michael R. Conover.

Wildlife managers use a variety of direct and indirect management techniques to increase avian recruitment, such as habitat improvements and restoration, and predator control (Lokemoen 1984). However, many of these techniques are expensive, controversial, or inadequately tested (Trautman et al. 1974, Sargeant and Arnold 1984, Clark and Nudds 1991, Sargeant et al. 1995, Greenwood and Sovada 1996).

The breeding ecology of ground-nesting birds is complex (Sargeant and Raveling 1992). Factors affecting recruitment include predation of hens and nests (Cowardin et al. 1985) mediated by habitat variables such as nesting cover and alternative prey to predators (Crabtree and Wolfe 1988, Clark and Nudds 1991). When birds are nesting on farms, agricultural practices, such as plowing and mowing (Greenwood et al. 1995) and livestock management also can influence nesting success (Kruse and Bowen 1996). In this paper, we reviewed the literature to examine the effectiveness of non-lethal management techniques in increasing recruitment of ground-nesting birds.

Methods

We reviewed methods designed to reduce predation rates on ground-nesting birds to assess their efficacy, cost effectiveness, and consistency of results. We emphasized studies conducted in the Prairie Pothole region of North America because the region has one of the more serious problems with nest predation.

Many of the studies reviewed assess nesting success using artificial nests. Although extrapolation of artificial nest studies to natural conditions has been criticized (Storaas 1988, Willebrand and Marcström 1988, Roper 1992, Major and Kendal 1996, Martin et al. 1996, Guyn and Clark 1997), these data are acceptable for comparative purposes (Wilson et al. 1998). We included artificial nest studies when information on natural nests was unavailable.

Results

Indirect predator management techniques

Exclusion with fences. Fences of different sizes have been used to protect patches of habitat, colonies, or individual nests. Structures to exclude predators include wire mesh exclosures (Nol and Brooks 1982), electric fences (Sargeant et al. 1974, Foster 1975, Minsky 1980), and metal barriers (Post and Greenlaw 1989).

Fences to protect individual nests. Wire mesh fences have successfully protected the nests of several species (Table 4-1). Estelle et al. (1996) improved daily survival rate of pectoral sandpiper (*Calidris melanotus*) nests using wire mesh fences to exclude arctic foxes in Alaska. Each fence took 30 minutes to construct and cost $4.00. Deblinger et al. (1992) examined the results of different studies to protect individual piping plover nests and concluded that fences were effective in reducing predation rates to 10%. They reported that exclosure effectiveness was related to fence characteristics. Successful fences enclosed areas either <3 m^2 or >6 m^2 in size, were triangular, covered on top, built with walls higher than 122 cm, using mesh size 5x5 cm, and buried deeper than 10 cm. One drawback of these fences was an increased nest abandonment by the parents. Inside these fences, 10% of the nests were abandoned by the adult birds, especially when the fences enclosed smaller areas or were covered on top (Vaske et al. 1994).

Nol and Brooks (1982) excluded gulls (*Larus* spp.) from killdeer (*Charadrius vociferus*) nests with mesh exclosures. However, raccoons were able to insert their forefeet through the holes, rendering the fences ineffective. In Florida, hardware cloth and metal barrier exclosures were used to protect seaside sparrow (*Ammodramus maritimus*) nests from garter snakes (*Thamnophis sirtalis*), Norway rats (*Rattus norvegicus*), rice rats (*Oryzomys palustris*), and fish crows (*Corvus ossifragus*) (Post and Greenlaw 1989). These fences increased hatch success from 6% to 48%.

Electric fences have also been tested (Table 4-1). Sargeant et al. (1974) used electric fences to protect individual nests of sharp-tailed grouse (*Tympanuchus phasianellus*) and upland-nesting ducks (*Anas* spp.) in North Dakota and Manitoba. Nest success increased from 21% to 67%, even though predators such as fox, raccoon, skunk, and mink (*Mustela vison*) could pass through the fence.

Fences to protect colonies and habitat patches. Foster (1975) and Patterson (1977) used electrified fences to improve recruitment in sandwich tern (*Sterna sandvicensis*) and eider (*Somateria mollissima*) colonies by excluding foxes (Table 4-1). Foxes avoided the fences and rarely trespassed. The fences proved valuable when predator removal was impossible or undesirable. In North Dakota, Mayer and Ryan (1991) fenced out mammalian predators from 4 beaches where piping plovers nested semi-colonially. Birds nesting within the enclosures enjoyed 71% greater nest survival rates, even though the exclosures did not restrict mink and gull access. The cost of fence material was $1.20/m, and required 48 person-hr/fence in labor, and fences were left in place with little maintenance costs.

Several studies evaluated the use of electric fences to exclude mammalian predators from habitat patches where ducks nested (Table 4-1). Beauchamp et al. (1996*a*) analyzed 21 studies and concluded that nest success in fenced habitat patches was comparable to that on islands and in both cases it was higher than on unmanaged sites. Duck nest densities and hatched nests in habitat patches enclosed with an electrified fence in North Dakota increased from 0.17 to 0.54 nests/ha and 0.02 to 0.42 nests/ha, respectively (Arnold et al. 1988). In North Dakota and Minnesota, exclosures produced 7.8 and 6.9 more duckling/ha, respectively, than outside areas (Lokemoen et al. 1982). Greenwood et al. (1990) reported nest success improved from 7 to 36% within exclosures. Seasonal predator control further increased nest success to 81%. The total cost of fence materials and herbicide for a 16.2-ha fence in 1989 was $4,500, excluding labor cost for construction, maintenance, and trapping. A fence that exclosed 16 ha of upland habitat in Iowa, and cost $7,240 (1985 dollars), improved nest success of mallards (*Anas platyrhynchos*) and blue-winged teals (*Anas discors*) from 13 to 32% (LaGrange et al. 1995). However, the fence delayed the exit of the broods, which increased mortality. Pietz and Krapu (1994) and Howerter et al. (1996) subsequently demonstrated that the survival of ducklings could be improved by modifying the ground-level exits.

Fences are not completely predator proof. Despite improvements in the design, minks, weasels (*Mustela* spp.), small mammals, foxes, coyotes (*Canis latrans*), badgers (*Taxidea taxus*), raccoons, and skunks occasionally entered exclosures (Lokemoen et al. 1982, Lokemoen and Messmer 1994, Howerter et al. 1996). Thus, some predator control is needed to maintain nest success rates (Greenwood et al. 1990, LaGrange et al. 1995). Given that avian predators will not be excluded with top-open fences, the use of fences is recommended for regions where nest predators are mainly terrestrial as in the southern half of the Prairie Pothole region (Sargeant et al. 1993).

Use of fences to exclude predators has generally proved useful in small areas where nest predation has been a consistent and significant limiting factor (Melvin et al. 1992, Goodrich and Buskirk 1995). Fences, although costly to construct, require low maintenance and endure for several years. When the costs are amortized over the expected life of the fence, this method can be more cost-effective than other techniques (Lokemoen 1984, Goodrich and Buskirk 1995). Hence, when mammalian predation was limiting, fences proved to be effective. Cover has been placed over single-nest fences to reduce avian predation (Pietz and Krapu 1994, LaGrange et al. 1995), but this procedure may not be practical for larger exclosures. One problem with fences is that in open grasslands, the fence itself could serve as a perch, therefore attracting raptors. To further reduce avian predation, the removal of potential perches was suggested (Greenwood et al. 1990, see also Preston 1957).

In general, single-nest fences have been successfully used to improve recruitment of solitary-nesting shorebirds and colonial species (Table 4-1). Solitary nesters are more expensive to protect than colonial species. Thus, single-nest fences may only be justified when predation by terrestrial species is high or the targeted species has a high conservation value.

Likewise, dabbling duck production has increased with protection of nesting patches using electrified fences. Use of these structures is usually easy to justify economically because these species nest in high densities in upland areas where mammalian predation is high. However, electrified fences are not a panacea.

As circles or rectangles get bigger, the area they encompass increases faster than their perimeter. Hence, it is more cost effective to fence a large area than a small one in terms of cost per unit area. For this reason, the cost of producing additional young with small fences may be extreme. Conversely, the cost per additional young produced could be generally lowered if larger areas are protected. However, because of the larger linear length of a fence, problems with terrestrial predators trespassing will more likely to become a problem. Additionally the use of fencing on uneven terrain will increase construction costs and the risks of predator access to the exclosure.

Use of nesting structures. Elevated artificial nesting structures (i.e., baskets, hay bales, floating platforms) have reduced mammalian predation on waterfowl nests (Losito et al. 1995), especially mallards (Doty and Lee 1974, Doty et al. 1975, Doty 1979). In Iowa, mallards used 33% of the structures and had an 87% hatch success with densities up to 0.3 nests/ha (Bishop and Barratt 1970). In the Prairie Pothole region, mallards used 38% of the structures; 83% of the nests in baskets hatched (Doty et al. 1975). Open-top baskets received higher use than mailbox-type structures (Sidle and Arnold 1972), and "horizontal cones" were used the most (Doty 1979). Horizontal cones provided protection from mammals and reduced predation by gulls by concealing the eggs from above. Baskets were better accepted when they were located in small openings in emergent vegetation and were lined with barley (*Avena* spp.) straw or brome (*Bromus* spp.) hay (Doty et al. 1975, Doty 1988). Structures lasted beyond 7 years where they were not impacted by wind, waves, or ice (Doty et al. 1975). Raccoons, apparently attracted by pipping sounds, were the only mammal that could reach the nests. This could be prevented with the use of "truncated metal cones" or metal sheet on support poles (Doty et al. 1975, Doty 1979). Considering maintenance over 20 years, the cost per duckling produced in baskets was $1.48 (1974 prices, Doty et al. 1975, Table 4-1).

In the Prairie Pothole region, nesting structures were largely used by mallards. The number of ducklings produced using these structures in wetlands is relatively low, probably limited by the fact that high densities of structures might attract avian predators, creating the opposite results than desired. For similar reasons, given the relatively high cost per young produced per area (Table 4-1), the use of nesting structures is recommended where mallards are targeted, mammalian predation is high, and upland area is limited or of poor quality; otherwise, other techniques such as fences have proven to be more cost effective.

Use of islands and peninsulas. Gadwalls (*Anas strepera*) and mallards typically nest on islands, isolated from mammalian predators (Vermeer 1970, Willms and Crawford 1989). Nest densities as high as 389 nests/ha have been reported on islands (Duebbert et al. 1983). However, predation by mink and raccoon, which may swim to nearby islands, can reduce duck nest success (Duebbert 1966, Willms and Crawford 1989, Fleskes and Klaas 1991, Beauchamp et al. 1996*a*).

Consequently, constructed islands have been used effectively to increase recruitment (Table 4-1, Lokemoen and Messmer 1993). Generally, both nest density and hatch success are high on islands (Higgins 1986*a*, 1988; Lokemoen and Messmer 1993). Gadwall nests densities of 62/ha with 65% nest success have been reported on constructed islands. This is much higher than in upland habitats (Hines and Mitchell 1983). Duebbert (1982) suggested an optimal island size of 0.5 - 5 ha, which is large enough to support numerous nests, but too small to support resident mammalian predators.

Use of constructed islands may decline if soil and vegetation for nesting are eroded due to wave action (Higgins 1986*a*). To construct more durable islands, Higgins (1986*a*, 1988) and Lokemoen and Messmer (1993) suggest building them higher and in smaller wetlands. However, wetlands must be large enough to impede immigration of predators from the mainland. This condition is met by large (>5 ha) permanent wetlands with water depths > 1 m. After ice break up, predators may have to be removed from islands (Lokemoen and Messmer 1993). The construction costs of artificial islands was $31 per duckling (Higgins 1986*a*). This estimate was similar to Lokemoen's (1984) estimate ($23).

Lokemoen and Woodward (1993) compared duck breeding on 20 peninsulas in North Dakota, 8 of them isolated from mainland by electric fences and 2 by water-filled moats. Isolated peninsulas exhibited 3 times the nest success and produced 9 times more ducklings/ha than nonisolated ones (Table 4-1). The cost per duckling produced was lower on fenced ($22) than on moated peninsulas ($114, Lokemoen and Woodward 1993). Problems with raccoons crossing moats were detected. Lokemoen and Messmer (1994) provide comprehensive guidelines and cost estimates for constructing fences and moats to reduce predator access to peninsulas. Duckling production on fenced peninsulas costs less than on man-made earthen islands or small rock islands (Lokemoen and Messmer 1993). Costs were similar to nest baskets methods, but higher than electrified fences in upland nesting habitat (Lokemoen 1984). Although production of ducklings on islands and moated peninsulas was high, construction costs resulted in higher costs per individual bird produced than other practices (Table 4-1, Lokemoen 1984).

Considering the effectiveness and cost per additional duckling produced, fenced peninsulas are more efficient than moated peninsulas or man-made islands. However, peninsulas that have high densities of nests and are large enough to protect many nests often are absent, in which case, the construction of islands may be the only option available. Predator problems caused by swimming (i.e., raccoon and mink) and avian predators will not be solved by fenced peninsulas and constructed islands. Thus, seasonal predator management may still be required. The use of fenced peninsulas and constructed islands is more effective in areas of the Pothole region where avian and aquatic nest predators are less abundant and the construction of upland exclosures is cost prohibitive.

Conditioned taste-aversion. Taste aversion conditioning is the process by which animals develop avoidance to the flavor of a food that makes them ill (Nicolaus et al. 1983). Although this approach has not succeeded in stopping depredation on natural nests (Conover 1989, 1997), additional research continues to explore its effectiveness for use on birds and mammals (Conover 1997).

Taste aversion research on avian predators has included captive fish crows (Avery and Decker 1994), free-ranging American crows (Nicolaus et al. 1983), and ravens (*Corvus corax*, Avery et al. 1995*a*, 1995*b*). Nesting crows and ravens learned to avoid treated eggs placed within their own territories (Nicolaus et al. 1983, Avery and Decker 1994), and depredation on least tern (*Sterna antillarum*) nests close to these nesting ravens declined (Avery et al. 1995*a*, 1995*b*). Apparently, the nesting ravens and crows indirectly protected the eggs from other ravens and crows while defending their territory (Avery et al. 1995b).

Conover (1989, 1990) pioneered research on mammalian egg predators by teaching captive raccoons to avoid treated food. However, field tests produced mixed results. Sheaffer and Drobney (1986) reported no difference in South Dakota between waterfowl nest successes in treated and untreated plots during the first year, and reduced nest success in treated plots during the second year. Conover (1990) was also unsuccessful in reducing egg depredation on treated sites in Connecticut. Greenwood and Sovada (1996) contended that because foxes seldom eat eggs immediately upon encounter, the technique would not work for this species. Although laboratory data suggested that mammals can learn to avoid treated eggs, the effectiveness of this technique under field conditions has not been demonstrated (Clark et al. 1996).

Limitations regarding the use of taste-aversion techniques are that some predators require frequent exposure to achieve continuous conditioning (Sheaffer and Drobney 1986, Conover 1990, Avery and Decker 1994), and responses differ among individual conspecifics (Conover 1990, Avery and Decker 1994, Avery et al. 1995b). Additionally, predators can learn to discriminate between treated and untreated eggs (Conover 1990, 1997; Avery et al. 1995b). Given a highly diverse and dynamic predator community, aversive agents may not deter all predators, and lastly, conditioning may not be strong enough to overcome certain innate predatory behaviors (Clark et al. 1996). Field tests on natural nests, where treated eggs are deployed well in advance of the availability of natural eggs, have been suggested as a means to overcome these problems (Sheaffer and Drobney 1986; Conover 1990, 1997; Avery and Decker 1994).

The fact that mammalian predators use a variety of senses to assess food items also may explain the lack of success in the ability of conditioned taste aversion to protect eggs. In contrast, its effectiveness in reducing avian predation seems more promising, and it could be used when territorial avian predators are responsible for nest depredation. It could also complement other techniques that manage terrestrial but not avian predators (see above). However, the development of the use of conditioned taste aversion is in its early development and more research is needed, especially to assess its effectiveness under field conditions.

The cost effectiveness of using conditioned taste aversion techniques cannot be analyzed because costs involved have not reported in the literature. However, given that predators need repeated exposure to treated foods, it would require intensive manpower, which would render its application expensive, thus, impractical for managing large blocks of nesting cover. Nonetheless, this technique might be effective on small areas where traditional management options are limited.

Fertility control for predators. Fertility control may reduce nest predation by curtailing predator reproduction. This short-term numerical response would be effective if predators with no offspring had lower food demands (functional response). Despite the fact that the development of fertility control techniques is in its infancy, ongoing research under laboratory conditions has produced promising results. However, these techniques have not yet been field tested. More research is necessary before fertility control can be considered as an applied management tool to reduce predation on breeding birds.

Currently, predator fertility control includes surgical/chemical sterilization, endocrine perturbation, and immunocontraception (De Liberto et al. in press). Surgical sterilization has been effective on domestic animals, feral cats (*Felis domesticus*) (Neville 1983, Neville and Remfry 1984), red foxes (Bailey 1992), and Canada geese (*Branta canadensis*) (Converse and Kennelly 1994). Given that most nest predators are territorial, sterilizing individuals may be better than removal, because they will keep out immigrants, which would readily colonize the vacant habitat. For instance, coyotes without pups require less prey biomass, but still maintain their territorial behavior (Till and Knowlton 1983). Consequently, this technique should be most promising for large species, which have large territories. In addition, large species are generally long-lived (e.g. coyote versus skunk). Thus, the costs and benefits associated with the capture and use of surgical techniques could be amortized over several years. Research using this technique on coyotes is ongoing (E. Gese, pers. comm.).

Use of endocrine perturbation has been limited by undesirable side effects to the animals (Asa and Porton 1991) and the inability to find species-specific, reliable compounds that work consistently and with a single application or oral dosage (Bradley 199', De Liberto et al. in press). Thus, aside from the technical aspects of drug delivery and acceptance by the target individuals, which still remain to be solved, changes in hormonal levels could disrupt the social behavior and potentially make territorial individuals nonterritorial, therefore rendering the technique ineffective. A nonterritorial predator would not keep out other conspecifics. In addition, the effects of these drugs wear off over time. Hence, repeated application of the drug would be necessary and this might make it inapplicable under field conditions. Hence, for the technique to be useful, these limitations need to be overcome by innovative research.

Immunocontraception research on captive coyotes effectively reduced litter size, but also requires frequent doses to establish a titer (De Liberto et al. in press). However, it is unknown if other important nest predators will respond in the same way.

Although these findings are encouraging, the effectiveness of fertility control techniques in protecting ground-nesting birds has not been evaluated. This is a promising yet almost unexplored line of research. The search for cost-effective, socially acceptable fertility control that does not affect nontarget species (Curtis et al. 1997, Trewhella et al. 1991) or negatively affect the gene pool (Nossal 1989) continues. Costs of using fertility control of predators was not reported in the literature. For an extended annotated bibliography on these techniques, see McIvor and Schmidt (1996).

Modifying the predator community. Several authors have recognized the relative effectiveness of specific predators and the context of predation events on nesting birds (Kalmbach 1938, Maxson and Oring 1978, Johnson et al. 1989, Miller and Knight 1993, Sargeant et al. 1993, Niemuth and Boyce 1995). Generalist predators typically have the greatest effect on breeding birds (Greenwood 1981; Sargeant et al. 1984, 1986, 1993; Andrén 1992; Harris and Saunders 1993; Clark et al. 1995; Goodrich and Buskirk 1995).

As a result of selective harvesting and local extirpation of larger predators (e.g., wolves, coyotes), populations of smaller medium-sized predators that are more efficient nest predators (e.g., red foxes, raccoons, skunks) have increased in density and expanded their ranges (Robinson 1961, Wagner and Graetz 1981, Sargeant et al. 1984, Cowardin et al. 1985, Schmidt 1986, Johnson et al. 1989, Langen et al. 1991, Goodrich and Buskirk 1995). Changes in the species composition and abundances of nest predators in the Prairie Pothole region of North America are described by Johnson and Sargeant (1977), Sargeant (1982), and Sargeant et al. (1993), and in northern Europe by Angelstam (1986) and Andrén and Angelstam (1988).

Control of the smaller predators responsible for most of the nest predation in the North American prairies has been proposed by encouraging coyote reestablishment in vacant areas (Sargeant and Arnold 1984, Klett et al. 1988). Given their low densities and larger home ranges, coyotes pose less of a threat to breeding hens and their nests than red foxes (Greenwood et al. 1987, Sovada et al. 1995). By allowing coyotes to repopulate areas where fox populations have expanded, we may be able to enhance reproductive output of local birds, because coyotes do not tolerate red foxes and drive them out from their territories (Sargeant et al. 1987, Sargeant and Allen 1989). In fact, 1 coyote pair can displace 5 pairs of red foxes (Sargeant et al. 1987). This may be used to increase nest success in ducks (Johnson et al. 1989, Ball et al. 1995). Correlational evidence from a study in the Prairie Pothole region supports this idea. Sovada et al. (1995) found that areas with coyotes and no red foxes had 32% nest success in breeding ducks, whereas areas with no coyotes but with foxes had 17% nest success. A similar biological method has been proposed for controlling arctic foxes with sterilized red foxes in the Aleutian Islands (Schmidt 1985, Bailey 1992). In this case, red foxes would exclude arctic foxes, but would be unable to reproduce.

Another example of competitive interaction among nest predators was described by Henry (1969) in Tennessee. He found that predation by foxes, dogs, and snakes on artificial grouse and turkey nests was lower in areas with high hog (*Sus scrofa*) populations than on areas with fewer hogs. Henry (1969) speculated that hogs, which are inefficient nest predators, may drive foxes and dogs away and prey on snakes.

Although the idea of selectively changing the predator community to improve nest success is appealing, to our knowledge, the only 3 studies that consider this approach experimentally show discouraging results. Greenwood (1986) selectively removed striped skunks and Clark et al. (1995) and Parker (1984) removed crows, but ground-nest success improved little or not at all. The authors speculated that compensatory predation by other local predators may have occurred. Further, removal methods may be socially unacceptable and would require constant effort due to repopulation from the periphery (Greenwood 1986). To be effective, changing the predator community would need to occur over extended areas and for multiple years of effort, which would be costly.

The management of the landscape (e.g., removing shelterbelts or secondary roads) to favor certain predator species might be a more feasible goal. Hence, it may be more reasonable to manage the resource base for predators rather than the demography of the predator themselves. This, combined with changes in local attitudes of people towards predators (i.e., to keep certain species) could produce the desired effects. So far, this approach is speculative and requires testing. Associated costs are unknown.

Protective umbrella or associational defense. Dyrcz et al. (1981) coined the term "protective umbrella" to describe the propensity of some species to nest close to a more pugnacious species that attack or mob predators. This behavior can increase reproductive output of the species unable to protect themselves. In Europe, species employing the protective umbrella strategy include waders and passerines nesting close to lapwings (*Vanellus vanellus*) and godwits (*Limosa limosa*, Dyrcz et al. 1981, Elliot 1985); godwits (*Limosa lapponica*) protected by whimbrels (*Numenius phaeopus*, Larsen and Moldsvor 1992); curlews (*Numenius arquata*) protected by nesting kestrels (*Falco tinnunculus*, Norrdahl et al. 1995); and artificial nests close to lapwing (Eriksson and Götmark 1982), grey plover (*Pluvialis squatarola*, Larsen and Grundetjern 1997), and kestrel nests (Norrdahl et al. 1995). In North America, species extending protective umbrellas include herring gulls (*Larus argentatus*) for savannah sparrows (*Passerculus sandwichensis*, Wheelwright et al. 1997); snowy owls (*Nyctea scandiaca*) for brent (*Branta b. bernicla*, Underhill et al. 1993) and snow geese (*Chen caerulescens*, Tremblay et al. 1997); and common terns (*Sterna hirundo*) for pintails (*Anas acuta*) and lesser scaups (*Aythya affinis*, Vermeer 1968). Vermeer (1968) documented >90% hatch success for waterfowl nesting in association with gulls (*Larus californicus*, *L. delawarensis*). However, gull predation on ducklings resulted in almost complete reproductive failure.

The protective umbrella behavior can be used as a nonlethal tool to improve the recruitment of certain birds by favoring and protecting the aggressive species, such as small-sized gulls and terns nesting in mixed colonies with ducks. Although not currently practiced in management, the strategy shows potential. Potential costs have not been reported.

Providing alternative prey for predators. Most nest predators are opportunistic species that eat a variety of food items. It has been hypothesized that alternative prey abundance buffers the effect of predators on nests. Predators may respond to alternative prey by changing their search image for food, altering their prey selection (i.e., dietary shift or functional response), or increasing their numbers in the area of abundant prey (i.e., numerical response) through immigration or increased reproduction.

Information on the effects of alternative prey on bird recruitment is mainly anecdotal, and based on correlations of nest success and abundance of alternative prey. Alternative prey abundance can be correlated either positively or negatively with nest success. When positively correlated, alternative prey presumably draw the attention of predators away from searching for nests. Several Scandinavian studies have assumed or documented a positive relationship between nest success and the abundance of alternative prey for black grouse (*Tetrao tetrix*, Angelstam et al. 1984), willow ptarmigan (*Lagopus lagopus*, Parker 1984), oldsquaw (*Clangula hyemalis*, Phersson 1986), tetraonids (Marcström et al. 1988), curlews (Norrdahl et al. 1995), and artificial nests (Huhta 1995, Larsen and Grundetjern 1997). A positive relationship also was documented for black brants (*Branta bernicla nigricans*) in Alaska (Anthony et al. 1991), and for brant geese and wading birds in Russia (Summers and Underhill 1987, Underhill et al. 1993). In these studies, the main predators were foxes, mustelids, and corvids and the alternative prey were small mammals with cyclic population dynamics.

Similar positive relationships were reported for nest success of wader species and vole (*Microtus* spp.) abundance in the Netherlands (Beintema and Müskens 1987), for duckling predation by mink and American coot (*Fulica americana*) abundance in the Prairie Pothole region (Bennett 1938 and Low 1945 in Eberhardt 1973; Sowls 1955), blue-winged teal nest success and small mammal abundance in the Prairie Potholes (Byers 1974, Weller 1979), bobwhite quail nest success (*Colinus virginianus*) and small mammals in Iowa (Scott and Klimstra 1955), ruffed grouse (*Bonasa umbellus*) nest success and small mammals in New York (Darrow 1945), and for waterfowl nest success and “availability of buffer prey” in the Canadian prairies (Greenwood et al. 1995) and Prairie Pothole region (Trevor 1989, Johnson et al. 1989).

Sometimes the availability of alternative prey may be inversely related to nest success. In these cases, the interpretation is that predators are attracted to the area where the birds are nesting, resulting in higher predation rates. Alternative prey that seem to have increased nest depredation include quail and small mammals eaten by foxes and skunks in Illinois (Komarek 1937), and arctic foxes preying on cyclic lemmings

(*Lemmus sibiricus*, *Dicrostonyx torquatus*) and brent geese in western Europe (Ebbinge 1989). The affected birds in these cases include meadowlark (*Sturnella magna*) nests, bobwhite quail nests, and prairie voles (*Microtus ochrogaster*) in Illinois (Roseberry and Klimstra 1970, Klimstra and Roseberry 1975), and for passerine nests and invertebrates preyed upon by skunks in Maine (Vickery et al. 1992). The inverse relationship of abundance of alternative prey and nest success is likely a reflection of random encounters of nests by predators when they are foraging for other prey items (Angelstam 1986, Vickery et al. 1992, Pasitschniak-Arts and Messier 1995).

Only 2 studies experimentally tested the effect of alternative prey on ground-nesting bird nest success (Crabtree and Wolfe 1988, Greenwood et al. 1998). Crabtree and Wolfe (1988) mimicked increased alternative prey by providing carp (*Cyprinus carpio*) and pet food in a Utah wetland. They found an increased nest success of gadwalls during June, but not in July. Apparently, predators other than skunks did not respond to the treatment. However, this study lacked replication. Similar approaches were used on nesting waterfowl in North Dakota using frozen fish (Greenwood et al. 1998) and chicken eggs (King et al., unpublished data) as alternative prey for skunks. However, King et al. (unpublished) and Greenwood et al. (1998) did not detect changes in nest success in their experimental areas.

Wildlife managers choosing to manipulate the prey base for predators to enhance the nesting success by birds should consider the mixed results of these studies. Additionally, although vegetative cover or plant species composition can be manipulated to increase or decrease the desired small mammal species, nesting birds and predators respond themselves to type and quality of cover (see below).

Currently, the results of alternative prey studies on recruitment of ground-nesting birds are mixed and based mainly on circumstantial evidence. These results could be due to many reasons, including differences in local predator composition and abundance, the ability of predators to track fluctuating resources, predators' prey preferences and thresholds, the availability of other nonaccounted resources to predators, the density, spatial dispersion and mixing of nests and other prey, or a combination thereof. Research must be conducted to determine causality rather than associations, if manipulation of predators prey base or food resources can truly be evaluated regarding its role in increasing nest success.

Supplemental feeding (Boutin 1990) apparently does not effectively decrease nest predation, but could be a short-term solution. It also may not be cost effective. Furthermore, numerical responses of predators might counteract the benefits over short (through immigration into a rich source of food) or longer time periods (through reproduction, Phersson 1986, Crabtree and Wolfe 1988, Ebbinge 1989).

Removal of mammalian den sites and perch sites for avian predators

Fleskes and Klaas (1991) and Herkert (1994) contend that by removing den sites (e.g., abandoned farm buildings, rock piles, and hollow trees) and nesting and perching structures (i.e., trees), the abundance and composition of the predator community could be managed. In addition to protecting large tracts of grasslands, Burger et al. (1994) and Greenwood et al. (1995) suggested removing brush (contrary to Sugden and Beyersbergen's 1987 proposal) where nest predation is high. To our knowledge, none of these practices have been implemented and evaluated.

Improving cover

Cover for breeding birds provides crucial shelter from climatic conditions and concealment for both the hen and nest (Riley et al. 1992, DeLong et al. 1995). Quality of cover can be measured by vegetation height, horizontal visibility, overhead visibility, vegetation density, and physical obstruction to movement. The spatial scale of measurement is also important (Bowman and Harris 1980). Changing scale can produce opposite results (Huhta 1995). Cover at a large spatial scale appears to have more influence on nest predation than at the immediate nest surrounding (Schranck 1972, Warner et al. 1987, Ritchie et al. 1994).

Milonski (1958), Duebbert (1969), Schranck (1972), Duebbert and Kantrud (1974), Kirsch et al. (1978), Livezey (1981), Mankin and Warner (1992), Riley et al. (1992), Kantrud 1993, Gregg et al. (1994), Leimgruber et al. (1994), Huhta (1995), and Nummi and Pöysä (1995) found greater waterfowl nest success in taller and denser cover. The dependence of breeding birds on concealment is also supported by increased duck recruitment (Schranck 1972, Sugden and Beyersbergen 1986, Greenwood et al. 1995, Beauchamp et al. 1996*b*), higher pheasant (*Phasianus colchicus*) nesting success (Chesness et al. 1968), and greater survival of artificial nests as cover grows during the season (Pasitschniak-Arts and Messier 1996).

Studies on the effect of cover on nest predation have produced conflicting results (Sugden and Beyersbergen 1986). Clark and Nudds (1991) found that the importance of cover varied with predator species. Dense cover conceals nests from visually oriented predators such as crows (*Corvus* spp., Dwernychuk and Boag 1972, Horkel et al. 1978, Wray and Whitmore 1979, Angelstam 1986, Sugden and Beyersbergen 1987), magpies (*Pica pica*, Jones and Hungerford 1972), herring gulls (*Larus argentatus*, Brouwer and Spaans 1994), and coyotes (Keppie and Herzog 1978). The same visual concealment that protects nests from avian predators may not protect them against predators that rely on olfaction, such as skunks and foxes (Glover 1956, Crabtree and Wolfe 1988, Fleskes and Klaas 1991, Sargeant et al. 1993), or snakes (Zimmerman 1984). Most cover fails to protect nesting waterfowl from mammalian predation (Schranck 1972, Hines and Mitchell 1983).

Cover can also provide structural heterogeneity around the nest. Bowman and Harris (1980) experimentally demonstrated the importance of spatial heterogeneity (i.e., habitat structure) in decreasing nest predator foraging efficiency. Heterogeneity increased searching time and reduced the number of clutches found. Local habitat heterogeneity is more important than visual concealment for protecting nests (Bowman and Harris 1980, Lima 1998, Mankin and Warner 1992). In fact, dense cover appeared not to act as an olfactory barrier for skunks (Crabtree et al. 1989). Zimmerman (1984) also found higher nest predation by snakes in more heterogeneous habitats.

Other studies have reported no relationship between nest success and cover (Kalmbach 1938, Hammond 1940, Glover 1956, Hammond and Forward 1956, Steel et al. 1956, Urban 1970, Byers 1974, Trevor 1989, Fleskes and Klaas 1991). This lack of pattern has not been fully explained but may be the result of incidental encounters of nests by predators (Best 1978, Livezey 1981, Zimmerman 1984, Angelstam 1986, Sugden and Beyersbergen 1986, Yahner and Voytko 1989, Vickery et al. 1992, Pasitschniak-Arts and Messier 1995).

Contrary to Clark and Nudds' (1991) conclusions that cover protects nests against avian, but not mammalian predators, Erikstad et al. (1982) found that crows robbed well-concealed willow ptarmigan (*Lagopus lagopus*) nests at higher rates than poorly concealed nests. They claimed that crows located nests by watching hen movements to and from the nests. The same behavior was described by Kalmbach (1938), Hammond and Forward (1956), and Preston (1957) for crows preying upon duck nests located in dense cover and by Preston (1957) for red grouse (*Lagopus scoticus*) nests. Nest concealment offered little protection from walking crows (Sugden and

Beyersbergen 1986). High losses of spruce grouse (*Dendragapus canadensis*) nests in sparse vegetation, likely due to predation by coyote, which rely primarily on vision to locate prey (Redmond et al. 1982), constitutes another exception to Clark and Nudds' (1991) conclusions.

Several authors emphasized the importance of residual vegetation from previous growing seasons for nesting birds. Fields with little residual cover had lower nest densities, and lower nest success than fields with denser residual cover (Gates 1965, Martz 1967, Chesness et al. 1968, Jarvis and Harris 1971, Kirsch 1974, Gjersing 1975, Mundinger 1976, Duebbert and Lokemoen 1977, Kirsch et al. 1978, Higgins and Barker 1982, Warner et al. 1987, Kantrud and Higgins 1992, Kantrud 1993, Gregg et al. 1994). Early nesting species, such as pintails, prefer stubble fields for nesting. Litter depth appears important for blue-winged teal (Byers 1974) and some passerines (Igl and Johnson 1995).

A main paradigm in managing breeding grounds for upland-nesting waterfowl has been that dense nesting cover improves nesting success (U.S. Fish and Wildlife Service 1986) by deterring predators and decreasing their feeding efficiency (Duebbert 1969, Schranck 1972, Livezey 1981, Redmond et al. 1982, Hines and Mitchell 1983, Sugden and Beyersbergen 1987, Crabtree et al. 1989, DeLong et al. 1995, Greenwood et al. 1995, Guyn and Clark 1997). Although widely accepted, this hypothesis remains untested. In fact, isolated patches of dense nesting cover may act as ecological traps (Ratti and Reese 1988, Pasitschniak-Arts and Messier 1995) by attracting and concentrating nesting hens (Duebbert and Lokemoen 1980, Haensly et al. 1987, Crabtree et al. 1989, Fleskes and Klaas 1991), and mammalian predators (Milonski 1958, Schranck 1972, Choromanski-Norris et al. 1989, Greenwood and Sovada 1996) that may destroy the nests (Labisky 1957, Hines and Mitchell 1983, Sugden and

Beyersbergen 1987, Trevor 1989, Clark and Nudds 1991, Greenwood et al. 1995). Similarly, vegetation managed to deter predators in New Zealand resulted in the opposite effect, by attracting predators and thus increasing depredations on nesting birds (Alterio et al. 1998).

Pheasant nesting studies along linear patches and rights-of-way (Chesness et al. 1968, Haensly et al. 1987, Mankin and Warner 1992) support the ecological trap hypothesis (small habitat patches attract nesting birds, but their nests suffer higher predation than nests in larger patches, Ratti and Reese 1988, but see Joselyn et al. 1968). Instead of being sources for recruitment, small patches of dense nesting cover might serve as sinks for nesting birds (Clark and Diamond 1993). Given that concentrations of nesting birds and dense cover appear to attract predators, it may be necessary to increase the area of dense nesting cover to disperse the nests (Duebbert and Lokemoen 1976, Taylor 1976, Sugden and Beyersbergen 1986, Crabtree et al. 1989, Kantrud 1993).

The relationship between protective vegetation cover and predation is complex. Management of cover alone may not improve nest success (Trevor 1989, Fleskes and Klaas 1991). Greater knowledge of predators' searching behaviors is necessary (Erikstad et al. 1982, Sugden and Beyersbergen 1986, Greenwood et al. 1995). The dynamic composition of predator communities is a significant obstacle in gaining this understanding (Sargeant et al. 1993). Clark et al. (1995) suggested establishing vigorous stands of natural vegetation only where avian predation occurs. However, Sullivan and Dinsmore (1990) claimed that this practice may not be effective against predation by crows. Erikstad et al. (1982) showed that by removing the offending crows and preventing them from nesting, egg loss of willow ptarmigans was reduced.

Therefore, fields of dense nesting cover should be managed according to the predators present (Millenbach et al. 1996).

Manipulating vegetation by burning

Fire is one management tool for improving wildlife habitat. Kirsch et al. (1973) and Kirsch (1974) proposed periodic burning of grasslands to improve prairie chicken (*Tympanuchus cupido*) and waterfowl habitat by arresting succession (Page and Cassel 1971). To improve nesting habitat, periodic burning is preferred over mowing (Kirsch et al. 1978). Frequency of burns should not exceed every 2 or 3 breeding seasons (Forde et al. 1984). Response of nesting birds to burned areas is species-specific. For instance, sandpipers (*Bartramia longicauda*) nested more successfully in grasslands burned 2 out of 5 years (Kirsch and Higgins 1976).

The timing of the burn also is important. Higgins (1986*b*) recommended burning before May or after July, whenever there are fewer birds breeding. Fall burns produce taller cover and enhance waterfowl productivity (Higgins 1986*b*). Denser regrowth may reduce nest predation through greater concealment (Mankin and Warner 1992). Spring burns decrease species richness and abundance of nongame birds during the year of the burn (Huber and Steuter 1984) or later years (Forde et al. 1984), and destroy most duck nests (Glover 1956, Fritzell 1975).

Burning cover to enhance recruitment of breeding birds may conflict with livestock and agricultural activities. However, this tool could be used well in areas set aside from production, such as low-productive fields, waterfowl production areas, and wildlife refuges. Cost-benefit analysis of burning is not possible because the required information is unavailable.

Manipulating vegetation through grazing

Grazing is often used to reduce litter, improve plant vigor, alter plant species composition (Bowen and Kruse 1993, Johnson et al. 1994), and open up dense monotypic stands (Kantrud 1986). However, it is generally detrimental to nesting birds (Kirsch 1969, Bowen and Kruse 1993, Hothem and Welsh 1994), especially in wetlands and riparian areas (Kirby et al. 1992). Cattle graze and trample protective cover (Gjersing 1975, Ammon and Stacey 1997), and step on nests (Gjersing 1975, Beintema and Müskens 1987, Bowen and Kruse 1993, Hothem and Welsh 1994), and their presence deters nesting birds (Kantrud and Higgins 1992). Some studies found a direct negative correlation between grazing intensity and nest success for teal (*Anas* spp., Glover 1956), bobwhite (Klimstra and Roseberry 1975), and waders (Beintema and Müskens 1987). However, grazing can be beneficial for upland-nesting waterfowl and nongame birds (Kantrud and Higgins 1992). Moderate grazing improved nesting habitat for blue-winged teal (Burgess et al. 1965, Duebbert et al. 1986) and may be beneficial for species that require sparse or low cover such as upland sandpipers (Kirsch and Higgins 1976) and lesser prairie chickens (*Tympanuchus pallidicinctus*, Riley et al. 1992). Although Johnson et al. (1994) found that grazing was detrimental for 14 avian species, it was beneficial for 11 others. Keith (1961), Barker et al. (1990), and Kruse and Bowen (1996) found no effect of grazing on upland-nesting ducks. Intensive browsing by deer on eastern forests has altered the vegetation structure, which has negatively impacted passerine reproduction (DeGraaf et al. 1991).

To decrease negative impacts of grazing on breeding birds, managers should delay grazing until past the peak of hatching (Bowen and Kruse 1993) and incorporate rotational grazing (Gjersing 1975, Mundinger 1976, Duebbert et al. 1986, Messmer and Goetz 1988, Kruse and Bowen 1996). The cost of these practices should be balanced with the potential benefits. Thus far, this cost/benefit information, which is needed by decision makers, is not available.

Landscape and patch manipulation

The effects of habitat loss on breeding birds and their interactions with nest predators and nest parasites in forested systems and grasslands have been extensively reported both in Europe (Beintema and Müskens. 1987, Andrén and Angelstam 1988, Storch 1991, Nour et al. 1993, Huhta 1995) and North America (Cowardin et al. 1985; Robbins et al. 1986; Terborgh 1989; Langen et al. 1991; Patterson 1994; Bethke and Nudds 1995; Greenwood et al. 1995; Beauchamp et al. 1996*a*, 1996*b*; Donovan et al. 1997). At landscape levels, effects result from habitat fragmentation, loss, and conversion. In Canada, waterfowl nest success was correlated to the amount of grassland habitat available and decreased with an increase in the amount of cropland (Greenwood et al. 1987, 1995). Similar results were found by Ball (1996) in the Prairie Pothole Region and by Andrén (1992) for artificial nests in Sweden.

In grassland ecosystems, habitat fragmentation is considered the primary factor in the decline of many bird populations (Johnson and Temple 1986, 1990). However, few studies have examined avian reproductive responses to grassland fragmentation (Burger et al. 1994). As summarized and reported by Clark and Nudds (1991), the evidence for the relationship between nest success and patch size is inconclusive. There are studies that show positive relationships (Johnson and Temple 1986, 1990; Greenwood et al. 1987; Kantrud 1993; Burger et al. 1994), no relationships (Duebbert and Lokemoen 1976, Pasitschniak-Arts and Messier 1996, see Martz 1967 for pair use and Storch 1991, Nour et al. 1993), or negative relationships (Livezey 1981, Gatti 1987, Huhta 1995). Clark and Nudds (1991) suggest that other factors (e.g., effect of concealment and predator species) confound results. Rather than spending resources on untested practices, needed research should parallel management (Clark and Diamond 1993).

Another consideration is the matrix nature of the landscape (Huhta 1995). The shape and spatial arrangement of cover patches also affect bird recruitment. For example, even the most concealed pheasant nests were destroyed (Chesness et al. 1968) and waterfowl nests had one of the lowest nest success rates (Klett et al. 1988, Cowardin et al. 1985, Greenwood et al. 1987) in linear patches such as fence rows and rights-of-way. Opposite results were found by Warner et al. (1987, 1992) for pheasants and for waterfowl by Oetting and Cassel (1971) and Page and Cassel (1971). Local predator composition and abundance, as well as abundance of alternative prey, may have accounted for the differences.

Clark and Diamond (1993) outlined management practices at the landscape level that included increasing the size and density of habitat patches, and reducing patch isolation. However, the limited availability of large patches and the large spatial scale and time frames are difficult management problems to solve. Instead of site-specific efforts, Bethke and Nudds (1995) and Beauchamp et al. (1996*b*) recommend directing efforts toward encouraging extensive management, including the recovery of marginal farmland (Fleskes and Klaas 1991) and alternative farming practices (Warner and Etter 1985). Low-quality agricultural lands are used intensively by many wildlife species (Clark and Diamond 1993).

Conclusions

Productivity of ground-nesting birds can be increased through several nonlethal management techniques. Our review indicates a wide range in the quality and quantity of data accumulated, the success of different methods, and the spatio-temporal applicability of the techniques (Table 4-2). To fill the gaps, much research and experimentation is needed. In some cases, the evidence was weak, and requires more research. It was surprising that in most studies (Table 4-1) the effectiveness of the technique used was not evaluated in terms of cost per additional young produced, which is ultimately the common currency that wildlife managers will use when choosing competing techniques. This information is needed.

There are no panaceas for the problem of reducing predation on nesting birds. Instead, most techniques could be applied only under limited conditions and were designed to target a specific array of species. For instance, individual nests of shorebirds on sandy beaches were successfully protected with a simple fence around each scattered nest, colony-nesting terns were protected with electrified fences, prairie-nesting dabbling ducks were protected with larger electrified fences around upland dense nesting cover, mallards responded well to nesting baskets installed in wetlands, and artificial islands worked best for mallards and gadwalls (Table 4-1).

Because of this, no management practice is uniformly better than another for boosting bird recruitment. In fact, it appears that the different techniques are complementary rather than exclusive. Managers need to select the best technique based on the species that needs protection, predator community, local topography and area, and other management goals and constraints. Ideally, the decisions should be based on cost/benefit analysis of producing an additional young (Lokemoen 1984). We believe that with little research, but well-designed experiments and by adjusting the techniques available to other scenarios and different species, a much larger array of species could be helped to boost their recruitment.

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Table 4-1. Summary of information on studies using fences, nesting baskets, artificial islands, fenced and moated peninsulas to improve nest success on ground-nesting birds. The effectiveness column shows the method used to measure effectiveness and the data comparing control vs. treatment. Lokemoen et al. (1982), Greenwood et al. (1990), Lokemoen and Woodward (1993), and LaGrange et al. (1995) controlled predators in their experimental sites.

Species	Location	Protected unit	Costs/unit ($)	Effectiveness	Life expectancy	Authors
SIMPLE FENCES						
Pectoral sandpiper	Alaska	1 nest	4.00 (materials)	Daily surv. rate 0.717 vs 0.982	1 season	Estelle et al. 1996
Piping plover	Massachus.	1 nest	15.00	Chicks fledged/pair 0.12 vs 1.96	1 season	Melvin et al. 1992
Piping plover	Massachus.	1 nest	50.00	% Nests hatched 25 vs 92	1 season	Rimmer and Deblinger 1990
Killdeer	Ontario	1 nest	not provided	% Successful nests 70.6 vs 33.3	1 season	Nol and Brooks 1982
Seaside sparrow	Florida	1 nest	not provided	% Successful nests 5.8 vs 47.6	1 season	Post and Greenlaw 1989
ELECTRIFIED FENCES						
Sandwich tern	UK	1 colony	not provided	No. nesting pairs 80 vs 450	1 season	Foster 1975

Table 4-1. (Continued).

Species	Location	Protected unit	Costs/unit ($)	Effectiveness	Life expectancy	Authors
Sandwich tern+eiders	UK	1 colony	not provided	Kept foxes out	1 season	Patterson 1977
Piping plover	N. Dakota	95 nests (6.8 ha)	810.00 (materials)	Mayfield nest succ. 0.27 vs 0.41 Chicks fledged/pair 0.66 vs 1.00	3 seasons	Mayer and Ryan 1991
Dabbling ducks	N. Dakota	1 nest	not provided	% Successful nests 21.2 vs 72.7	1 season	Sargeant et al. 1974
Dabbling ducks	N. Dakota	45 ha	not provided	Nests/ha 0.38 vs 0.83 Successf. nests/ha 0.05 vs 0.11	3 seasons	Arnold et al. 1988
Dabbling ducks	N. Dakota	8.6 ha	1.44/m (total) 0.65/additnl. young	Nest success 45 vs 65 Chicks/ha 12.0 vs 19.8	20 years	Lokemoen et al. 1982
Dabbling ducks	Minnesota	17.0 ha	1.84/m (total) 0.87/additnl. young	Nest success 16.5 vs 54.0 Chicks/ha 3.2 vs 10.1	20 years	Lokemoen et al. 1982

Table 4-1. (Continued).

Species	Location	Protected unit	Costs/unit ($)	Effectiveness	Life expectancy	Authors
Dabbling ducks	N. Dakota	40 ha	4,500 (1989 mat. costs) for a-16.2-ha fence)	Nest success 7 to 36	not provided	Greenwood et al. 1990
Mallard	Iowa	19 ha	7,240 (1985 mater.+labor)	Nest success 14 vs 39	not provided	LaGrange et al. 1995
Blue-W. teal	Iowa	19 ha	7,240 (1985 mater.+labor)	Nest success 14 vs 30	not provided	LaGrange et al. 1995
NESTING BASKETS						
Mallard	Prairie Poth. Reg.	NA	1.48/duckling (1974 prices)	Production of 2.6 ducklings/basket/y	20 years	Doty et al. 1975
ARTIFICIAL ISLANDS						
Gadwall	Saskatch.	0.03 ha	not provided	Nest densi. 62/ha Nest success 65	not prov.	Hines and Mitchell 1983
Mallard	N. Dakota	0.0025 ha	50.00 31.25/ducklg.	Nest succ. 38 to 52 0.8ducklings/island	15 years	Higgins 1986a

Table 4-1. (Continued).

Species	Location	Protected unit	Costs/unit ($)	Effectiveness	Life expectancy	Authors
PENINSULAS WITH ELECTRIC FENCES						
Dabbling ducks	N. Dakota	not prov.	1,259 22.2/duckl.	Nest succ. 17 vs 54 Duckl/ha 1.9 vs 17.6	20 years	Lokemoen and Woodward 1993
PENINSULAS WITH MOATS						
Dabbling ducks	N. Dakota	not prov.	18,944 114.8/duckl.	Nest succ. 14 vs 75 Duckl/ha 1.2 vs 21.8	50 years	Lokemoen and Woodward 1993

Table 4-2. Applicability of different techniques to improve recruitment in ground-nesting birds.

Management technique	Time span	Spatial extent	Type of evidence	Quality of evidence	Likelihood of success
Exclusion with fences	1 - >15 yrs	Nest/patch/ site	Experimental	Good	High
Construction of nesting structures	>15 yrs	Nest	Experimental	Good	High
Construction of islands and peninsulas	>20 yrs	Patch	Experimental	Good	High
Conditioned-taste-aversion	Days - months	Patch/site	Experimental	Poor	Low
Fertility control for predators	1 - few yrs	Site	Untested	Proposed	Unknown
Changing the predator community	1 - several yrs	Landscape	Correlational/ experimental	Poor	Low
Protective umbrella or associational defense	Weeks	Site/ landscape	Experimental	Good	Low
Providing alternative prey to predators	Weeks - months	Site	Correlational/ experimental	Poor	Low
Improving cover	Months - yrs	Patch/ landscape	Correlational/ experimental	Good	Low

Table 4-2. (Continued).

Management technique	Time span	Spatial extent	Type of evidence	Quality of evidence	Likelihood of success
Burning	1 - several yrs	Patch/ landcape	Correlational/ experimental	Poor	Low
Grazing	Weeks - yrs	Patch/ landscape	Correlational/ experimental	Poor	Low
Landscape/patch manipulation	Several yrs	Landscape	Observational	Poor	Unknown

CHAPTER 5

CONCLUSIONS

Concern exists regarding long-term decline of dabbling duck populations in North America. One of the main causes for this decline is the steady decline in nest success of ducks on their main breeding grounds, the grassland and wetland complexes of the Prairie Pothole Region of North America (PPR). Almost invariably, studies have shown that the low nest success of prairie-nesting ducks is due to intense predation on the nests and incubating hens. Two major factors seem to have converged to produce the low nest success documented. The landscape in the PPR has been converted almost entirely to intensive agricultural production, leaving only few and scattered habitat patches that dabbling ducks use for nesting. Thus, most of the nesting habitat is gone, and what is left is extremely fragmented. The second factor is the increase in numbers and in range expansion of several generalist and medium-sized carnivores, which apparently have taken advantage of the human-altered landscape, and the resources provided by farming activities. Hence, nesting hens in the PPR face two main problems: lack of habitat and a landscape swamped by efficient nest predators.

The working hypothesis of wildlife managers is that ducks concentrate their nests in high densities in small patches of planted nesting cover, and that these nest concentrations attract predators to these patches. Another hypothesis is that dense nesting cover, which attracts nesting hens, will decrease predation, either by deterring predators to enter and forage in patches with that vegetation, or by decreasing their foraging efficiencies.

The main predictions derived from these hypotheses are that: (1) nest predation is density dependent. Patches with higher nest density should show lower nest success;

(2) given that larger patches would allow hens to disperse their nests, predation should be lower in larger patches; and (3) that predation should be lower in patches with denser cover. The evidence to support the predictions derives from a few studies that have produced contradictory results. A series of variables that might have added to the discrepancy is often mentioned but rarely quantified. The most quoted are the effects of density of predators, predator species present at the sites, and the abundance of alternative prey for predators. Here, the predictions are that nest success would be higher in patches with fewer predators (abundances and number of species) and with higher abundances of alternative prey. These assumptions are so often cited, mentioned, and even used to manage duck recruitment, without much base, that they have became a paradigm ingrained in the literature and in the manager's mind.

I evaluated the relationship of these variables at the level of the habitat patch, considering all of them simultaneously. I analyzed each one while accounting for the effect of the others. My results did not agree with any of the predictions, and therefore I rejected the hypotheses proposed. Nest success, as a consequence of intense predation, was generally low. Although it was highly variable both in space and time, nest success was unrelated to patch size, nest density, predator abundance, predator richness, height of vegetation cover, obstruction to movement of vegetation, and abundances of two types of alternative prey (small mammals and insects).

To have a better understanding of the process of predation on nests, which might be operating at another spatial scale, I examined the effect of 14 variables on the probability of a nest to be depredated. At the spatial scale of the nest and its neighborhood I quantified the effect of predator abundance at the site, the presence/absence of each of the five main carnivores at the site, nest concealment, heterogeneity of the vegetation around the nest, vegetation types at the nest, distance to potential sources of predators, such as wetland meadows and man-made edges, nest initiation date, and each of the six duck species involved. Variables unrelated to nest predation risk included vegetation type and heterogeneity at and around the nest, distance of a nest to an edge, and the presence or absence of skunks and badgers at the site. The effect of presence/absence of foxes, raccoons, and minks was significant, but opposite for the two years considered, and therefore, the pattern was inconsistent. Nests established late in the season, closer to a wetland, at spots with low vegetation cover, and on sites with abundant nest predators had higher probabilities of being depredated. As repeatedly reported, duck species showed different predation vulnerabilities, likely associated to species-specific ecological differences.

The height of the vegetation cover and the abundance of predators at the habitat patch level had different effects on nest success than at the nest level. Effects of these variables were detected only at the latter level. This is unfortunate, because at that small spatial scale, no management option is feasible.

For the reasons already explained, I failed to build a predictive model to explain nest success at the patch level. Apparently, the lack of pattern in the analysis was due to too much variability in the data, at two spatial and at two temporal scales. Here, there is room to speculate on the potential effects of variables not considered, complex indirect effects, concentration of wetlands, and landscape matrix. However, approached from a traditional perspective (i.e., using variables already thought to be affecting nest vulnerability), the evidence points out that predation on nests is extremely complex. It appears that we do not even have a grasp of how it operates, what are the scales, and the factors involved in determining nest vulnerability to predation.

My findings, in addition to the extreme variability on nest predation observed, indicate that so far, management actions intended to help duck recruitment have no scientific basis. Given that we cannot generalize, not even across years, I feel that the current management options for upland nesting waterfowl, when applied, are, at best, educated guesses, set in practice based on trial and error. Some of them, such as the effect of patch size and edge effects, based mainly on experiments with artificial nests mimicking passerine bird nests in forested landscapes, may also be misleading. Predation on nests in grasslands appears different than in forests. The facile solutions often proposed (i.e., improving nesting cover), according to my results, are a waste of resources.

In spite of the above, we have to keep in mind that my conclusions are based on correlations and associations, and do not imply causality. We need better and more reliable knowledge. I strongly agree with a few previous studies, which emphasize the need of well-designed experiments. Otherwise, if managers keep applying the same untested "management techniques," it is likely that duck populations will continue declining as tax dollars are wasted.

APPENDIX

Table A-1. Plant species detected on the study sites during the breeding season of 1998.

COMMON NAME	*SCIENTIFIC NAME*	NELSON S	NELSON N	EIDNESS	SEITZ	GETTE	MELLIN	BABCOCK	HALL	HOWS	EDWARDS	POLLESTAD	PUNG	STINKEOWAY	STORLIE	THORSON	WENGLER W
ALFALFA	*Medicago sativa*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
HOP CLOVER	*Trifolium agrarium*														x		
SWEET CLOVER	*Melilotus spp.*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
WHITE CLOVER	*Trifolium repens*					x	x		x						x		
RED CLOVER	*Trifolium pratense*														x		
PURPLE PRAIRIE CLOVER	*Dalea purpurea*												x		x		
AMERICAN VETCH	*Vicia americana*				x			x			x	x					
AMERICAN LICORICE	*Glycyrrhiza lepidota*	x					x	x					x		x	x	x
SILVERLEAF SCURFPEA	*Psoralea argophylla*												x				
SMOOTH BROME	*Bromus inermis*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
KENTUCKY BLUEGRASS	*Poa pratensis*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
SWITCHGRASS	*Panicum spp.*					x	x		x			x		x	x	x	x
WHEATGRASS	*Agropyron spp.*	x				x	x		x	x	x	x	x	x	x	x	x
QUACKGRASS	*Agropyron repens*										x	x			x	x	
CREEPING FOXTAIL	*Alopecurus arundinaceus*														x	x	
ORCHARD GRASS	*Dactylis glomerata*														x		
GREEN MUHLY	*Muhlenbergia spp.*										x				x	x	
REED CANARYGRASS	*Phalaris arundinacea*					x		x	x			x		x	x	x	
GREEN NEEDLEGRASS	*Stipa viridula*												x		x	x	
PRAIRIE CORDGRASS	*Spartina pectinata*							x							x	x	
FOXTAIL BARLEY	*Hordeum jubatum*	x	x	x	x	x	x		x		x				x		
MUSK THISTLE	*Carduus nutans*	x				x	x		x	x	x	x	x	x	x	x	x
SOWTHISTLE	*Sonchus arvensis*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
CANADA THISTLE	*Cirsium arvense*	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
BULL THISTLE	*Cirsium vulgare*		x	x	x	x		x	x	x		x	x	x	x		
WHITE COCKLE	*Lychnis alba*					x	x										
YELLOW GOATSBEARD	*Tragopogon major*	x	x	x	x	x	x	x	x		x		x	x	x	x	x
DAISY FLEABANE	*Erigeron strigosus*	x		x				x					x		x	x	
COMMON CHICORY	*Cichorium intybus*		x	x	x	x	x		x	x			x	x		x	
WHITE ASTER	*Aster ericoides*						x			x					x	x	x
ASTER	*Aster spp.*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
BLACK-EYED SUSAN	*Rudbeckia hirta*			x		x	x	x		x		x			x	x	x
PRAIRIE-CONEFLOWER	*Ratibida spp.*			x			x	x		x	x		x			x	
COMMON YARROW	*Achillea millefolium*				x		x	x	x	x	x		x				
STINGING NETTLE	*Urtica dioica*	x			x	x			x		x					x	
STIFF SUNFLOWER	*Helianthus rigidus*						x								x	x	
ABSINTH WORMWOOD	*Artemisia absinthium*			x	x	x	x	x	x	x	x	x	x	x	x	x	x
WHITE SAGE	*Artemisia ludoviceana*				x									x			
SMART WEED	*Polygomum spp.*								x						x		
THIMBLE WEED	*Anemone virginiana*						x								x	x	
CURLY DOCK	*Rumex crispus*	x	x			x	x		x		x	x			x	x	x
WILD MUSTARD	*Brassica kaber*				x	x	x	x	x						x	x	x
SHOWY MILKWEED	*Asclepias speciosa*			x	x		x	x	x		x	x	x			x	
MILKWEED	*Asclepias spp.*	x	x	x	x		x		x		x				x	x	x
GOLDENROD	*Solidago spp.*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
BLUEBELL	*Campanula rotundifolia*												x				
WOOD LILY	*Lilium philadelphicum*			x													
FIELD BINDWEED	*Convolvulus arvensis*		x	x	x												x
FIELD MINT	*Mentha arvensis*			x			x		x	x				x			
LEAFY SPURGE	*Euphorbia esula*	x		x		x					x				x	x	
FIELD PENNY	*Thlaspi arvense*						x										
EVENING-PRIMROSE	*Oenothera biennis*		x				x										
PRAIRIE WILD ROSE	*Rosa arkansana*	x	x					x	x	x		x	x				
COMMON RAGWEED	*Ambrosia artemisiifolia*			x													
COMMON PLANTAIN	*Plantago major*			x	x							x			x		x
YELLOW LADY SLIPPER	*Cypripedium calceolus*			x				x					x		x		
WESTERN SNOWBERRY	*Symphoricarpos occidentalis*			x	x			x	x	x	x		x			x	x
DOGWOOD	*Cornus spp.*				x			x		x	x			x	x	x	
RUSSIAN OLIVE	*Eleagnus angustifolia*	x		x	x	x		x	x		x		x				x
SIBERIAN ELM	*Ulmus pumila*					x			x		x						
CARAGANA	*Caragana arborescens*					x										x	
WILLOW	*Salix spp.*	x	x	x		x	x	x	x	x	x	x	x		x	x	x
WINTERBERRY	*Ilex verticillata*					x											
QUAKING ASPEN	*Populus tremuloides*												x				
COTTONWOOD	*Populus deltoides*	x	x				x	x	x	x		x	x	x		x	
GREEN ASH	*Fraxinus pennsylvanica*					x											
WILD PLUM	*Prunus spp.*		x				x	x	x			x				x	x

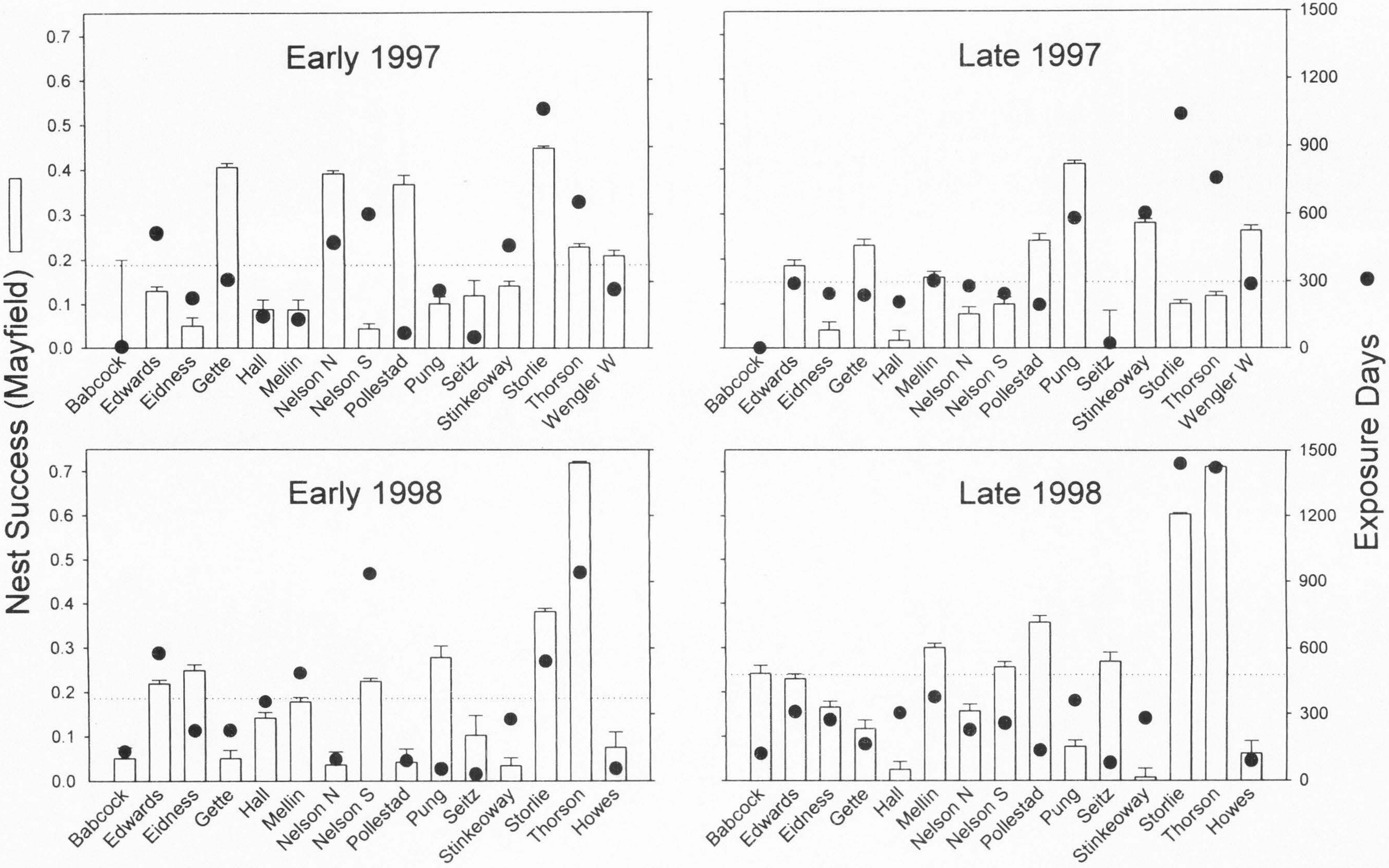

Figure A-1. Nest success of ducks in North Dakota by site and year, during early and late breeding seasons. Shown are means and 1 SE. The dotted line indicates the mean nest success among sites.

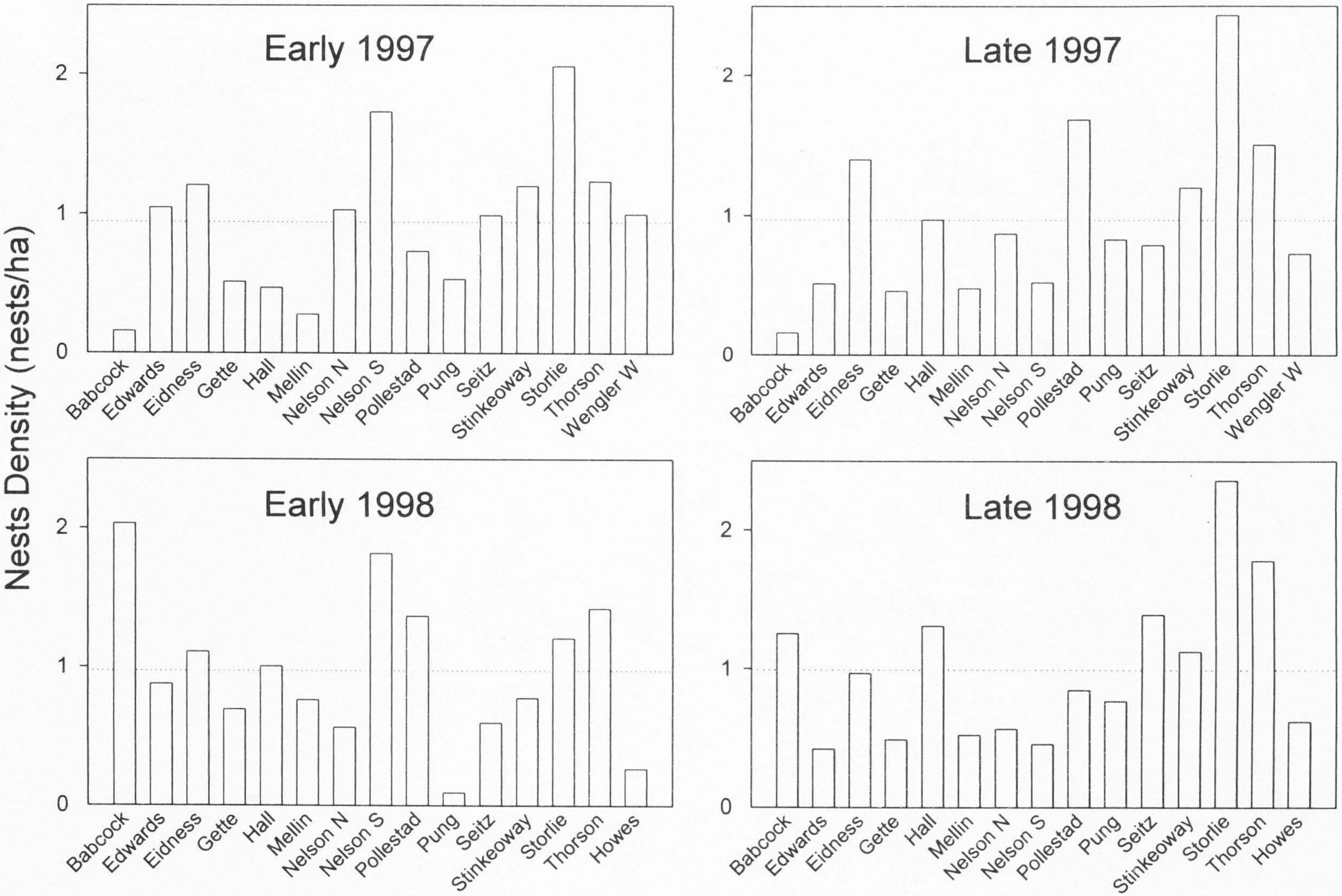

Figure A-2. Density of duck nests found in North Dakota by site and year, during early and late duck breeding seasons. The dotted line indicates the mean among sites.

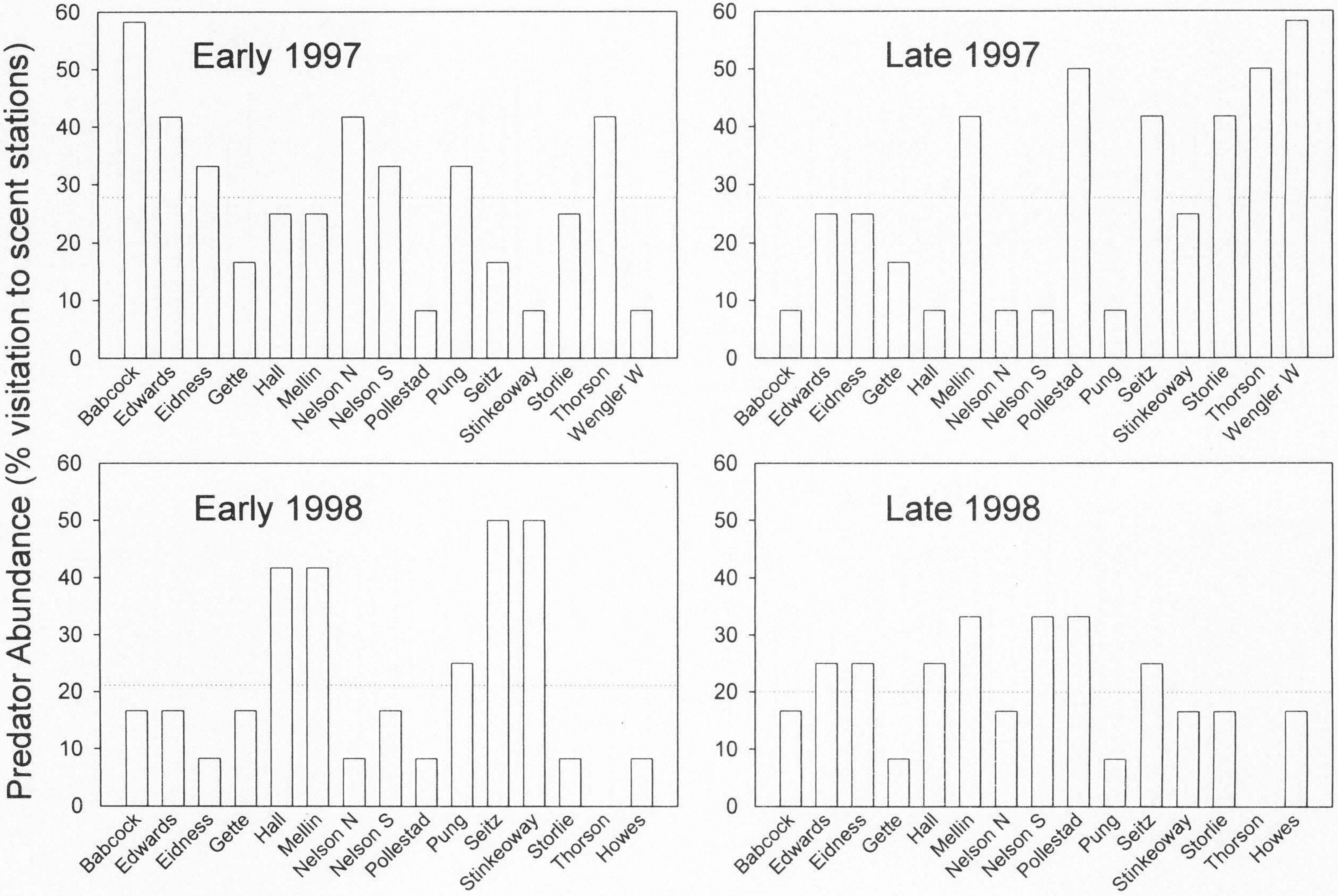

Figure A-3. Predator abundance in North Dakota by site and year, during early and late duck breeding seasons. The dotted line indicates mean abundances among sites.

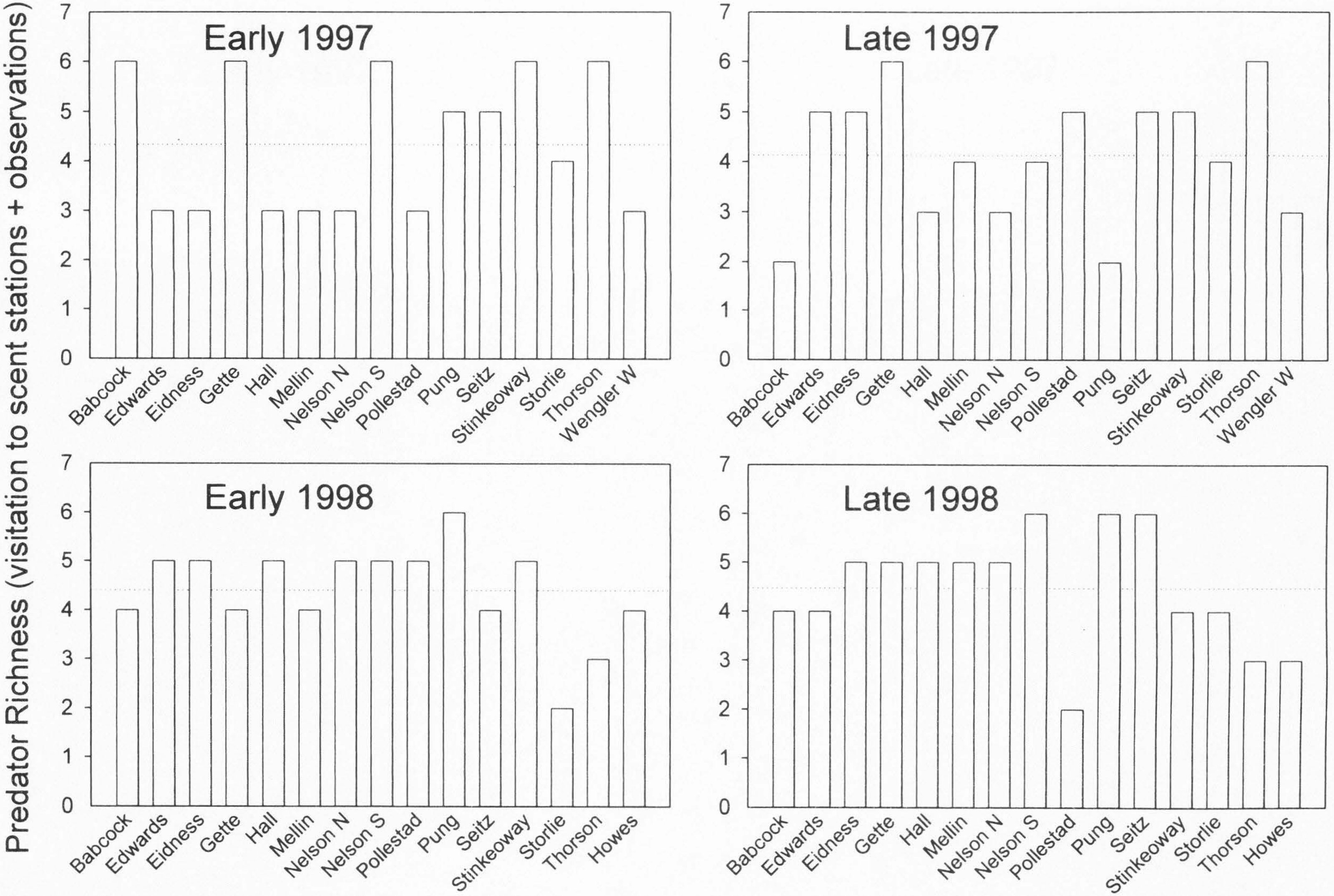

Figure A-4. Predator richness in North Dakota by site and year, during early and late duck breeding seasons. The dotted line indicates mean abundances among sites.

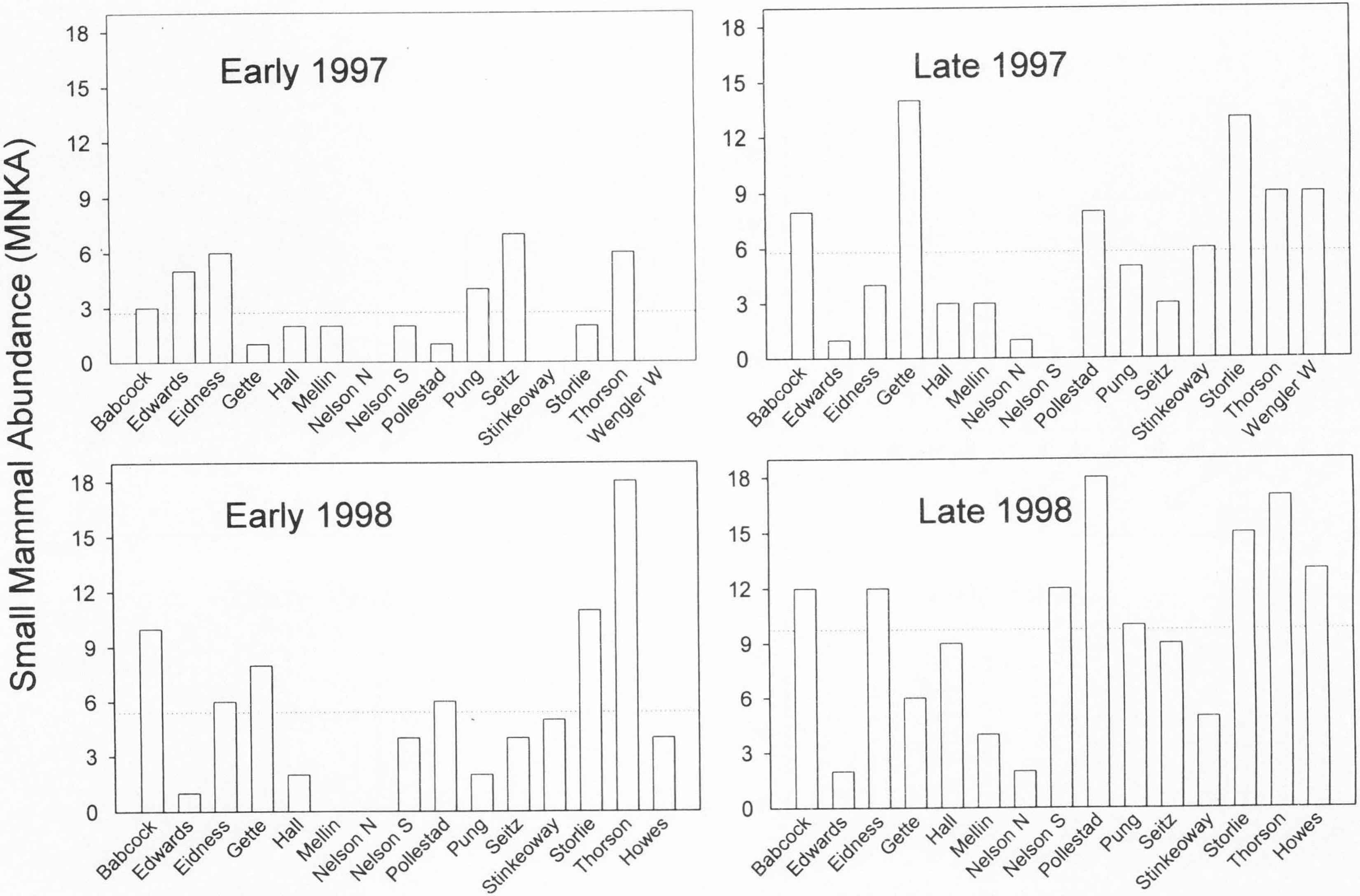

Figure A-5. Small mammal abundance (estimated as the minimum number known alive) in North Dakota by site and year during early and late duck breeding season. The dotted line indicates the mean among sites.

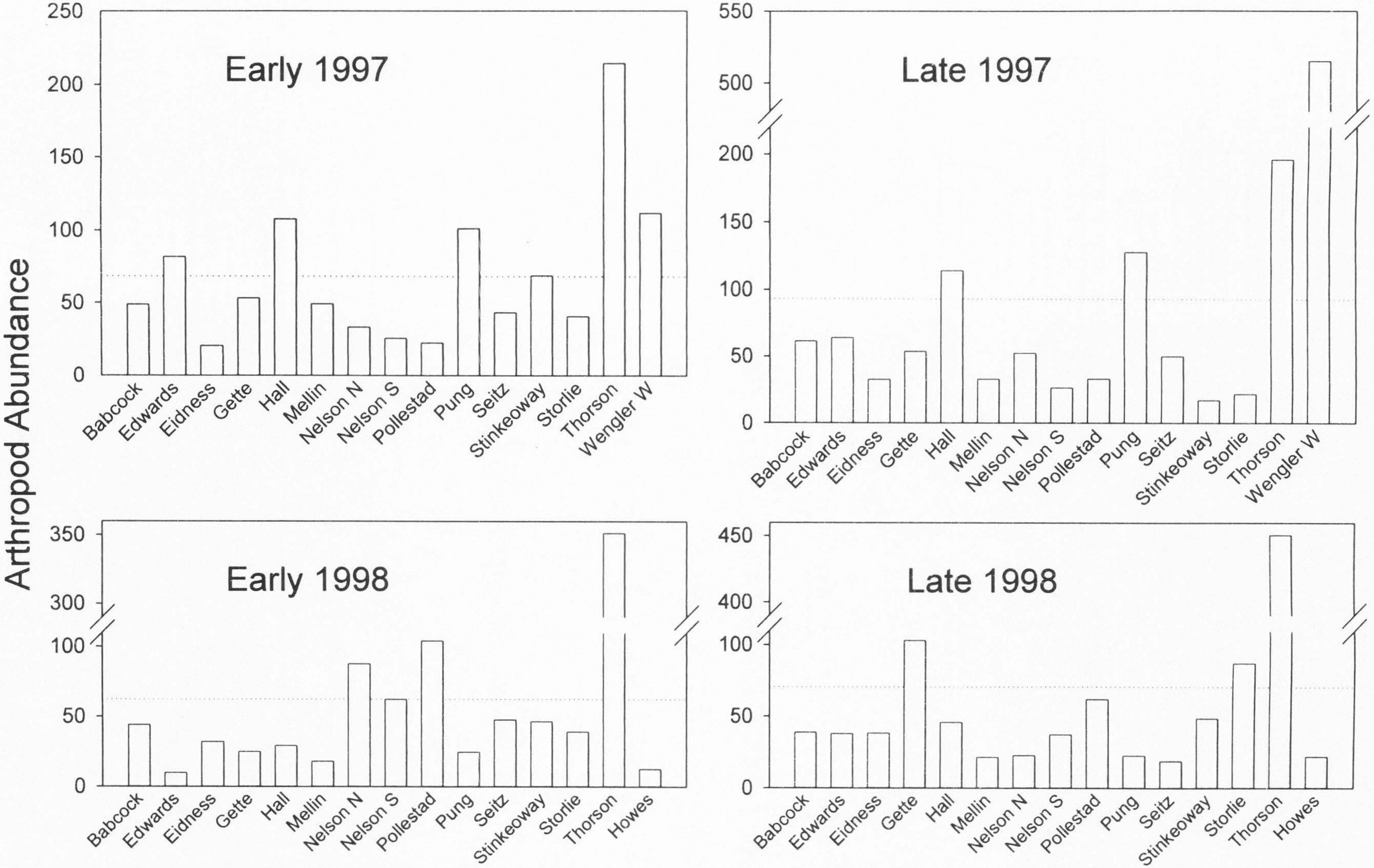

Figure A-6. Arthropod abundance (estimated as the numbers caught in pit-fall traps) in North Dakota by site and year during early and late duck breeding season. The dotted line indicates the mean among sites.

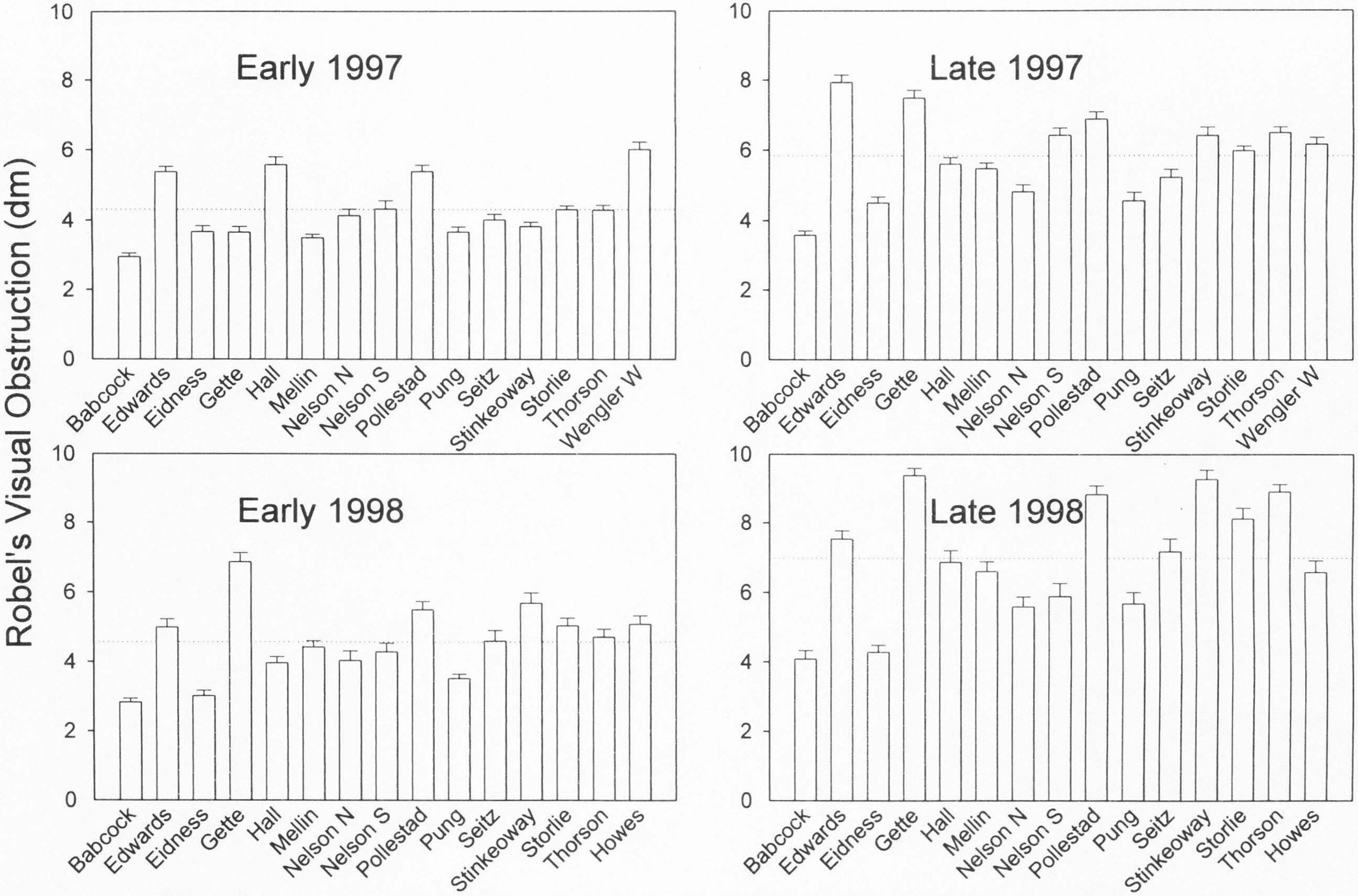

Figure A-7. Visual obstruction of the vegetation in North Dakota by site and year during early and late duck breeding season. Shown are means and 1 SE. The dotted line indicates the mean among sites.

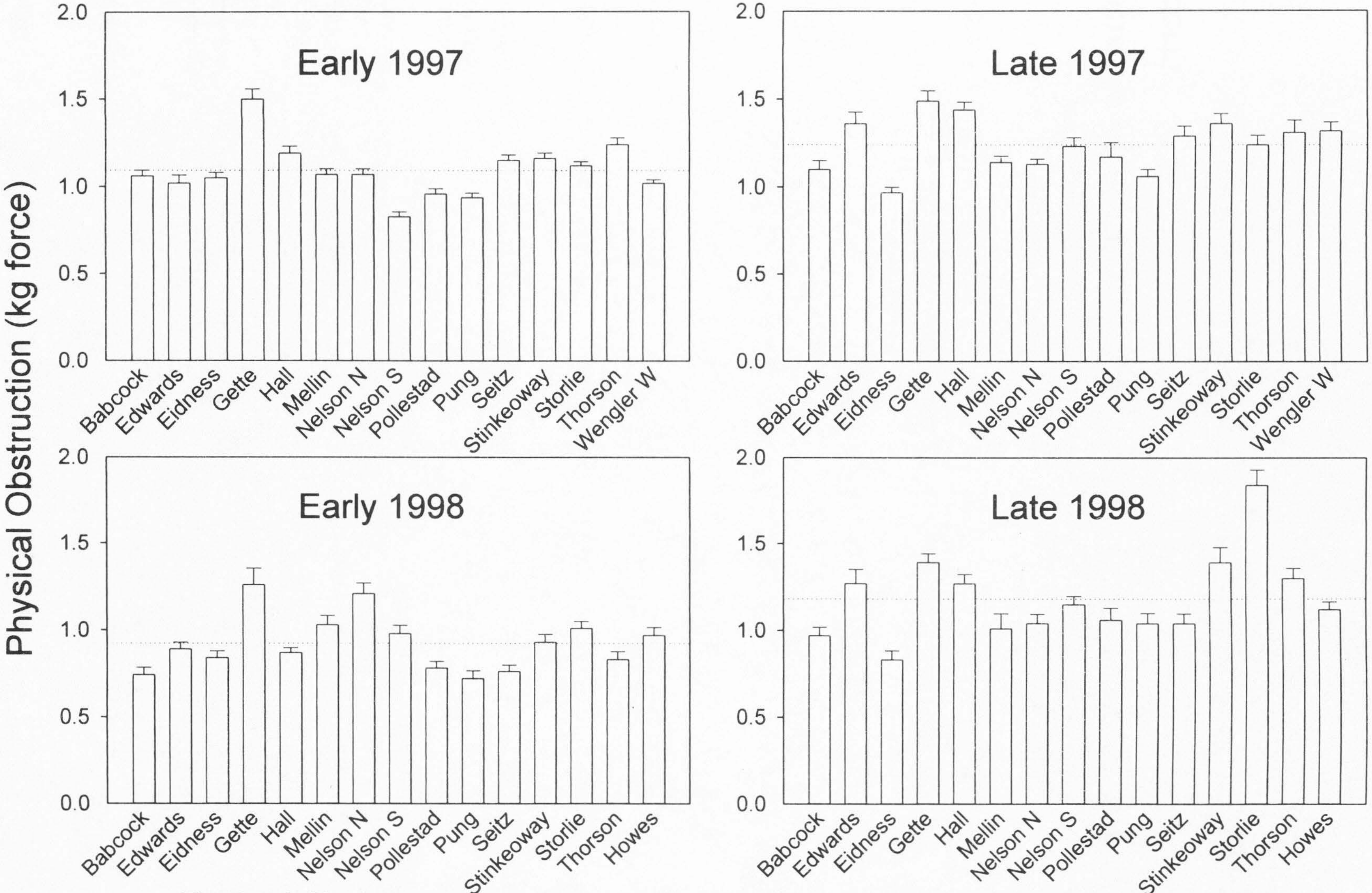

Figure A-8. Physical obstruction of the vegetation in North Dakota by site and year during early and late duck breeding season. Shown are means and 1 SE. The dotted line indicates the mean among sites.

CURRICULUM VITAE

Jaime Enrique Jiménez

COLLEGE EDUCATION

1979--1984: Licenciatura degree (similar to a M. S.) in Biological Sciences. Faculty of Biological Sciences, Catholic University of Chile, Santiago. Chile. Supervisors Drs. F. M. Jaksić and J. C. Castilla. Thesis title: "[Behavioral ecology of three sympatric buteonine hawks in central Chile]."

1990--1993: Master of Science. Department of Wildlife and Range Sciences, University of Florida, Gainesville. Supervisors: Drs. K. H. Redford, P. Feinsinger, L. C. Branch, M. E. Sunquist, and R. A. Kiltie. GPA 4.00/4.00. Thesis title: "Comparative ecology of *Dusicyon* foxes at the Chinchilla National Reserve in northcentral Chile."

1993–1999: Ph. D. in Wildlife Ecology in the Department of Fisheries and Wildlife, Utah State University. Supervisors: Drs. R. D. Dueser, M. R. Conover, J. A. Bissonette, T. A. Messmer, E. W. Schupp, and F. H. Wagner. GPA 3.79/4.00. Dissertation title: "Nest success of dabbling ducks in a human-modified prairie: effects of predation and habitat variables at different spatial scales."
In addition, completed 8 extra-curricular courses both in Chile and abroad.

HONORS AND PRIZES

At the Catholic University was honored by the president's fellowship for excellency of performance as undergraduate student and was later awarded a graduate scholarship. Was also awarded 3 fellowships to travel abroad and a first prize in photography.

Received a Fulbright, LASPAU (Latin American Scholarship for American Universities), and an AmCham (American Chamber of Commerce) graduate scholarship for two years to study in the U. S. and a graduate scholarships from the Program for Studies in Tropical Conservation and from the Tropical Conservation and Development Program, both of the University of Florida.

At Utah State University received a Quinney Ph. D. fellowship, fellowships from the Graduate School, the Ecology Center, and the Jack Berryman Institute to study in the Department of Fisheries and Wildlife. Was named to the School of Graduate Studies Honor Roll.

LANGUAGES

Spanish is my native language. I read, write, and speak english and german with fluency.

PROFESSIONAL SOCIETIES

Currently belongs to 12 professional societies (including COS, WOS, AOU, AFO, NOS, RRF, TWS, ASM, SCB, ESA) and to Sigma Xi. Is a member of the IUCN/SSC Deer Specialist group.

RESEARCH AND TEACHING APPOINTMENTS

Was appointed as research affiliate and later as research associate at the Department of Ecology, Catholic University of Chile, Santiago, Chile. Was PI of: "The Chilean chinchilla conservation project (WWF-1297)" for almost 4 years; "Predation by foxes (*Dusicyon* spp.) and the last wild chinchillas in Chile," and "Responses of pudus (*Pudu puda*) to human disturbances in Neotropical temperate rainforests," both funded by the Lincoln Park Zoo Scott Neotropic Fund; "Nest success of dabbling ducks in a human-modified prairie: effects predation and habitat variables at different scales." Participated as co-PI in: 2 projects on the Darwin's fox; a third on predator guild dynamics and a fourth on the coexistence of two sympatric foxes. Also participated as research assistant in 7 other projects, and as collaborator in 4. Was teaching assistant in 4 courses and was invited lecturer in 3 other courses. In addition, was teaching assistant in Conservation Biology at University of Florida, Gainesville.

PROFESSIONAL CONSULTING, ADVICE, AND FIELD GUIDANCE

Worked 6 times as scientific advisor (to set up exhibits, in environmental education, for television and newspaper series), 4 times as consulting assistant for environmental impact assessment throughout Chile and once consulting for the Virginia Museum of Natural History, Virginia.

CONGRESSES, WORKSHOPS, AND SYMPOSIA

Co-organized the "[First Workshop for the Evaluation of the Chilean Chinchilla Conservation Project]" at the National Chinchilla Reserve, Illapel, Chile. Co-authored and presented 12 papers to Chilean and international meetings.

REVISION OF MANUSCRIPTS FOR PROFESSIONAL JOURNALS AND PROPOSALS

Served as a reviewer of manuscripts for the following professional journals:

- Biological Conservation (United Kingdom)
- Condor (USA)
- Ecotrópicos (Venezuela)
- El Hornero (Argentina)
- Journal of Field Ornithology (USA)
- Journal of Raptor Research (USA)

Revista Chilena de Historia Natural (Chile)
Vida Silvestre Neotropical (Costa Rica)
Wilson Bulletin (USA)
...and reviewed proposals for COLCIENCIAS (Colombia's NSF).

CHAPTER OF BOOKS

01) Jaksić, F. M., J. A. Iriarte, and J. E. Jiménez. 1999. The raptors of Torres del Paine National Park: their ecology, community structure, and trophic guilds. In A Patagonia Gem, the Ecology and Natural History of a World Biosphere Reserve: Torres del Paine National Park, Chile. W. L. Franklin and W. E. Johnson, editors. (In press).

PUBLICATIONS, PAPERS, AND MANUSCRIPTS IN PROCESS

01) Jiménez, J., and R. Rageot. 1979. [Notes on the biology of the "monito del monte" (*Dromiciops australis* Philippi 1893)]. Anales del Museo de Historia Natural de Valparaíso (Chile) 2:83-88.

02) Jaksić, F. M., and J. E. Jiménez. 1986. The conservation status of raptors in Chile. Birds of Prey Bulletin 3:95-104.

03) Jaksić, F. M., and J. E. Jiménez. 1986. Trophic structure and food-niche relationships of Nearctic and Neotropical raptors: an inferential approach. Proceedings of the International Ornithological Congress (Ottawa, Ontario, Canada) 19:2336-2347.

04) Jaksić, F. M., R. Rozzi, A. Labra, and J. E. Jiménez. 1987. The hunting behavior of Black-shouldered Kites (*Elanus caeruleus leucurus*) in central Chile. Condor 89:907-911.

05) Jiménez, J. E. 1987. [Relative efficiency of six trap types for live trapping of small mammals, with emphasis on *Chinchilla lanigera*]. Medio Ambiente (Chile) 8:104-112.

06) Medel, R. G., J. E. Jiménez, S. F. Fox, and F. M. Jaksić. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. Oikos 53:321-324.

07) Jiménez, J. E., and F. M. Jaksić. 1988. Ecology and behavior of southern South American Cinereous Harriers, *Circus cinereus*. Revista Chilena de Historia Natural 61:199-208.

08) Iriarte, J. A., J. E. Jiménez, L. C. Contreras, and F. M. Jaksić. 1989. Small-mammal availability and consumption by the fox, *Dusicyon culpaeus*, in central Chilean scrublands. Journal of Mammalogy 70:641-645.

09) Jiménez, J. E., and F. M. Jaksić. 1989. Biology of the Austral Pygmy-owl. Wilson Bulletin 101:377-389.

10) Jiménez, J. E. 1989. [Use of the smoked-card technique for the effectivity testing of small mammal baits, with emphasis on *Chinchilla lanigera*]. Medio Ambiente (Chile) 10:84-91.

11) Jiménez, J. E., and F. M. Jaksić. 1989. Behavioral ecology of Grey Eagle-buzzards, *Geranoaetus melanoleucus*, in central Chile. Condor 91:913-921.

12) Medel, R. G., J. E. Jiménez, J. L. Yáñez, J. J. Armesto, and F. M. Jaksić. 1990. Discovery of a continental population of the rare Darwin's Fox, *Dusicyon fulvipes* (Martin, 1837) in Chile. Biological Conservation 51:71-77.

13) Jaksić, F. M., J. E. Jiménez, R. G. Medel, and P. A. Marquet. 1990. Habitat and diet of Darwin's Fox (*Pseudalopex fulvipes*) on the Chilean mainland. Journal of Mammalogy 71:246-248.

14) Jiménez, J. E., and F. M. Jaksić. 1990. Diet of Gurney's Buzzard in the Puna of northernmost Chile. Wilson Bulletin 102:344-346.

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16) Jiménez, J. E., and M. Lorca. 1990. [American trypanosomiasis in wild vertebrates and its relationship with the vector *Triatoma spinolai*]. Archivos de Medicina Veterinaria (Chile) 22:171-183.

17) Castro, S. A., J. E. Jiménez, and F. M. Jaksić. 1991. Diet of the racerunner *Callopistes palluma* in north-central Chile. Journal of Herpetology 25:127-129.

18) Jiménez, J. E., and F. M. Jaksić. 1991. Behavioral ecology of Red-backed Hawks in central Chile. Wilson Bulletin 103:132-137.

19) Jiménez, J. E., P. A. Marquet, R. G. Medel, and F. M. Jaksić. 1991. Comparative ecology of Darwin's fox (*Pseudalopex fulvipes*) in mainland and island settings of southern Chile. Revista Chilena de Historia Natural 63:177-186.

20) Jaksić, F. M., J. E. Jiménez, S. A. Castro, and P. Feinsinger. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia 89:90-101.

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22) Pavéz, E. F., C. A. González, and J. E. Jiménez. 1992. Diet shifts of Black-chested Eagle (*Geranoaetus melanoleucus*) from native rodents to European rabbits.

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25) Jiménez, J. E., and F. M. Jaksić. 1993. Observations on the behavioral ecology of Harris' Hawk in central Chile. Journal of Raptor Research 27:143-148.

26) Jiménez, J. E. 1993. Notes on the diet of the Aplomado Falcon (*Falco femoralis*) in northcentral Chile. Journal of Raptor Research 27:161-163.

27) Jiménez, J. E., and F. M. Jaksić. 1993. [Seasonal diet of the Austral Pygmy-owl (*Glaucidium nanum*) in Chile, and its relationship to prey abundance]. El Hornero (Argentina) 13:265-271.

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30) Jiménez, J. E. 1995. [Natural history of the Red-backed Buzzard *Buteo polyosoma*: a review]. El Hornero (Argentina) 14:1-9.

31) Jiménez, J. E. 1995. Conservation of the last wild chinchilla (*Chinchilla lanigera*) archipelago: a metapopulation approach. Vida Silvestre Neotropical 4:89-97.

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Juniper Mountain, southeastern Oregon. Great Basin Naturalist 57:74-78.

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38) Jiménez, J. E. Accepted. Effect of sample size, plot size, and observation time on assessment of avian diversity and abundance in a Neotropical temperate rainforest. Journal of Field Ornithology.

39) Jiménez, J. E. In review. Continued decline of wild chinchillas: the hypothesis of predation by foxes and the role of protection. Biological Conservation.

40) Jiménez, J. E., and M. R. Conover. Submitted. Analysis of non-lethal methods to reduce predation on ground-nesting birds and their nests. Wildlife Society Bulletin.

41) Jiménez, J. E., M. R. Conover, T. A. Messmer, and R. D. Dueser. Submitted. Effects of environmental variables on prairie duck nest success: a multivariate approach at the landscape level. Ecological Applications.

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43) Jiménez, J. E. In preparation. Importance of habitat variables on the spatial distribution of the endangered wild chinchilla (*Chinchilla lanigera*).

44) Jiménez, J.E. In preparation. Convergence in the ecology, behavior, and morphology of small forest ruminants: predictions for the Southern pudu, *Pudu puda* (Artiodactyla, Cervidae).