The validity of using artificial nests to assess nest-predation rates in prairie nesting ducks
by Michael A Butler

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Artificial nests have been used in numerous studies of nest success because they provide adequate sample sizes and can be placed according to experimental designs. However, concerns regarding the validity of their use in studying avian nesting ecology have been raised. For the use of artificial nests to be valid, nest success for artificial and natural nests must be strongly correlated. Additionally, increased knowledge of factors that affect artificial-nest survival would be useful. If correlates of survival can be identified, further refinement of the technique may be possible, thus improving its performance. Therefore, I conducted research to evaluate the validity of the artificial-nest technique by comparing rates of artificial- and natural-nest success, examining characteristics of artificial-nest predation, and evaluating the effects of corvid abundance and nest vegetation on artificial-nest survival.

I estimated survival of artificial ($n = 1,210$) and natural ($n = 1,318$) nests of upland-nesting waterfowl at 16 sites across northern Montana, in a variety of habitats, and over 2 nesting seasons. Correlations between artificial- and natural-nest success estimates were highly variable by year and habitat type (e.g., all nests from 1993 and 1994: $R2 = 0.20$, $P = 0.08$; nests in planted nesting cover in 1994: $R2 = 0.87$, $P = 0.02$; nests in native grass cover in 1993 and 1994: $R2 = 0.01$, $P = 0.86$). Thus, artificial nest success was not consistently correlated to natural nest success in all habitats or years. Artificial nests were depredated at a higher rate during daylight hours than at night ($t = -4.93$, $P < 0.0001$), were depredated at a higher rate during the first 10 days of exposure ($P < 0.005$), and were depredated less as the nesting season progressed (Log-rank test, $P = 0.0007 - 0.07$). Corvid abundance and nest vegetation were not good predictors of nest survival (logistic regression fit = 0.1127).

My results indicated that artificial nests may lead to erroneous conclusions regarding nest survival. Thus, I conclude that (1) the technique should not be used for upland-nesting ducks in the mid-continent and (2) researchers working in other areas/species should evaluate the usefulness of the technique over the range of habitats and nest-success rates they wish to consider.

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of

Master of Science

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Fish and Wildlife Management

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

May 1996

APPROVAL

of a thesis submitted by

Michael A. Butler

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

This project, by nature, was logistically difficult, and would not have been possible without the cooperation of many people. Dr. Jay Rotella, with his guidance, knowledge, and patience, was instrumental to my personal success, and that of this project. The members of my committee, Dr. Andy Hansen and Dr. Bob White, provided advice and review of this thesis. I thank The Rob and Bessie Welder Wildlife Foundation staff for their encouragement and funding for this project

Dr. I. J. Ball of the Montana Cooperative Wildlife Research Unit (MCWRU) provided wisdom and advice regarding the artificial-nest technique. Tom Fondell (MCWRU), Steve Martin (Benton Lake NWR), Fritz Prellwitz (Bowdoin NWR), Ted Gutski (Medicine Lake NWR), Mike Rabenburg (Medicine Lake NWR), and Terry Lonner and Shawn Bayless of Montana Fish Wildlife and Parks provided access to research sites, nesting-waterfowl data, housing, and equipment. Dr. Dan Gustafson provided graphical assistance and programming assistance with data analyses. Special thanks go to my field assistants, Toby Swank and Julie Arrington, for their dedication and hard work.

I would also like to thank my colleagues and office mates of Montana State University for their discussion and debate of ideas concerning wildlife biology and my project. Lastly, I thank my parents for their continued love, support, and belief in me, and my ability to turn my dreams into reality.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

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My results indicated that artificial nests may lead to erroneous conclusions regarding nest survival. Thus, I conclude that (1) the technique should not be used for upland-nesting ducks in the mid-continent and (2) researchers working in other areas/species should evaluate the usefulness of the technique over the range of habitats and nest-success rates they wish to consider.

CHAPTER 1

INTRODUCTION

Since the late 1960's, numerous species of migrant birds have significantly declined in number (Bohning-Gaese et al. 1993). This trend has been corroborated by a number of studies investigating continental bird-population trends (Kerlinger and Doremus 1981, Robbins et al. 1989, Terborgh 1992, Bohning-Gaese et al. 1993). Understandably, avian ecologists have attempted to identify environmental factors that might be responsible for these declines. Factors such as habitat loss and fragmentation resulting from intensive agriculture, suburban development, and urbanization, as well as increased nest depredation and parasitism are widely thought to contribute to population declines (Kerlinger and Doremus 1981, Robbins et al. 1989, Bohning-Gaese et al. 1993). However, it is difficult to evaluate how these factors affect avian population dynamics. Most avian ecologists agree that these factors lower the productivity of populations of birds (Robbins et al. 1989, Bohning-Gaese et al. 1993).

In avian populations, a common measure of reproductive productivity is recruitment rate, which can be defined as the number of young females in the fall population divided by the number of adult females in the spring population (Cowardin and Blohm 1992). Because nest success is one of the most important factors affecting recruitment rates of birds, biologists have sought nest-success information for many species (Ricklefs 1969, Martin and Guepel 1993). However, estimating nest success is typically problematic because nesting studies are expensive, time consuming, and logistically troublesome (Hammond and Forward 1956, Klett and Johnson 1982). Additionally, when working with natural nests it is difficult to meet the demands of experimental designs required for tests of many hypotheses (e.g., distance from edge of a habitat patch vs. nest success) (Rearden 1951, Balser et al. 1968, Willebrand and Marcstrom 1988). This has prompted many researchers to use artificial nests when studying nest success and associated factors (Henry 1969, Kurnat 1991, Burger et al. 1994, Thurber et al. 1994, Haskell 1995b).

Although artificial nests have been used often to test hypotheses and to develop management recommendations (Angelstam 1986, Yahner and Cypher 1987, Burger et al. 1994), concerns exist about the validity of inferences drawn from artificial-nest studies (Martin 1987, Storass 1988, Willebrand and Marcstrom 1988, Haskell 1995a). The greatest concerns regard inconsistencies and differences in the rates at which artificial and natural nests are depredated.

Surprisingly, only a few studies have attempted to explain why artificial nests experience different rates of depredation than natural nests (e.g., Storass 1988, Willebrand and Marcstrom 1988, Kulesza 1980, Kurnat 1991, Guyn and Clark In Press). For these reasons, I designed nest experiments to investigate these concerns.

Chapter 2 of this thesis addresses whether artificial-nest success can be used as a valid index to natural-nest success. If the artificial-nest technique is to be used validly, it must be shown that the most critical assumption of the technique is met: that nest success estimates from artificial nests and the natural nests they are designed to mimic are highly correlated. Chapter 3 addresses the effects of nest vegetation and corvid abundance on artificial-nest survival. Nest vegetation and corvid abundance have been identified as 2 factors that may influence nest survival, and I attempt to develop a model that will predict artificial-nest survival. Chapter 4 is an overall discussion of my research conclusions.

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CHAPTER 2

THE VALIDITY OF USING ARTIFICIAL NESTS TO ASSESS NEST-PREDATION RATES IN PRAIRIE-NESTING DUCKS

Introduction

Because nest success is one of the most important factors affecting recruitment rates of birds, biologists have sought nest-success information for many species for a wide variety of uses (Ricklefs 1969, Martin and Guepel 1993). However, estimating nest success is typically problematic because nesting studies are expensive, time consuming, and logistically troublesome (Hammond and Forward 1956, Klett and Johnson 1982). Additionally, when working with nests, it is difficult to meet the demands of experimental designs required for tests of many hypotheses (e.g., distance from edge vs. nest success) (Rearden 1951, Balser et al. 1968, Willebrand and Marcstrom 1988). Collectively, the restrictions associated with nesting studies have prompted many researchers to use artificial nests when studying nest success and associated factors (Henry 1969, Kurnat 1991, Burger et al. 1994, Thurber et al. 1994, Haskell 1995b).

By using artificial nests, investigators are able to achieve necessary sample sizes of nests at locations dictated by experimental designs. Research on artificial nests requires less expense, time, equipment, and manpower than conventional nesting studies (Storass 1988). Finally, nest-initiation dates, destruction dates, and population sizes are known, providing higher precision when estimating artificial-nest success.

Although artificial nests have been used often to test hypotheses and to develop management recommendations (Angelstam 1986, Yahner and Cypher 1987, Burger et al. 1994), concerns exist about the validity of inferences drawn from these studies (Martin 1987, Storass 1988, Willebrand and Marcstrom 1988, Haskell 1995a). Storass (1988) stated that the relationship between depredation of natural and artificial nests has not been properly evaluated. Similarly, Willebrand and Marcstrom (1988) noted that results of artificial-nest studies are often used without determining whether they are similar to results of studies of natural nests.

Results of studies that have examined the strength of the correlation between survival rates of artificial and natural nests are variable and conflicting. Chesness et al. (1968), Gottfried and Thompson (1978), Gotmark et al. (1990), and Kurnat (1991) found depredation rates of artificial and natural nests to be similar. However, Balser et al. (1968), Dwernychuk and Boag (1972), Martin (1987), Storass (1988), Willebrand and Marcstrom (1988), and Guyn and Clark (In Press) found depredation rates for artificial and natural nests to be markedly different.

Similarly, the relationship between vegetative structure and nest success has also been shown to vary for artificial and natural nests. Dwernychuk and Boag (1972) and Storass (1988) found nest concealment to have no effect on natural-nest success, but reported a positive relationship between nest concealment and artificial-nest success. However, Guyn and Clark (In Press) found no relationship between nest concealment and artificial-nest survival and a positive relationship between nest concealment and natural-nest success. Dwernychuk and Boag (1972) felt that the effect of nest concealment on survival differed for the 2 nest types because vegetation disturbance advertised artificial-nest locations to sight-oriented predators (e.g., corvid and larid species). Additionally, they felt that the lack of a relationship between nest concealment and natural-nest success resulted from the presence of the hen and her maintenance of concealing nest cover at the nest site. Storass (1988) hypothesized that differences in the effect of nest vegetation on survival were a result of the type of nest predator attracted to each nest type. He concluded that nest concealment of artificial nests was an important factor affecting survival when the primary predator was avian, but that odor associated with natural nests was an important factor affecting survival when the primary predator was mammalian. Willebrand and Marcstrom's (1987) results supported Storass' (1988) hypothesis that artificial nests are more vulnerable to avian depredation and natural nests are more vulnerable to mammalian depredations by finding their artificial nests eaten by corvids and natural nests eaten by mammals. Additionally, Guyn and Clark (In Press) found their nest predators to be mammalian, and observed no relationship between nest concealment and artificial-nest success.

Given potential differences between artificial- and natural-nest success and the factors affecting their survival, it appears that artificial nests may be inappropriate for evaluating natural-nest success. However, for the technique to be useful, it is not necessary for the 2 types of rates to be similar. Rather, it is necessary only for there to be a consistent and known relationship between survival of artificial and natural nests on the area of interest. Surprisingly, this relationship has not been properly evaluated (Storass 1988). Given the experimental advantages that the artificial-nest technique provides, I designed this study to further investigate the validity of using artificial-nest success as an index to natural-nest success in waterfowl and to evaluate the possible effect of vegetation density on nest success.

Specifically, I tested for a consistent relationship between survival rates of artificial and natural nests using duck nests. I chose duck nests because: (1)

there are important landscape-level hypotheses regarding duck population dynamics that can be tested with artificial nests (Clark and Nudds 1991) and (2) duck nests can be found, with great effort, in large enough samples to properly evaluate the relationship between the 2 nest types. To increase the inference space of the results, I tested the relationship over a broad geographic area on sites having a wide range of nest-success rates and 2 different habitat types.

To determine the possible effect of vegetation density on nest success, I investigated the relationship between vegetation density and artificial- and natural-nest success. I also discuss potential impacts of other ecological factors on nest survival.

Study Areas

I selected 4 study areas across the state of Montana (Fig. 1). The Ninepipe study area (47^{0}26’N, 114^{0}7’W), Benton Lake National Wildlife Refuge (NWR) (47^{0}40’N, 111^{0}20’W), Bowdoin NWR (48^{0}25’N, 107^{0}41’W), and Medicine Lake NWR (48^{0}28’N, 104^{0}26’W) were selected to ensure variation in nesting habitats, geographic regions, and predator communities. All study areas had a semi-arid continental climate.

Within study areas, I selected research sites (Fig. 1) based upon historical densities of nesting waterfowl and habitat abundance. The Ninepipe

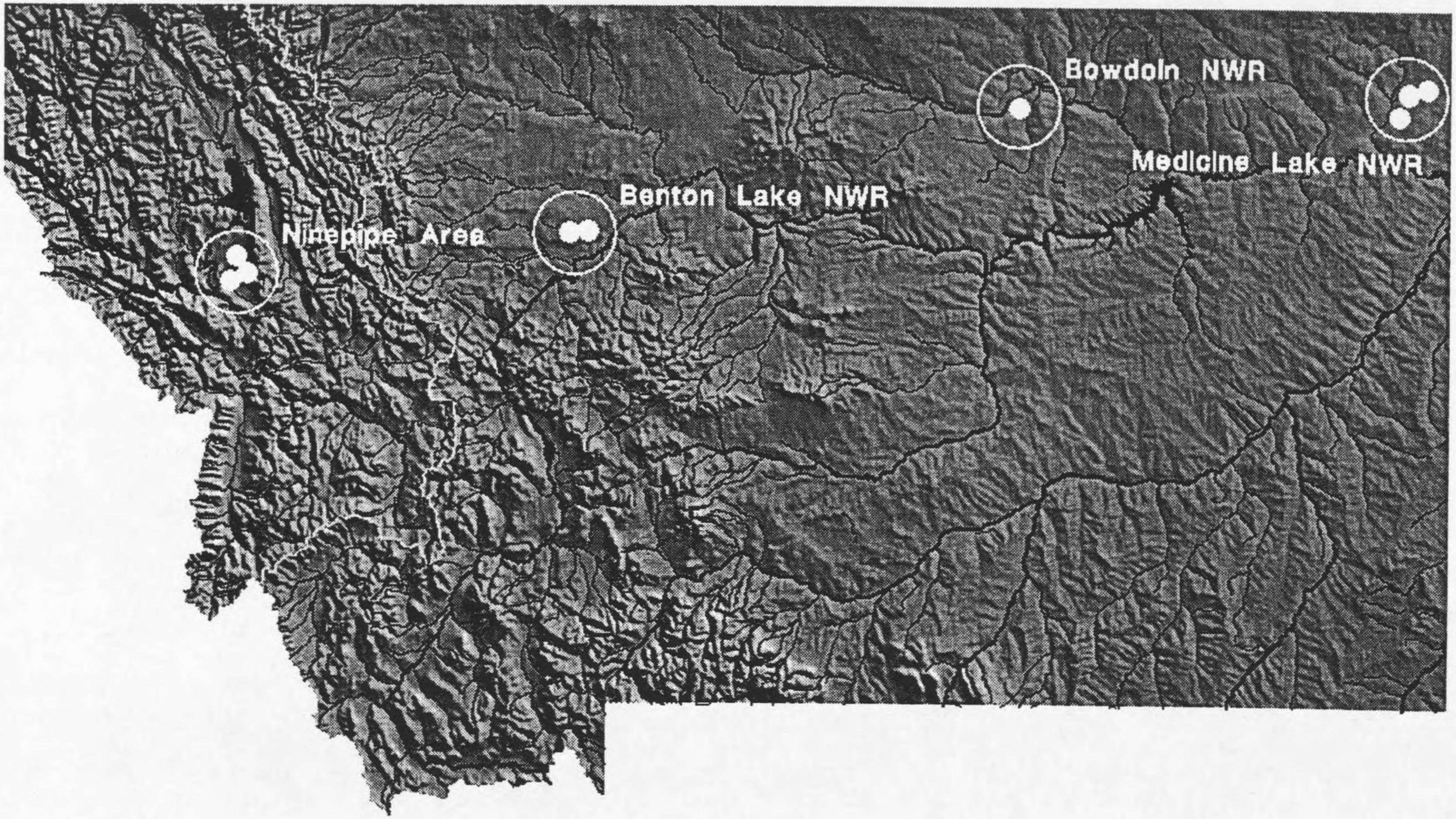

Figure 1. Study areas and research sites used for comparing survival rates of artificial and natural nests of ducks in northern Montana, 1993-1994.

area contained 3 sites (Sandsmark and North Kicking Horse Waterfowl Production Areas [WPA], Sloan Lake private lands project), Benton Lake NWR contained 2 sites, Bowdoin NWR contained 1 site, and Medicine Lake NWR contained 3 sites (Homestead NWR, Medicine Lake dense-nesting cover [DNC], and Medicine Lake native short-grass prairie [NGS]). I evaluated nest success of artificial- and natural-duck nests for 2 habitat types during both field seasons: planted DNC and NGS. Although I attempted to locate and use equal numbers of DNC and NGS research sites, actual numbers were determined by availability of sites and logistical feasibility with respect to scheduling placement of artificial nests and conducting searches for duck nests. In 1993, 6 DNC sites and 3 NGS sites were chosen. In 1994, 5 of the 6 DNC and 2 of the 3 NGS sites from the 1993 field season were chosen. The 2 sites were dropped in 1994 because small samples of duck nests were found at these sites in 1993.

Primary species composition of vegetation in DNC was quackgrass; western, crested, intermediate, and tall wheatgrasses (*Agropyron spp.*); orchard grass (*Dactylis glomerata*); alfalfa (*Medicago sativa*); sweet clover (*Melilotus officinalis*); smooth brome (*Bromus inermis*); and cheatgrass (*Bromus tectorum*). Primary species composition of NGS was western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), green needlegrass (*Stipa virdula*), needle-and-thread (*Stipa comata*), fringed sagebrush (*Artemisia frigida*), silver sagebrush (Artemisia cana), greasewood (Atriplex patula), and prairie junegrass (Koeleria cristata).

All study areas contained ephemeral, temporary, seasonal, semipermanent, and permanent wetlands (Stewart and Kantrud 1971). Lokemoen (1966) likened the Flathead Valley to pothole habitat in the prairie pothole region of Canada. All other areas were characterized by permanent ponds and lakes, and large managed wetland blocks. Benton Lake NWR, Bowdoin NWR, and Medicine Lake NWR contained alkali ponds and lakes.

Methods

Data Collection

Artificial nests. A circuit of placement and retrieval for artificial nests was coordinated for all research sites across Montana. In 1993 and 1994, 3 placement circuits of 20 nests/site/circuit were made. Thus, each site received 60 artificial nests, which were placed as 3 replicates of 20 nests. Placement of artificial nests began at the western-most study area (Ninepipe) and continued eastward until all artificial nests were placed. During subsequent placement circuits, previously placed nests were retrieved prior to placing a new sample of 20 nests. One placement circuit (i.e., placement of artificial nests across the state from west to east) took approximately 14-16 days. New artificial-nest locations were randomly selected during each circuit. In 1993, nest placement began on 7 May and retrieval concluded on 22 July. In 1994, nest placement began on 12 May and retrieval concluded on 8 August.

Specific artificial-nest locations for the 3 replicates of 20 nests were determined by randomly selecting nest locations from within each research site. I overlaid a grid of 1-hectare plots onto aerial photos of DNC and NGS polygons for each research site, orientated the grid along cardinal directions, and fixed 1 corner of the grid in the south-westernmost corner of each site which caused some 1-hectare plots to fall along habitat edges. In this way, grid placement allowed some nests to fall near edges where depredation may be higher (Gates and Gysel 1978, Yahner and Wright 1985, Ratti and Reese 1988, Angelstam 1986). I randomly selected 20 plots from each grid and placed 1 artificial nest in the center of each plot. A plot center was located using the aerial photo, grid, measurements, and landmarks in the field. If the center of a selected plot was outside the research-site boundary, in water, or on other unsuitable habitat (e.g., rock), that plot was excluded and another plot was randomly selected. I placed only 1 artificial nest/plot to avoid potential density-dependent increases in depredation rates of nests (Goransson et al. 1975, Sugden and Beyersbergen 1986).

Artificial nests were designed to simulate upland-nesting duck nests in the laying stage. An artificial nest consisted of 1 chicken egg dyed to resemble a mallard (Anas platyrhynchos) or gadwall (A. strepera) egg, duck nesting down, a timer device (Ball et al. 1994), and a nest marker. Timers recorded the exact time of destruction for each nest, and necessitated the use of 1 egg/nest. Markers used to identify nest locations were identical in type and placement to those used in marking natural-duck nests (Picozzi 1975). I used 2 types of nest markers: cut willows (Salix spp.), and orange plot flags.

Twenty-one days after placement, I revisited each artificial nest, determined its fate (e.g., successful or destroyed), and, if necessary, recorded time to nest destruction. After all nesting data were recorded, fragments of destroyed nests, whole eggs of survived nests, and all nesting materials were removed from each nest location.

Natural-duck nests. Samples of upland-nesting duck nests were found in DNC and NGS using the cable-chain drag method described by Klett et al. (1986). Nest drags were conducted by U.S. Fish and Wildlife personnel and technicians during the spring and summer months of 1993 and 1994. A series of ≥ 3 drags took place during both years of the study. In 1993, drags began between 29 April and 14 May and nest rechecks were concluded by 27 July. During 1994, drags began between 30 April and 26 May and rechecks were concluded by 29 July. Once a nest was located, its status was checked every 7-12 days until destruction or hatching occurred. Data recorded during nest visits included nest initiation date, status of the nesting hen (if seen), status of the nest, stage of incubation, presence/absence of parasitic eggs, species, habitat, clutch size, fate of nest, and if necessary, the cause of nest failure, and vegetation type (DNC or NGS). A nest was considered successful if $\geq$ 1 egg hatched (Klett et al. 1986).

Vegetation measurements. Upon placing an artificial nest, I used Robel et al.'s technique (1970) to measure height and density of vegetation in each cardinal direction at each artificial-nest site. These four measurements were then used to calculate a mean vegetative height-density (MVHD) measurement for each nest site. Nest-site MVHD measurements were then used to calculate a research-site MVHD. Because artificial-nest locations were randomly selected, vegetation measurements taken at nest locations provided a random sample of the MVHD for each research site, habitat type, and year. Thus, I used MVHD measurements to investigate changes in vegetation between habitat types and years and to explore relationships between research-site MVHD and nest success.

Predator-community composition. I estimated the presence/absence of species of mammalian predators at each research site using scent stations (Roughton and Sweeny 1982). In 1993 and 1994, transects of scent stations were placed on the shoulder of refuge and county roads that bordered research sites. Each transect was 4.8 km long, consisted of a scent station placed on alternating sides of the road every 0.48 km, and contained 10 scent stations. I placed scent tablets at stations in the late afternoon and checked for tracks at first light the following day. I attempted to place scent stations each day, however weather conditions limited scent station samples to 269 stations in 1993 and 110 stations in 1994.

In 1994, I also estimated avian-nest predator abundance using roadside point-count surveys (Ralph et al. 1993). Point-count transects were established on the same roads used for scent-station transects. A point-count transect consisted of 25 point-count stations, each spaced 0.16 km apart. Thus, each point-count transect was 4 km long. At each point, observers recorded all species within and outside of a 50-m radius circle. Each count lasted 5 minutes, and birds were identified by visual characteristics, flight characteristics, and vocalizations. An attempt was made to visually confirm all birds identified by vocalizations. All point-counts were conducted in conjunction with scent station checks and began at first light. A complete list of potential nest predators was compiled from scent-station data, point-count surveys, and observations made by refuge trapping personnel.

Data Analysis

Nest success. I estimated survival of artificial nests by research site and vegetation type using the binomial method (White and Garrot 1990: 208). Daily-survival rates were obtained by taking the twenty-first root of each nest-success estimate (21 days was the maximum number of days that an artificial nest was exposed to possible depredation). Daily-survival rates were then raised to the thirty-fifth power (on average a mallard takes 35 days to lay and incubate a typical clutch of eggs, Bellrose 1980) to produce an artificial-nest success estimate comparable to duck-nest success estimates.

Nest-success estimates for duck nests were calculated using Mayfield's (1961, 1975) method as modified by Johnson (1979). I used SAS (SAS Institute, Inc. 1989) and code written by the Northern Prairie Wildlife Research Unit to calculate the estimates and associated 95% confidence intervals for each habitat type and research site possible.

Changes in artificial- and natural-nest success between years (e.g., 1993 and 1994) were compared using paired t-tests. I used the arcsine square-root transformation to normalize the distributions of nest-success estimates (Zar

1984: 239). Additionally, I used a t-test to determine if the mean change in nest success between years, for both artificial and natural nests, was similar. I considered all differences to be significant at $P \leq 0.10$.

Artificial- and duck-nest mortality resulting from activities of researchers and/or managers ranged from actual crushing of a nest to inadvertent flooding of nest sites. For both nest types, these nest destructions resulted in removal of the affected nest(s) from samples. Presence of parasitic eggs also led to exclusion of duck nests from samples.

Vegetation analyses. I pooled MVHD measurements from all artificial-nest sites within habitat types and years. I used a Wilcoxon matched-pairs test (Conover 1980: 280) to test for differences in MVHD between years, and I determined differences between mean DNC and NGS MVHD using a t-test. I considered differences to be significant at $P \leq 0.10$.

Correlation of artificial- and natural-nest success. I used correlation analysis to determine if artificial-nest success can be used as a valid index to duck-nest success using STATISTICA's correlation subroutine (StatSoft, Inc. 1994). An overall analysis was performed using artificial- and duck-nest success estimates for all research sites and vegetation types. Subsequent analyses divided nest success estimates by year, habitat type, and a year-habitat type combination. A correlation was considered to be significant at $\underline{P} \leq 0.10$.

In all correlation analyses, nest-success estimates were treated as having no associated variances. Thus, only the point estimates for nest success were used. Because I placed and knew the fate of each artificial nest, I censused rather than sampled their fates. Therefore, no estimates of variance were applied to artificial-nest success. If duck-nest success variances were included, the strength of any correlation between artificial- and duck-nest success estimates would be weakened. This approach provides correlation results representing the maximum number of possible correlations and mimics the way all previous reports of the relationship have been reported (Kurnat 1991, Guyn and Clark In Press).

Vegetation correlation analysis. I also used correlation analysis to investigate the relationship between research-site MVHD and nest success of artificial and natural nests. An overall analysis was performed using research-site MVHD and nest success for artificial and natural nests. Subsequent analyses were conducted on data from each year. Correlation analysis was conducted using STATISTICA's correlation subroutine (StatSoft, Inc. 1994), and correlations were considered to be significant at $\underline{P} \leq 0.10$.

Results

During 1993-1994, I placed 1,210 artificial nests. Nesting histories were available for 1,318 upland-nesting duck nests over the same time period. Nests were well dispersed among years, research sites, and habitat types (Table 1). Nests were found and monitored for American green-winged teal (Anas crecca), American wigeon (Anas americana), blue-winged teal (Anas discors), canvasback (Aythya valisineria), cinnamon teal (Anas cyanoptera), gadwall, lesser scaup (Aythya affinis), mallard, northern pintail (Anas acuta), northern shoveler (Anas clypeata), and redhead (Aythya americana). Gadwall nests were the most abundant, accounting for 43% and 31% of all duck nests found across the state of Montana in 1993 and 1994, respectively (Table 2). Mallard nests were the second most abundant, accounting for 17% and 27% of all duck nests found in 1993 and 1994, respectively. Northern shoveler nests were the third most abundant, accounting for 15% of all nests found in both 1993 and 1994.

Nest success

Nest-success rates ranged widely for both artificial (0.08 - 0.80) and natural nests (0.23 - 0.80) (Table 1). Additionally, differences between paired estimates of artificial- versus natural-nest success were highly variable. For

Table 1. Nest success for artificial and upland-nesting duck nests monitored at 9 research sites across northern Montana, 1993-1994.

		1993					1994				
		Artificial		Natural			Artificial		Natural		
Research Site	Habitat Type[a]	n	Success	n	Success	95% CI	n	Success	n	Success	95% CI
Sandsmark WPA[b]	DNC	52	0.19[c]	166	0.46[d]	0.37-0.57	60	0.67	263	0.58	0.50-0.67
North Kicking Horse WPA	DNC	53	0.18	44	0.25	0.14-0.45	62	0.52	35	0.29	0.16-0.54
Sloan Lake	DNC	57	0.25	24	0.26	0.12-0.54	NE[e]	NE	NE	NE	0.68-0.93
Benton Lake NWR[f]	DNC	56	0.80	190	0.69	0.61-0.79	127	0.71	77	0.80	0.68-0.93
Benton Lake NWR	NGS	60	0.41	36	0.27	0.14-0.50	60	0.39	25	0.74	0.52-1.00
Bowdoin NWR	NGS	55	0.08	39	0.57	0.40-0.81	55	0.43	54	0.61	0.45-0.82
Homestead NWR	DNC	60	0.43	73	0.39	0.27-0.57	60	0.62	155	0.69	0.59-0.80
Medicine Lake NWR	DNC	55	0.39	46	0.23	0.12-0.42	61	0.52	58	0.24	0.14-0.41
Medicine Lake NWR	NGS	20	0.49	33	0.72	0.53-0.96	NE	NE	NE	NE	NE

[a] DNC=planted dense-nesting cover, NGS=native short-grass prairie.

[b] Waterfowl production area.

[c] Binomial estimator used (White and Garrot 1990).

[d] Mayfield estimator used (Johnson 1979).

[e] NE=no estimate for this year.

[f] NWR=national wildlife refuge.

Table 2. Percent composition of duck species' nests by research site for 9 research sites across northern Montana, 1993-1994.

		% composition in 1993 (n = 651)							% composition in 1994 (n = 668)						
Research Site	Habitat Type[a]	Mall[b]	Gadw[c]	Nosh[d]	Nopi[e]	Amwi[f]	Teal[g]	Divers	Mall	Gadw	Nosh	Nopi	Amwi	Teal	Divers
Sandsmark WPA[h]	DNC	30	26	19	4	3	13	5	51	14	11	3	5	10	6
N. Kicking Horse WPA	DNC	39	26	12	0	7	16	0	41	15	15	0	9	17	3
Sloan Lake	DNC	17	21	29	4	0	29	0	NE[i]	NE	NE	NE	NE	NE	NE
Benton Lake NWR[j]	DNC	3	58	14	20	1	4	0	3	69	9	9	2	8	0
Benton Lake NWR	NGS	0	36	25	39	0	0	0	4	40	36	16	0	4	0
Bowdoin NWR	NGS	5	43	21	5	0	26	0	2	24	37	11	2	24	0
Homestead NWR	DNC	16	54	4	1	7	11	7	5	40	18	5	3	29	0
Medicine Lake NWR	DNC	4	55	13	0	4	4	20	18	41	12	2	4	16	7
Medicine Lake NWR	NGS	52	36	3	0	0	0	9	NE	NE	NE	NE	NE	NE	NE

[a] DNC=planted dense-nesting cover, NGS=native short-grass prairie.

[b] Mall=Mallard.

[c] Gadw=Gadwall.

[d] Nosh=Northern Shoveler.

[e] Nopi=Northern Pintail.

[f] Amwi=American Wigeon.

[g] Teal catagory contains Blue-winged, Green-winged, and Cinnamon Teal nests.

[h] WPA=waterfowl production area.

[i] NE=no estimate for this year.

[j] NWR=national wildlife refuge.

sites where artificial-nest success was 0.40, duck-nest success ranged from 0.20 - 0.75. Similarly, given duck-nest success of 0.50 - 0.70, artificial-nest success varied from 0.08 - 0.80. Many research sites found to have artificial-nest success greater or less than natural-nest success in 1993 experienced the opposite in 1994 (Table 1).

Overall, nest success increased for both artificial (1993 = 0.35, 1994 = 0.55, $\underline{P} \leq 0.05$) and natural (1993 = 0.41, 1994 = 0.56, $\underline{P} \leq 0.05$) nests from 1993 to 1994. Additionally, the mean difference in nest success between years for both nest types was similar (artificial-nest success change $\bar{x}$ = 0.20, natural-nest success change $\bar{x}$ = 0.16, $\underline{P}$ = 0.74). However, the direction of the change in nest success among research sites (e.g., increase vs. decrease) was not consistent for both nest types. Artificial-nest success increased at every research site except for the 2 sites located at Benton Lake NWR. In contrast, natural-nest success increased at every research site from 1993 to 1994.

Vegetation analyses

Vegetative height-density measurements differed significantly between DNC ($\bar{x}$ = 2.51, SE = 0.86) and NGS ($\bar{x}$ = 1.33, SE = 0.52) ($\underline{P} < 0.01$). Vegetative height-density increased ($\underline{P}$ = 0.06) from 1993 ($\bar{x}$ = 2.07, SE = 0.85) to 1994 ($\bar{x}$ = 2.40, SE = 0.98) and increased ($\underline{P} < 0.1$) at every research site between 1993 and 1994 except for the DNC research site at Benton Lake NWR.

Predator-community composition

Three hundred and seventy-nine mammalian scent stations were placed, and 656 point counts were conducted to monitor avian nest predators. Presence/absence data indicated similar predator communities at each study area, with the exception of ravens (Corvus corax) which were only present at the Ninepipe study area during 1993 and 1994 field seasons (Appendix A).

Relationship between artificial- and natural-nest success

Given the annual changes in nest success and that the 2 nest types experienced similar changes in success rates, the success rates for artificial and natural nests were only weakly correlated (Fig. 2.) ($F = 3.44$, $R^2 = 0.20$, $P = 0.08$). However, when nest-success data were analyzed by year, habitat type, and a year-habitat type combination, strength of relationships varied dramatically (Table 3). Survival rates of artificial nests and duck nests were significantly related within DNC in all years and when years were pooled ($R^2 = 0.52\text{-}0.87$, $P = 0.01 - 0.08$). However, results of analyses of other combinations were not significant ($R^2 = 0.00 - 0.20$, $P = 0.24 - 1.00$). Based on the weak and inconsistent relationship between survival rates of the 2 nest types, I conclude that artificial-nest success is not consistently a valid index to duck-nest success in Montana and should be applied with caution. In particular, the relationship

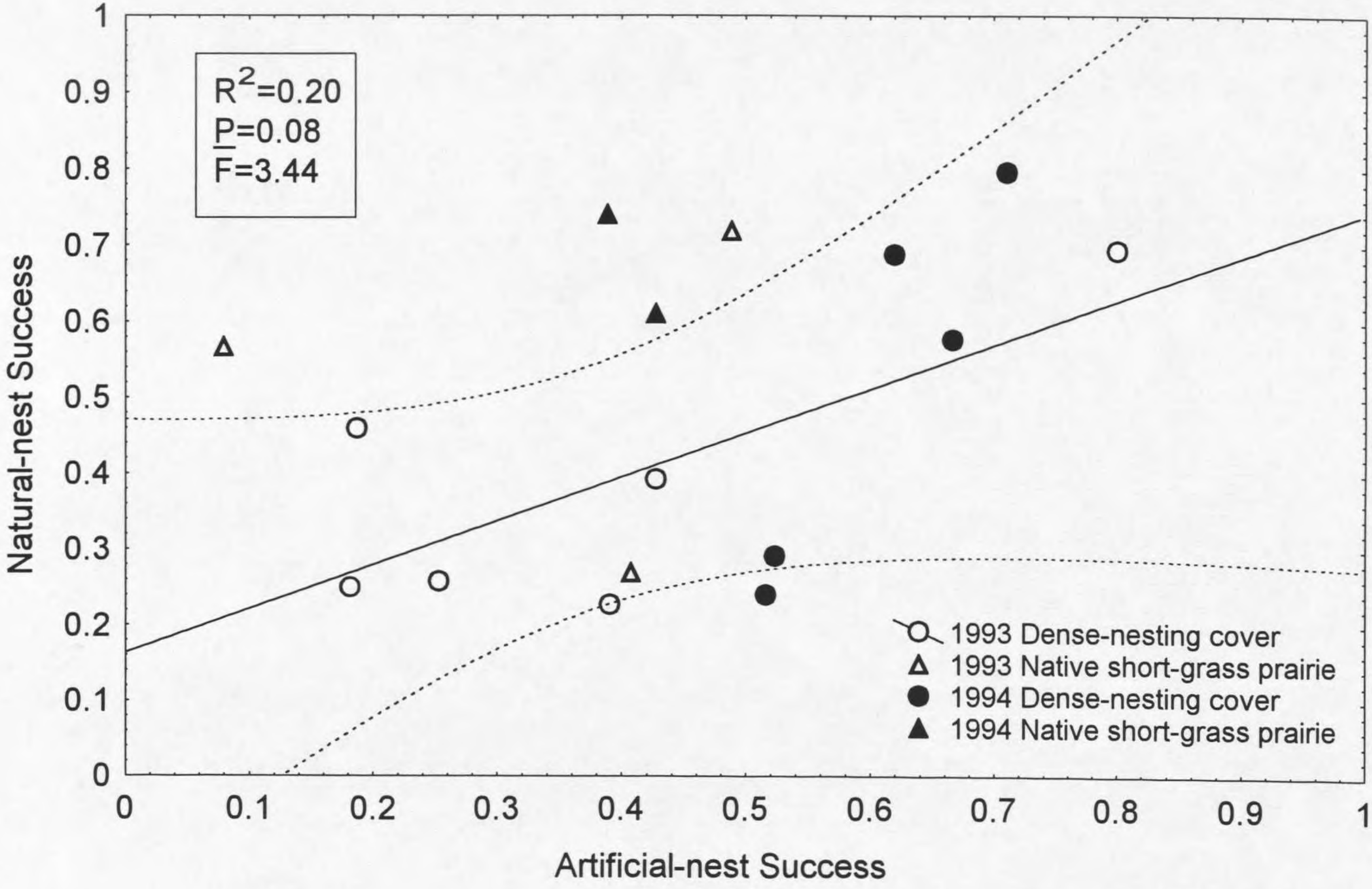

Figure 2. Correlation analysis of nest-success estimates for artificial versus natural duck nests for 16 research sites across northern Montana, 1993-1994.

Table 3. Correlations between nest-success estimates of artificial versus natural nests monitored at 16 research sites across northern Montana, 1993-1994.

	Habitat Type[a]								
	DNC			NGS			DNC & NGS		
Year	*n* sites[b]	R^2	*P*	*n* sites	R^2	*P*	*n* sites	R^2	*P*
1993	6	0.57	0.08	3	0.00	1.00	9	0.19	0.24
1994	5	0.87	0.02	2	NE[c]	NE	7	0.04	0.68
1993-94	11	0.52	0.01	5	0.01	0.86	16	0.20	0.08

[a] DNC=planted dense-nesting cover, NGS=native short-grass prairie.

[b] Number of research sites for which artificial- and natural-nest daily survival-rate estimates were available.

[c] NE=No estimate available; regression coefficient and corresponding p-value not calculable.

between survival rates of the 2 nest types does not appear consistently strong in all habitat types.

Relationship between nest vegetation and nest success

The relationship between research-site MVHD and nest success was different for artificial and natural nests. Correlation analysis indicated a weak, but significant, correlation between MVHD and artificial-nest success ($F = 5.07$, $R^2 = 0.26$, $P = 0.04$) (Fig. 3.). In contrast, MVHD was not significantly related to natural-nest success ($F = 0.01$, $R^2 = 0.001$, $P = 0.91$). Analyses by year resulted in 1 significant correlation between MVHD and artificial-nest success for 1993 ($F = 4.91$, $R^2 = 0.50$, $P = 0.08$).

Discussion

Numerous researchers have used artificial nests to study avian nesting ecology because of the difficulty of finding natural nests. The main focus of these studies has been on factors that potentially influence nest survival (Dwernychuk and Boag 1972, Vacca and Handel 1988, Sullivan and Dinsmore 1990, Esler and Grand 1993, Burger et al. 1994). I am aware of only 5 studies that conducted experiments designed to test whether artificial-nest success is

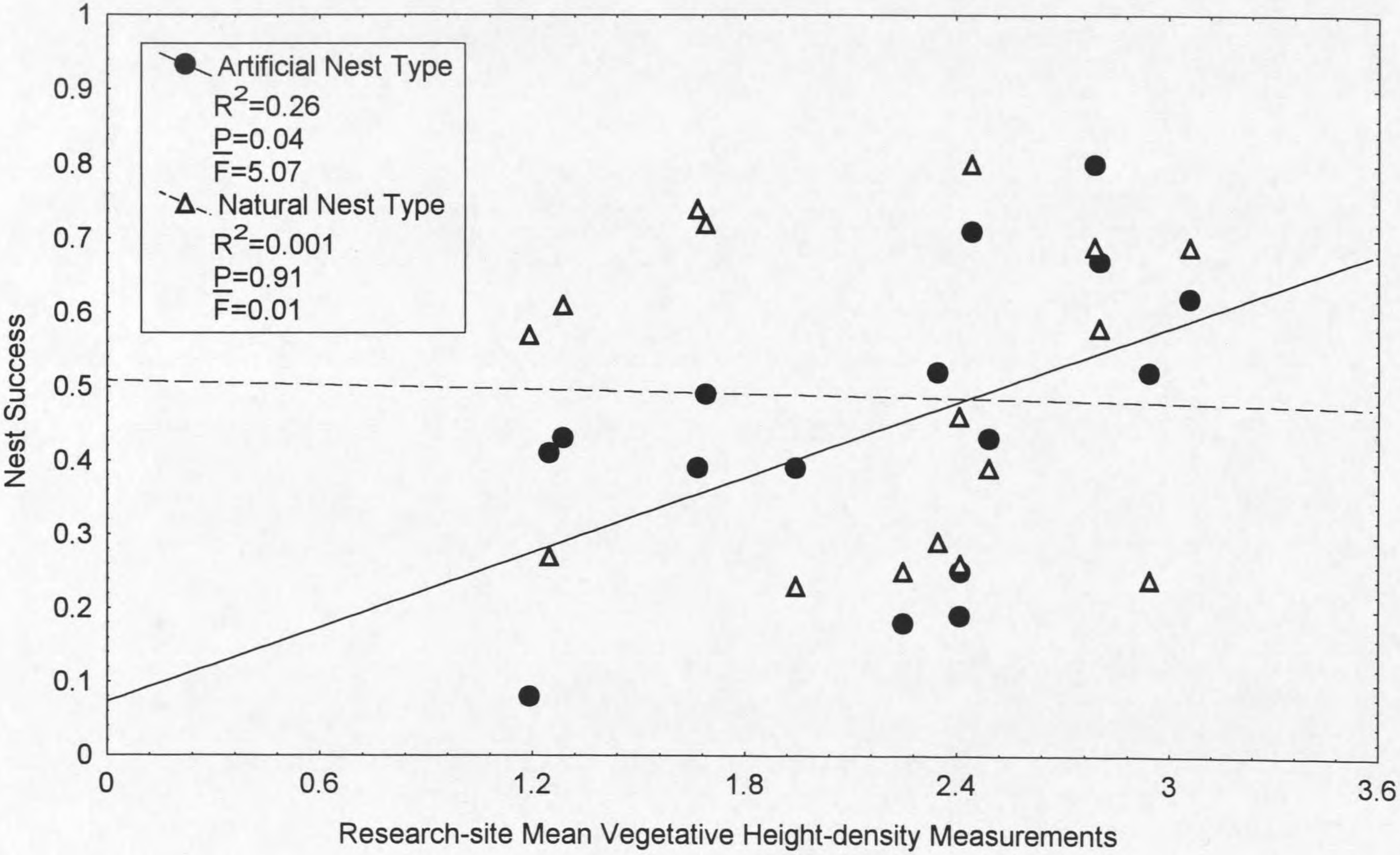

Figure 3. Correlation analysis of vegetative height-density and nest success for 2 nest types monitored at 16 research sites across northern Montana, 1993-1994.

directly related to natural-nest success and thus, a valid method for studying nest success.

Storass (1988) compared depredation rates on artificial- and natural-capercaille (Tetrao urogallus) nests, and found that artificial-nest success was not a valid index to natural-nest success. Similarly, Willebrand and Marcstrom (1988) compared depredation rates for artificial and natural nests of Eurasian black-grouse (Tetrao tetrix) and reported that artificial-nest success was not a reliable index to natural-nest success. Recently, Guyn and Clark (In Press) found no correlation between artificial- and natural-waterfowl nests in Saskatchewan. In contrast, Gotmark et al. (1990) and Kurnat (1991) found the results of artificial-nest success to be similar to natural-nest success in arctic loons (Gavia arctica) and upland-nesting ducks, respectively. Thus, results of evaluations of the artificial-nest technique have varied by study.

My results support those of Storass (1988), Willebrand and Marcstrom (1988), and Guyn and Clark (In Press): there was not a consistent relationship between survival of artificial and natural nests across the state of Montana. At some research sites, artificial-nest success was higher than natural whereas at other sites the reverse was true. The relationship between artificial- and natural-nest success was strongest at DNC research sites. However, the nature of the relationship (i.e., slope) differed greatly between years. Furthermore, the overall relationship between artificial- and natural-nest success was weak ($F = 3.44$, R^2

= 0.20, P = 0.08) (Fig. 2.). Thus, the relationship between survival of the 2 nest types does not appear strong enough to justify using artificial nests as surrogates for natural nests. For example, if artificial-nest success was 0.15, the 95% confidence interval for predicted natural-nest success would be 0.16 to 0.54 (Fig. 2.). If variance in natural-nest success estimates were incorporated into the correlation, the confidence interval for predicted natural-nest success would further widen.

The observed differences between artificial-nest success and natural-nest success are apparently the result of differential rates of depredation on the 2 nest types. Artificial and natural nests likely present different cues that differentially attract various species of nest predators to each nest type. Natural nests have attending hens which offer visual, olfactory, and auditory cues (Hammond and Forward 1956, Erikstad et al. 1982). Additionally, during incubation, hens camouflage their clutches of eggs with down and nest debris before they leave nests to feed. Visual cues provided by artificial nests appeared limited but varied with the amount of concealing nest vegetation available at the nest site. My artificial nests had duck-down linings but likely had less scent than natural nests. Thus, it is quite likely that my artificial nests differed from natural nests in terms of sight and scent. Furthermore, the nature of these differences, especially visual differences, probably changed from site to site and year to year with vegetation changes.

Clark and Nudds (1991) proposed that nest concealment may be most important when primary nest predators are avian. This hypothesis has been supported by observations of higher artificial-nest success in areas with heavier cover (Jones and Hungerford 1972, Sugden and Beyersbergen 1987, Mankin and Warner 1992, this study). Thus, during my study vulnerability of artificial nests probably varied dramatically. At sites or times with less concealing vegetation and/or more avian predators, artificial nests were probably more vulnerable. At sites or times with thick cover and/or fewer avian predators, artificial nests may have been quite secure.

Additionally, natural nests were probably variable in their vulnerability: I found no relationship between MVHD and natural-nest success (Fig. 3.). Given my results, I agree with Dwernychuk and Boag (1972) and Storass (1988): avian nest predators likely discover artificial nests at a different rate than they do natural nests, yielding different depredation rates for artificial and natural nests.

Although most researchers caution against using survival of artificial nests to estimate natural-nest success, many argue that the technique is a valid means of studying factors that influence nest survival (e.g., Yahner and Voytko 1989). Based on my results, I disagree. If artificial nests are used to study factors that influence nest depredation, the only information gained regards factors that influence artificial-nest depredation. Unlike other evaluations of the technique, this study incorporated numerous sites well dispersed across a wide geographic area (800 km E-W), encompassed a wide range of natural-nest success rates, and provided a rigorous test of the artificial-nest technique. I suggest that others conduct similar work over the range of areas and nest-success rates they wish to consider before using artificial nests. Additionally, they should evaluate the technique over a number of habitats and years.

Conclusion

My results clearly indicate that the strength of the relationship between artificial- and natural-nest success varies by year and habitat type. My results not only suggest that the relationship is weak, they also indicate that artificial-nest success may lead to wrong conclusions regarding natural-nest success in many situations. Thus, given the weak and variable relationship between artificial- and natural-nest success, I conclude that, (1) the technique should not be used for upland-nesting ducks in the mid-continent and (2) researchers working in other areas/species should evaluate the usefulness of the technique before implementing it.

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CHAPTER 3

EFFECTS OF NEST VEGETATION AND CORVID ABUNDANCE ON SURVIVAL OF ARTIFICIAL-DUCK NESTS IN MONTANA

Introduction

Numerous studies have used artificial nests as surrogates for natural nests when investigating factors that influence nest-depredation rates, despite the fact that many researchers have voiced concern over their use (Storass 1988, Willebrand and Marcstrom 1988). Many of these studies employed artificial nests to examine the effect of concealing vegetation on nest success. Results from these studies were mixed: 4 studies reported no effect of nest concealment on artificial-nest survival (Gottfried and Thompson 1978, Erikstad et al. 1982, Elser and Grand 1993, Kelly 1993), whereas 15 studies reported some positive relationship between nest concealment and artificial-nest survival (Odin 1957, Dwernychuk and Boag 1972, Jones and Hungerford 1972, Schrank 1972, Picozzi 1975, Boag et al. 1983, Gotmark and Ahlund 1984, Sugden and Beyersbergen 1986, Sugden and Beyersbergen 1987, Storass 1988, Vacca and

Handel 1988, Sullivan and Dinsmore 1990, Kurnat 1991, Mankin and Warner 1992, Leimgruber et al. 1994).

Because the results of these studies conflict, I investigated the effect of nest vegetation on survival of artificial-duck nests in northern Montana where habitat is managed intensively to increase nest concealment and reduce loss of nests to predators. I also documented predator-community composition at each study area in an effort to explain differences in artificial-nest success between areas, and thus, was able to investigate the effect of corvid, sight-oriented nest predators abundance (Kalmbach 1937, Gottfried and Thompson 1978, Loman and Gorannsson 1978, Johnson 1979). Some researchers have hypothesized that survival of artificial nests is biased low because sight-oriented predators destroy them at a higher rate than they do natural nests (Picozzi 1975, Angelstam 1986, Martin 1987, Storass 1988, Willebrand and Marcstrom 1988).

Study Areas

I selected 4 study areas across the state of Montana (Fig. 4). The Ninepipe study area (47^{0}26'N, 114^{0}7'W), Benton Lake National Wildlife Refuge (NWR) (47^{0}40'N, 111^{0}20'W), Bowdoin NWR (48^{0}25'N, 107^{0}41'W), and Medicine Lake NWR (48^{0}28'N, 104^{0}26'W) were selected to ensure variation in nesting

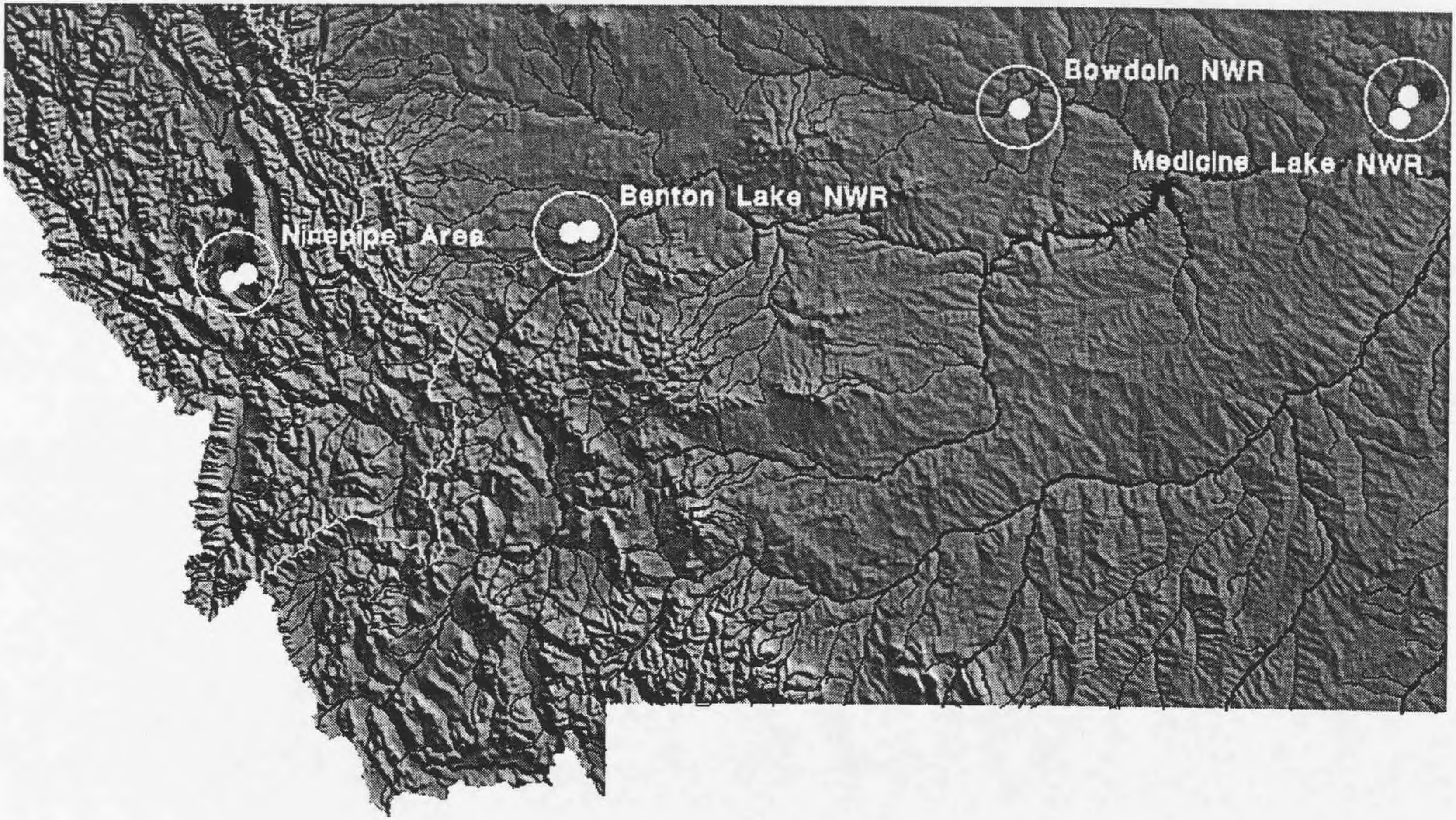

Figure 4. Study areas and research sites used for placement of artificial nests across northern Montana, 1994.

habitats, geographic regions, and predator communities. All study areas had a semi-arid continental climate.

Within each study area, I selected research sites (Fig. 4) based upon historical densities of nesting waterfowl and habitat abundance. In 1994, the Ninepipe area contained 2 sites (Sandsmark and North Kicking Horse Waterfowl Production Areas [WPA]), Benton Lake NWR contained 2 sites, Bowdoin NWR contained 1 site, and Medicine Lake NWR contained 2 sites (Homestead NWR and Medicine Lake dense-nesting cover (DNC).

I evaluated nest success of artificial-duck nests for 2 habitat types during both field seasons: planted DNC and native short-grass prairie (NGS). Although I attempted to locate and use equal numbers of DNC and NGS research sites, actual numbers were determined by availability of sites and logistical feasibility with respect to scheduling placement of artificial nests. In 1994, 5 DNC and 2 NGS sites were chosen.

Primary species composition of vegetation in DNC was quackgrass; western, crested, intermediate, and tall wheatgrasses (Agropyron spp.); orchard grass (Dactylis glomerata); alfalfa (Medicago sativa); sweet clover (Melilotus officinalis); smooth brome (Bromus inermis); and cheatgrass (Bromus tectorum). Primary species composition of NGS was western wheatgrass (Agropyron smithii), blue grama (Bouteloua gracilis), green needlegrass (Stipa virdula), needle-and-thread (Stipa comata), fringed sagebrush (Artemisia frigida), silver sagebrush (Artemisia cana), greasewood (Atriplex patula), and prairie junegrass (Koeleria cristata).

All study areas contained ephemeral, temporary, seasonal, semipermanent, and permanent wetlands (Stewart and Kantrud 1971). Lokemoen (1966) likened the Flathead Valley to pothole habitat in the prairie pothole region of Canada. All other areas were characterized by permanent ponds and lakes, and large managed wetland blocks. Only Benton Lake NWR, Bowdoin NWR, and Medicine Lake NWR contained alkali ponds and lakes.

Methods

Data Collection

Nest sample. A circuit of placement and retrieval for artificial nests was coordinated for all research sites across Montana. Three placement circuits of 20 nests/site/circuit were made. Thus, each site received 60 artificial nests, which were placed as 3 replicates of 20 nests. Placement of artificial nests began at the western-most study area (Ninepipe) and continued eastward until all artificial nests were placed. During subsequent placement circuits, previously placed nests were retrieved prior to placing a new sample of 20 nests. One placement circuit (i.e., placement of artificial nests across the state from west to east) took approximately 14-16 days. New artificial-nest locations were randomly selected during each circuit. Nest placement began on 12 May and retrieval concluded on 8 August.

Specific artificial-nest locations were determined by randomly selecting nest locations from within each research site. I overlaid a grid of 1-hectare plots onto aerial photos of DNC and NGS polygons for each research site, orientated the grid along cardinal directions, and fixed 1 corner of the grid in the south-westernmost corner of each site which caused some 1-hectare plots to fall along habitat edges. In this way, grid placement allowed some nests to fall near edges where depredation may be higher (Gates and Gysel 1978, Yahner and Wright 1985, Ratti and Reese 1988, Angelstam 1986). I randomly selected 20 plots from each grid and placed 1 artificial nest in the center of each plot. A plot center was located using the aerial photo, grid, measurements, and landmarks in the field. If the center of a selected plot was outside the research-site boundary, in water, or on other unsuitable habitat (e.g., rock), that plot was excluded and another plot was randomly selected. I placed only 1 artificial nest/plot to avoid potential density-dependent increases in depredation rates of nests (Goransson et al. 1975, Sugden and Beyersbergen 1986).

Artificial nests were designed to simulate upland-nesting duck nests in the laying stage. An artificial nest consisted of 1 chicken egg dyed to resemble a mallard (Anas platyrhynchos) or gadwall (A. strepera) egg, duck nesting down, a timer device (Ball et al. 1994), and a nest marker. Timers recorded the exact time of destruction for each nest, and necessitated the use of 1 egg/nest. Markers used to identify nest locations were identical in type and placement to those used in marking natural-duck nests (Picozzi 1975). I used 2 types of nest markers: cut willows (Salix spp.), and orange plot flags.

Twenty-one days after placement, I revisited each artificial nest, determined its fate (e.g., successful or destroyed), and, if necessary, recorded time to nest destruction. After all nesting data were recorded, fragments of destroyed nests, whole eggs of survived nests, and all nesting materials were removed from each nest location.

Vegetation measurements. Upon placing an artificial nest, I used a Robel et al.'s technique (1970) to measure height and density of vegetation in each cardinal direction at each artificial-nest site. These four measurements were then used to calculate a mean vegetative height-density (MVHD) for each nest site. Nest-site MVHDs were then used to calculate a research-site MVHD.

Predator-community composition. I estimated the presence/absence of species of mammalian predators at each research site using scent stations (Roughton and Sweeny 1982). Transects of scent stations were placed on the shoulder of refuge and county roads that bordered research sites. Each transect was 4.8 km long, consisted of a scent station placed on alternating sides of the road every 0.48 km, and contained 10 scent stations. I placed scent tablets at stations in the late afternoon and checked for tracks at first light the following day. I attempted to place scent stations each day, however weather conditions limited scent station samples to 110 stations in 1994.

I also estimated avian-nest predator abundance using roadside point-count surveys (Ralph et al. 1993). Point-count transects were established on the same roads used for scent-station transects. A point-count transect consisted of 25 point-count stations, each spaced 0.16 km apart. Thus, each point-count transect was 4 km long. Point-counts were conducted in conjunction with scent station checks at first light. A complete list of potential nest predators was compiled from scent-station data, point-count surveys, and observations made by refuge trapping personnel.

Data Analysis

I conducted data analysis using a 4-step approach: nest survival analysis, analysis of the effect of vegetation on nest survival, univariate analyses and screening of candidate variables for multivariate analysis, and multivariate analysis of factors affecting nest survival. I considered differences to be significant at $P \leq 0.10$. An explanatory variable was a candidate in multivariate analysis if results of univariate tests using the variable had $P \leq 0.15$. I chose P

≤ 0.10 as significant to balance Type I and Type II errors. All univariate analyses were conducted in STATISTICA (StatSoft, Inc. 1994). Multivariate analyses were conducted in SAS (SAS Institute, Inc. 1989).

Nest survival. I only used nest data from 1994 because I only had estimates of corvid abundance for 1994. Because I placed and knew the fate of each artificial nest, I censused rather than sampled their fates, and no estimates of variance were applied to nest success. Additionally, because I was only working with artificial nests in this chapter, I based all analyses on 21-day survival rates (rather than 35-day survival rates as in chapter 2). Nests destroyed by human causes (accidental crushing, inadvertent flooding of nest sites) or with defective timers were removed from the data set before analysis.

Nest timers allowed nest initiation and termination dates to be known, which made analyses that require specific time of destruction data possible. Nest destruction times allowed for investigation of when nests were being depredated with respect to daytime hours. I pooled artificial nests from all research sites and calculated a mean number of nest depredations/hour for each hour of a 24 hour day. Likewise, this analysis was repeated after I created subsets of artificial nests for both DNC and NGS habitats. Differences in depredation during daytime and nighttime hours were tested with a t-test.

I conducted further temporal nest survival analysis using the Kaplan-Meier product limit estimator (Kaplan and Meier 1958), and generated survivorship curves for nests by habitat type, placement circuit number (1, 2, or 3), and a combination of habitats and placement circuit numbers. I determined significant differences between survivorship curves using the log-rank test (Cox and Oakes 1984: 104).

I tested for differences in nest survival among study areas by analyzing a 4 X 2 contingency table (4 study areas X 2 possible fates) with Pearson's chi-square test (Conover 1980: 182). If the overall test was significant, I conducted pairwise chi-square analyses to determine where specific differences existed between study areas.

Vegetation analyses. I pooled nest-specific data for all nests within each research site/habitat type to calculate a MVHD for each research site and habitat type. I used Kruskall-Wallis analysis of variance (ANOVA) (Conover 1980: 229) to test for differences in MVHD between/among research sites. I determined differences between mean DNC and NGS MVHD using a Mann-Whitney U-test (Conover 1980: 215).

Point-count analysis. For each of the 4 study areas, I determined the mean number of corvids/point/study area and their corresponding standard errors. Because point-count data were not normally distributed (Shapiro-Wilk W=0.43, P<0.001), I used Kruskall-Wallis ANOVA to determine differences in corvid abundance among study areas (Conover 1980: 229).

Effects of vegetation on nest survival. I conducted correlation analysis for nest-site MVHD versus the number of days an artificial nest survived to determine if MVHD influenced survival of nests. I also examined the data set by habitat type and again tested for effects of MVHD on artificial-nest survival. Additionally, I examined correlation between average nest success for each research site and research-site MVHD. For this analysis, I estimated nest success by research site using the binomial method (White and Garrot 1990: 208).

Univariate analysis of factors affecting survival of artificial nests. I screened 6 candidate explanatory variables using univariate analyses to aid in the selecting of candidate explanatory variables for logistic regression analysis (Hosmer and Lemeshow 1989: 82). Any variable whose screening test met a significance level of $P \leq 0.15$ was entered into step wise logistic regression analysis.

I tested for differences in nest survival among research sites using a 7 X 2 contingency table (7 research sites X 2 possible nest fates) and Pearson's chi-square test. If the overall chi-square analysis indicated a difference between nest survival among research sites, I conducted pair-wise chi-square analyses to determine where specific differences existed.

To determine if habitat type influenced nest survival, I compared survival of nests in DNC and NGS chi-square tests. I tested for differences in nest survival by nest initiation date, nest-specific Robel mean, research-site specific Robel mean, and corvid abundance using t-tests.

Multivariate analysis of factors affecting survival of artificial nests. I used a step wise logistic regression procedure to test whether nest survival was related to the explanatory variables chosen as candidates by univariate screening (Hosmer and Lemeshow 1989). Analysis was conducted using the Logistic procedure in SAS, and significance was set at $P = 0.05$ for explanatory variables to enter and exit the regression model (SAS Institute, Inc. 1989). I used likelihood-ratio tests to determine the best available model and emphasized parsimony (Hosmer and Lemeshow 1989: 106). I estimated model fit for the logistic regression by dividing the model's chi-square statistic by the -2 X ln (likelihood) value for the null model. This criteria of model fit describes what percentage of the ln-likelihood is explained by the model, and is analogous to an R^2 value in multiple-regression analysis.

Results

Nest survival

During 1994, I placed 505 artificial nests with timers, and 309 timers provided useful data on time to destruction. When data from all sites were pooled, nest depredation rate between 6 am - 9 pm (5.13 nests/hour) was significantly greater ($\underline{P} < 0.0001$) than the rate between 9 pm - 6 am (1.78 nests/hour) (Fig. 5.). Hourly nest-depredation rate peaked (11 nests/hour) between 1 and 2 pm. Dense-nesting cover and NGS exhibited similar trends in depredation patterns, but depredation was not different between daytime and nighttime hours for DNC (daytime 2.47 nests/hour, nighttime 1.89 nests/hour, $\underline{P} = 0.63$). Depredation among native-grass site's was significantly different during daytime and nighttime hours (daytime 2.27 nests/hour, nighttime 0.56 nests/hour, $\underline{P} = 0.01$).

Kaplan-Meier survival analyses indicated that depredation of artificial nests was greatest during the first 10 days of exposure ($\underline{P} \leq 0.005$) (Fig. 6.). This pattern of depredation was spatially and temporally consistent: depredation rates were highest during the first 10 days of exposure for each placement circuit and research site (Fig. 8, Fig. 9; Appendix B). Additionally, Kaplan-Meier

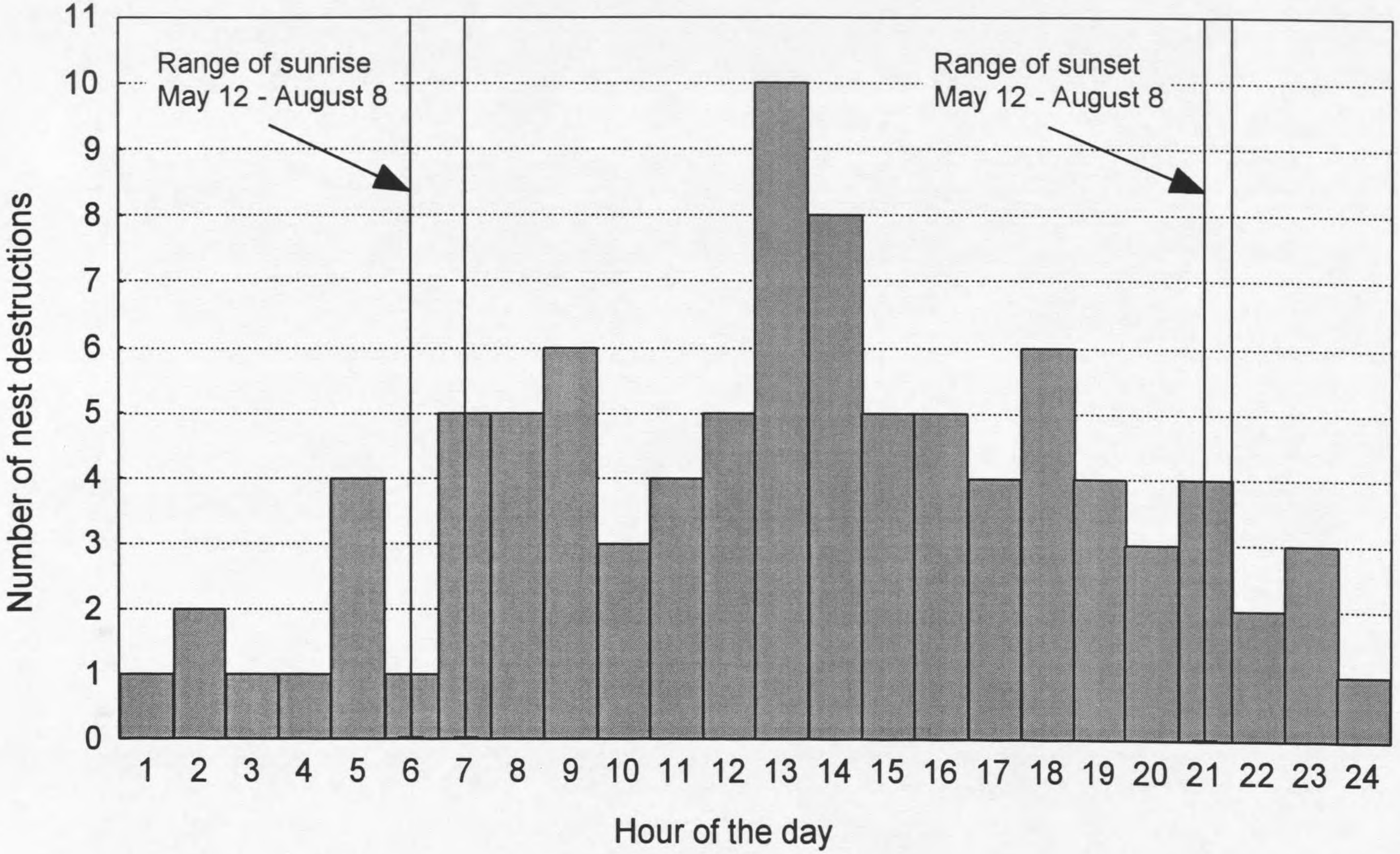

Figure 5. Hourly depredation of 93 artificial nests monitored at 7 research sites across northern Montana, 1994.

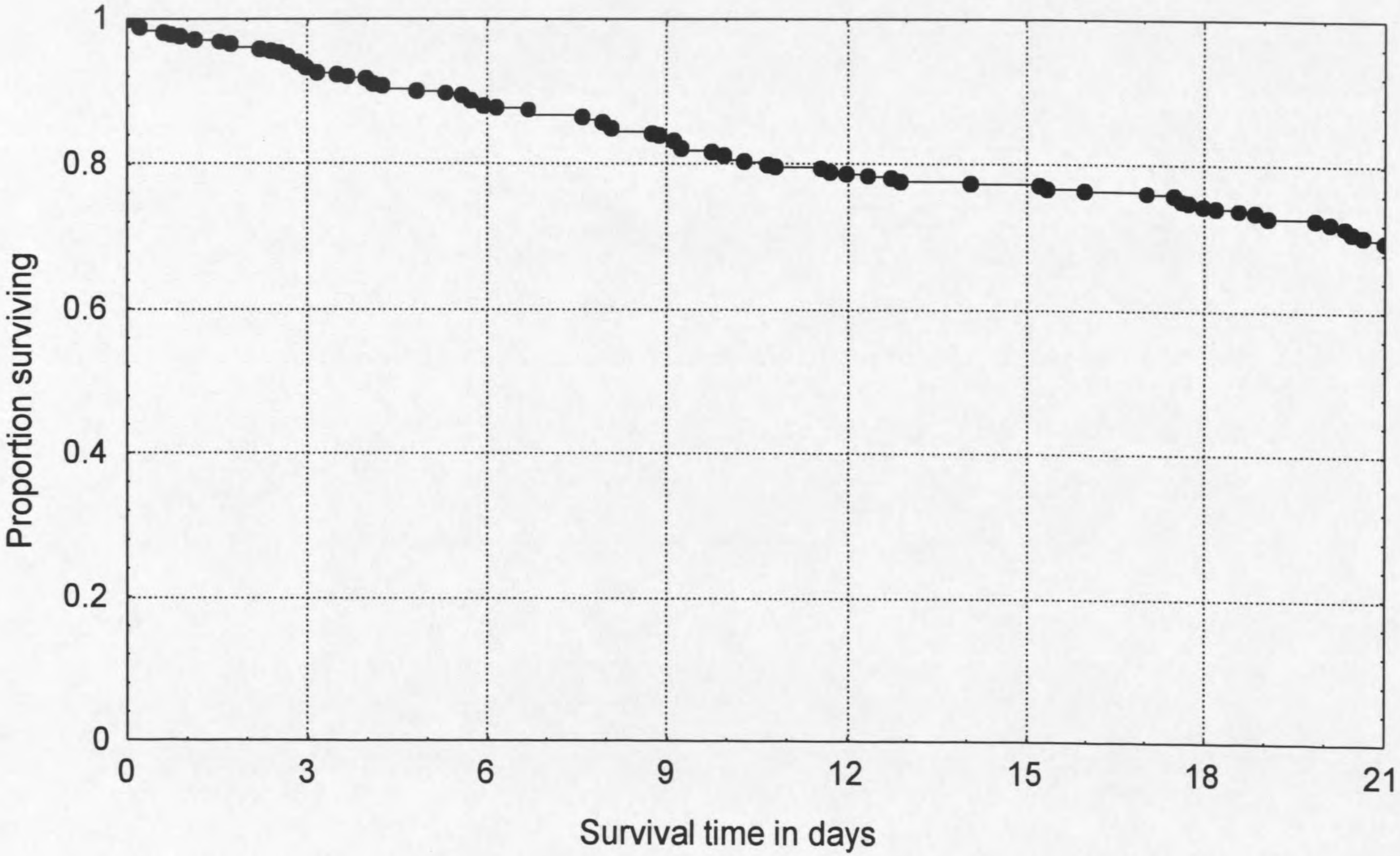

Figure 6. Kaplan-Meier survivorship curve for 309 artificial nests monitored at 7 research sites across northern Montana, 1994.

analyses indicated that depredation of nests was greatest earlier in the nesting season. Survivorship for placement circuits of artificial nests was significantly different between early and late nest placements for all but 2 pairs of placement curves. The second and third placement circuits in DNC and the first and second placement circuits in NGS were not different from each other (2nd vs. 3rd placements in DNC, Log-rank test, $P = 0.40$; 1st vs. 2nd placements in NGS, Log-rank test, $P = 0.39$). However, all other possible pairs of placements were highly significantly different (Log-rank test, $P = 0.0007 - 0.07$). Thus, nest survival was lowest during first placements and increased through the nesting season (third placement of nests). Nest survival ranged from 0.63 - 0.74 among study areas but was not significantly different among study areas ($X^2 = 1.72$, 3 d.f., $\underline{P} = 0.63$).

Vegetation analyses

Analysis of variance indicated that not all research sites had similar MVHD ($\underline{P} \leq 0.10$). Sixteen of a possible 21 paired comparisons of research-site MVHD were different ($\underline{P} \leq 0.10$) (Tables 4 and 5). Mean vegetative height-density was similar among research sites with the same habitat types (Table 5). These ANOVA results were supported by significantly different habitat MVHDs (DNC $\bar{x} = 2.68$, NGS $\bar{x} = 1.37$, $U = 1821.5$, $\underline{P} < 0.01$).

Table 4. Significance levels for results of Kruskall-Wallis tests comparing vegetation density between 7 research sites across northern Montana, 1994.

Study area[a]	Research site	Sandsmark WPA[b] (D[c])	North Kicking Horse (D)	Benton Lake (D)	Benton Lake (N[d])	Bowdoin NWR[e] (N)	Homestead NWR (D)	Medicine Lake (D)
1	Sandsmark WPA (D)	-	**0.021**[f]	0.176	**0.000**	**0.000**	**0.032**	0.129
1	N. Kicking Horse WPA (D)		-	0.136	**0.000**	**0.000**	**0.000**	**0.000**
2	Benton Lake (D)			-	**0.000**	**0.000**	**0.000**	**0.002**
2	Benton Lake (N)				-	0.212	**0.000**	**0.000**
3	Bowdoin NWR (N)					-	**0.000**	**0.000**
4	Homestead NWR (D)						-	0.511
4	Medicine Lake DNC (D)							-

[a] Study area: 1=Ninepipe area; 2=Benton Lake NWR; 3=Bowdoin NWR; 4=Medicine Lake NWR

[b] WPA=waterfowl production area

[c] D=dense-nesting cover

[d] N=native short-grass prairie

[e] NWR=national wildlife refuge

[f] Bold type indicates significance

Table 5. Artificial-nest success, corvid abundance, and mean vegetative height-density for 7 research sites used to study duck nests across northern Montana, 1994.

				Corvids/point		MVHD[a]	
Study area	Research site	n nests	Nest success	$\bar{x}$	SE	$\bar{x}$	SE
Ninepipe area	Sandsmark WPA[b]	40	0.75	1.47	0.14	2.76	0.15
Ninepipe area	N. Kicking Horse WPA	21	0.71	1.47	0.14	2.23	0.12
Benton Lake NWR[c]	Benton Lake DNC[d]	84	0.76	0.07	0.07	2.55	0.10
Benton Lake NWR	Benton Lake NGS[e]	48	0.56	0.07	0.07	1.47	0.06
Bowdoin NWR	Bowdoin NWR	48	0.63	0.10	0.19	1.27	0.08
Medicine Lake NWR	Homestead NWR	32	0.69	0.03	0.02	2.99	0.09
Medicine Lake NWR	Medicine Lake DNC	36	0.72	0.03	0.02	2.89	0.10

[a] MVHD=mean vegetative height-density

[b] WPA=waterfowl production area

[c] NWR=national wildlife refuge

[d] D=dense-nesting cover

[e] NGS=native short-grass prairie

Point-count analysis

Based on 656 point counts, corvid abundance was not the same for all study areas ($\underline{P} \leq 0.001$) (Table 5). Corvid abundance did not differ among Benton Lake NWR, Bowdoin NWR, and Medicine Lake NWR ($\underline{P} = 0.428 - 0.725$) but was significantly different at the Ninepipe area from all other study areas ($\underline{P} \leq 0.001$). Ninepipe was the only area where ravens were present.

Effects of vegetation on nest survival

Correlation analysis indicated a weak relationship between nest-site MVHD and the number of days that a nest survived (Fig. 7.) ($R^2 = 0.04$, $\underline{P} < 0.001$). Weak relationships were also found during analyses that investigated relationships between days survived and nest-site MVHD on a habitat type or research site basis ($R^2 = 0.02 - 0.11$, $\underline{P} = 0.002 - 0.22$). In contrast, research-site MVHD strongly correlated with nest success ($F = 8.11$, $R^2 = 0.62$, $P = 0.04$) (Table 5). Because only 7 research sites were used in 1994, further analyses of this relationship was not possible.

Overview of univariate analysis of factors affecting survival of artificial nests

Of six potential candidate explanatory variables, only 4 passed the screening criteria of $\underline{P} \leq 0.15$. Nest survival did not vary by research site ($X^2 = 9.13$, 6 d.f., $\underline{P} = 0.17$) or corvid abundance ($t = 0.70$, 307 d.f., $\underline{P} = 0.48$).

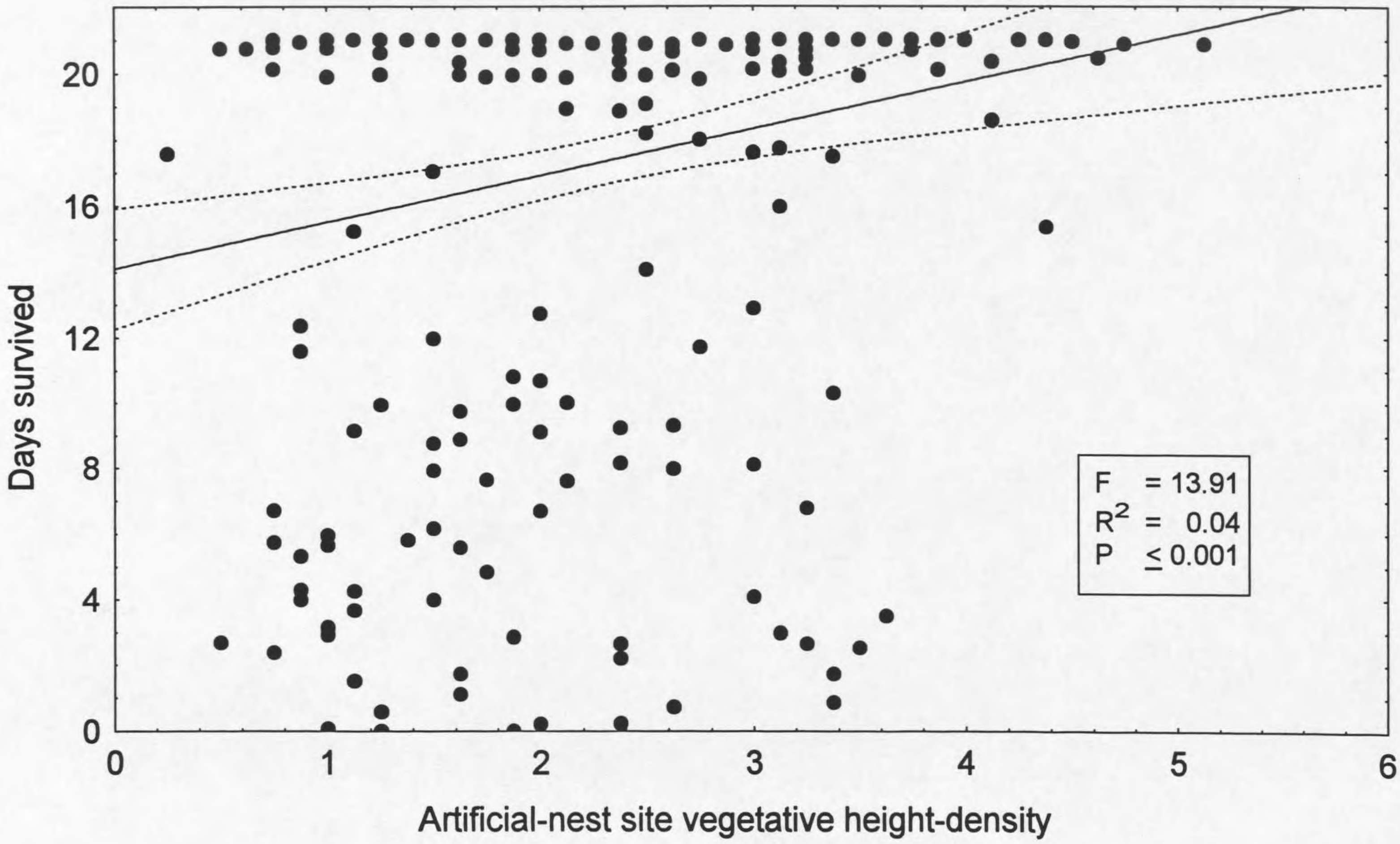

Figure. 7. Correlation analysis of nest-site mean vegetative height-density versus the number of days an artificial nest survived for 309 artificial nests monitored at 7 research sites across northern Montana, 1994.

However, nest survival did vary by habitat type ($X^2 = 7.34$, 1 .d.f., P < 0.01), nest-initiation date (t = 6.08, 307 d.f., P < 0.000001), nest-site MVHD (t = 2.89, 307 d.f., P = 0.004), and research-site MVHD (t = 2.36, 307 d.f., P = 0.019). Therefore, habitat type, nest-initiation date, nest-site MVHD, and research-site MVHD entered into the multivariate analysis as explanatory variables.

Multivariate analysis of factors affecting nest survival of artificial nests

Step wise logistic-regression analysis produced a model to explain nest survival that contained nest-initiation date and nest-site MVHD (X^2 for 2 variable model = 42.63, 2 d.f., P = 0.0001). The logit of the model was,

1241.1-0.036 (nest initiation date)-0.4 (nest-site MVHD).

Model P_1 explained a significant amount of the variation in nest survival but did not fit the data well (Model Fit = 0.1127, 11.27% of the log-likelihood was explained by the model). The model indicates that later nest-initiation date and higher nest-site MVHD were positively related to nest survival.

Discussion

Corvids are sight-oriented predators, and some researchers have hypothesized that survival of artificial nests is biased low because sight-oriented predators destroy them at a higher rate than they do natural nests (Picozzi 1975, Angelstam 1986, Martin 1987, Storass 1988, Willebrand and Marcstrom 1988). I was able to test various predictions taken from these hypotheses regarding the relationship between corvid abundance and nest survival.

Based upon these hypotheses, daytime depredation of nests should be greater than nighttime depredation if artificial nests are more easily detected by sight-oriented predators. Results of this study support this prediction: depredation of nests was greater during daylight hours. Additionally, it has been thought that areas of high corvid abundance should experience higher nest depredation than areas of low corvid abundance if artificial nests are biased towards depredation by sight-oriented predators (Andren et al. 1985). My results do not support this hypothesis. While abundance of corvid birds was highly significantly different between the Ninepipe area and all 3 study areas east of the continental divide, artificial-nest success was similar at all study areas (Table 5). Surprisingly, the high densities of corvids at the Ninepipe area appeared to have little effect on artificial-nest survival.

Another prediction supported by previous research is that artificial-nest depredation declines as the nesting season progresses (Gottfried and Thompson 1978, Sugden and Beyersbergen 1986). Some researchers have hypothesized that this decrease in depredation is due to changing vegetation height and density and/or prey switching by nest predators because of lower nest densities later in the nesting season (Johnson 1979). An increase in vegetation height and density could hinder sight-oriented predators in their ability to locate nests, and prey switching would result in fewer nests depredated. Like Gottfried and Thompson (1978) and Sugden and Beyersbergen (1986), my results showed a decrease in nest depredation through the nesting season, but were not designed to investigate causes for this decline. Additionally, results of previous studies of artificial nests indicated high rates of depredation during the first 10 days of nest exposure (Jones and Hungerford 1972, MacIvor et al. 1990). Artificial nests in my study experienced a higher rate of depredation during the first 10 days of exposure as compared to the last 11 days of exposure (Fig. 6).

I also examined other hypotheses regarding the role of nest vegetation on nest survival. Clark and Nudds (1991) proposed that nest concealment may be most important when primary nest predators are avian, and the hypothesis that artificial-nest survival is positively correlated with density, height, and/or weight of nest vegetation is supported by many studies (Jones and Hungerford 1972, Sugden and Beyersbergen 1987, Mankin and Warner 1992). However, results from my study were not conclusive. The consistently weak relationship between nest-site MVHD and nest survival (Fig. 7) did not support this hypothesis. However, the strong relationship between research-site MVHD and nest success did support this hypothesis. Confoundingly, logistic regression results, while weak, did indicate nest-site MVHD and nest-initiation date as significant covariates in the artificial-nest survival model. This may be due to the effects of nesting-cover vegetation growth being realized late in the growing/nesting season. Thus, it appears the ability to predict nest survival based upon nest vegetation measurements varies with regard to the scale at which the relationship is being evaluated. Survival of individual nests may be regulated more by a nest's proximity to a predators home range or slight variations in the nest site environment (Krasowski and Nudds 1986, Crabtree et al. 1989, Durner and Edward 1989). However, because nest vegetation and nest success of research sites is calculated from numerous nests and nest measurements, small variations that make a large impact at the individual nest scale may be masked at the research site scale. Therefore, a trend visible at one scale may not be visible at another.

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CHAPTER 4

DISCUSSION

While artificial nests have been widely used, the technique has undergone few critical evaluations of its performance (Storass 1988, Willebrand and Marcstrom 1988, Guyn and Clark In Press). This project provided a thorough evaluation of the validity of using the artificial-nest technique to predict nest success in upland-nesting ducks. I compared success rates of artificial and natural nests, examined characteristics of artificial-nest depredation, and evaluated the effects of corvid abundance and nest vegetation on nest survival. Additionally, sample sizes were adequate, and allowed for proper data analyses and experimental design. This study incorporated numerous sites well dispersed across a wide geographic area (800 km E-W), encompassed a wide range of natural-nest success rates, and provided a rigorous test of the artificial-nest technique. I chose to test this technique because it is still being used (e.g., Niemuth and Boyce 1995, Pasitschniakarts and Messier 1995), and is an appealing technique with regards to expense and effort.

The usefulness of artificial-nest success as an index to natural-nest success

Storass (1988) compared depredation rates on artificial- and natural-capercaille (Tetrao urogallus) nests, and found that artificial-nest success was not a valid index to natural-nest success. Similarly, Willebrand and Marcstrom (1988) compared depredation rates for artificial and natural nests of Eurasian black-grouse (Tetrao tetrix) and reported that artificial-nest success was not a reliable index to natural-nest success. Recently, Guyn and Clark (In Press) found no correlation between artificial- and natural-waterfowl nests in Saskatchewan. My results support those of Storass (1988), Willebrand and Marcstrom (1988), and Guyn and Clark (In Press): there was not a consistent relationship between survival of artificial- and natural-nests across the state of Montana. At some research sites, success was higher for artificial nests than it was for natural nests whereas at other sites the reverse was true. The relationship between artificial- and natural-nest success was strongest at DNC research sites. However, due to the overall weak relationship between artificial- and natural-nest success ($F = 3.44$, $R^2 = 0.20$, $P = 0.08$) (Fig. 2.) this relationship is not strong enough to justify using artificial nests as surrogates for natural nests. Thus, basing research or management decisions upon artificial-nest studies can be misleading.

The observed differences between artificial-nest success and natural-nest success are apparently the result of differential rates of depredation on the 2 nest types. Artificial and natural nests likely present different cues that differentially attract various species of nest predators to each nest type. Natural nests have attending hens which offer visual, olfactory, and auditory cues (Hammond and Forward 1956, Erikstad et al. 1982). Additionally, during incubation, hens camouflage their clutches of eggs with down and nest debris before they leave nests to feed. Visual cues provided by artificial nests appeared limited but varied with the amount of concealing nest vegetation available at the nest site. My artificial nests had duck-down linings but likely had less scent than natural nests. Thus, it is quite likely that my artificial nests differed from natural nests in terms of sight and scent. Furthermore, the nature of these differences, especially visual differences, probably changed from site to site and year to year with vegetation changes.

Clark and Nudds (1991) proposed that nest concealment may be most important when primary nest predators are avian. This hypothesis has been supported by observations of higher artificial-nest success in areas with heavier cover (Jones and Hungerford 1972, Sugden and Beyersbergen 1987, Mankin and Warner 1992, this study). Thus, during my study vulnerability of artificial nests probably varied dramatically. At sites or times with less concealing vegetation and/or more avian predators, artificial nests were probably more vulnerable. At sites or times with thick cover and/or fewer avian predators, artificial nests may have been quite secure.

Additionally, natural nests were probably variable in their vulnerability: I found no relationship between MVHD and natural-nest success (Fig. 3.). Given my results, I agree with Dwernychuk and Boag (1972) and Storass (1988): avian nest predators likely discover artificial nests at a different rate than they do natural nests, yielding different depredation rates for artificial and natural nests.

Factors influencing artificial-nest survival

Corvids are sight-oriented predators, and some researchers have hypothesized that survival of artificial nests is biased low because sight-oriented predators destroy them at a higher rate than they do natural nests (Picozzi 1975, Angelstam 1986, Martin 1987, Storass 1988, Willebrand and Marcstrom 1988). Based upon this hypotheses, daytime depredation of nests should be greater than nighttime depredation if artificial nests are more easily detected by sight-oriented predators. Results of this study support this prediction: depredation of nests was greater during daylight hours.

Additionally, it has been thought that areas of high corvid abundance should experience higher nest depredation than areas of low corvid abundance if artificial nests are biased towards depredation by sight-oriented predators

(Andren et al. 1985). My results do not support this hypothesis. While abundance of corvid birds was highly significantly different between the Ninepipe area and the 3 study areas east of the continental divide, artificial-nest success was similar at all study areas (Table 5). Surprisingly, the high densities of corvids at the Ninepipe area appeared to have little effect on artificial-nest survival.

Another prediction supported by previous research is that artificial-nest depredation declines as the nesting season progresses (Gottfried and Thompson 1978, Sugden and Beyersbergen 1986). Some researchers have hypothesized that this decrease in depredation is due to changing vegetation height and density and/or prey switching by nest predators because of lower nest densities later in the nesting season (Johnson 1979). An increase in vegetation height and density could hinder sight-oriented predators in their ability to locate nests, and prey switching would result in fewer nests depredated. Like Gottfried and Thompson (1978) and Sugden and Beyersbergen (1986), my study showed a decrease in nest depredation through the nesting season, but was not designed to investigate causes for this decline. Additionally, results of previous studies of artificial nests indicated high rates of depredation during the first 10 days of nest exposure (Jones and Hungerford 1972, MacIvor et al. 1990). Artificial nests in my study experienced a higher rate of depredation during the first 10 days of exposure as compared to the last 11 days of exposure (Fig. 6).

I also examined other hypotheses regarding the role of nest vegetation on nest survival. Although the hypothesis that artificial-nest survival is positively correlated with density, height, and/or weight of nest vegetation is supported by many studies (Jones and Hungerford 1972, Sugden and Beyersbergen 1987, Mankin and Warner 1992), results from my study were not conclusive. The consistently weak relationship between nest-site mean vegetative height-density (MVHD) and nest survival (Fig. 7) did not support this hypothesis. However, the strong relationship between research-site MVHD and nest success did support this hypothesis. Thus, it is possible that the ability to predict nest survival based upon nest-vegetation measurements varies with regard to the scale at which the relationship is being evaluated. Survival of individual nests may be regulated more by a nest's proximity to a predator's home range or slight variations in the nest site environment (Krasowski and Nudds 1986, Crabtree et al. 1989, Durner and Edward 1989). However, because nest vegetation and nest success of research sites is calculated from numerous nests and nest measurements, small variations that make a large impact at the individual nest scale may be masked at the research site scale. Therefore, a trend visible at one scale may not be visible at another.

Conclusion

Although most researchers caution against using survival of artificial nests to estimate natural-nest success, many argue that the technique is a valid means of studying avian nesting ecology (e.g., Yahner and Voytko 1989). Based on my results, I disagree. If artificial nests are used to study factors that influence nest depredation, the only information gained regards factors that influence artificial-nest depredation.

My results clearly indicate that the strength of the relationship between artificial- and natural-nest success varies by year and habitat type. Additionally, they not only suggest that the relationship is not strong, they suggest that artificial-nest success will lead to wrong conclusions regarding natural-nest success in many situations. Thus, given the weak and variable relationship between artificial- and natural-nest success, I conclude that, (1) the technique should not be used for upland-nesting ducks in the mid-continent and (2) researchers working in other areas/species should evaluate the usefulness of the technique over the range of areas and rates they wish to consider.

My study provided a good range of corvid abundance and nest vegetation measurements to test for effects of vegetative concealment on artificial-nest survival but was still unable to predict artificial-nest survival. Clark and Nudds

(1991) proposed that nest concealment may be most important when primary nest predators are avian. However, because knowledge of the type of predator was not available, the respective impact of mammalian and avian-nest depredation cannot be known.

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APPENDICES

APPENDIX A

Table 6. Presence/absence of nest predators at 4 study areas during the nesting season for ducks, April-August, 1993-1994.

Nest Predator	Scientific name	Ninepipe area	Benton Lake NWR[a]	Bowdoin NWR	Medicine Lake NWR
Striped skunk	Mephitis mephitis	Yes	Yes	Yes	Yes
Red fox	Vulpes vulpes	Yes	Yes	Yes	Yes
Raccoon	Procyon lotor	Yes	Yes	Yes	Yes
Coyote	Canis latrans	Yes	Yes	Yes	Yes
Bull snake	Pituophis melanoleucus	Yes	Yes	Yes	Yes
Richardson's ground squirrel	Spermophilus richardsonii	Yes	Yes	Yes	Yes
Mink	Mustela vison	Yes	Yes	Yes	Yes
Badger	Taxadea taxis	Yes	Yes	Yes	Yes
Long-tailed weasel	Mustela frenata	Yes	Yes	Yes	Yes
Domestic cat	Felis sylvestris	Yes	Yes	Yes	Yes
Domestic dog	Canis familiaris	Yes	Yes	Yes	Yes
California gull	Larus californicus	Yes	Yes	Yes	Yes
Ringbill gull	Larus delawarensis	Yes	Yes	Yes	Yes
Black-billed magpie	Pica pica	Yes	Yes	Yes	Yes
American crow	Corvus brachyrhynchos	No	Yes	Yes	Yes
Raven	Corvus corax	Yes	Yes	No	No

[a] NWR=National wildlife refuge

APPENDIX B

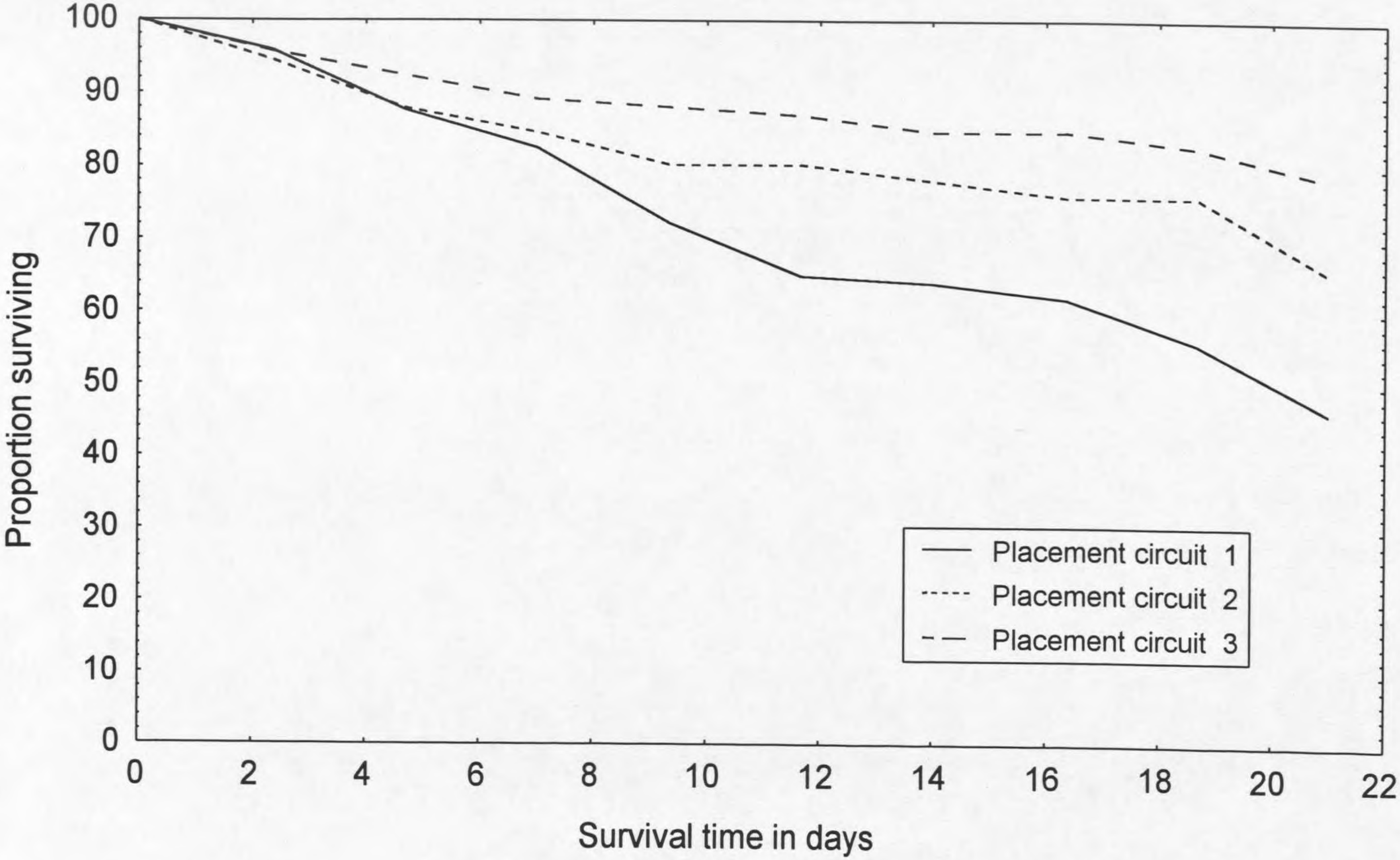

Figure 8. Kaplan-Meier survivorship curves for 3 placement circuits of artifical nests across northern Montana, 1994.

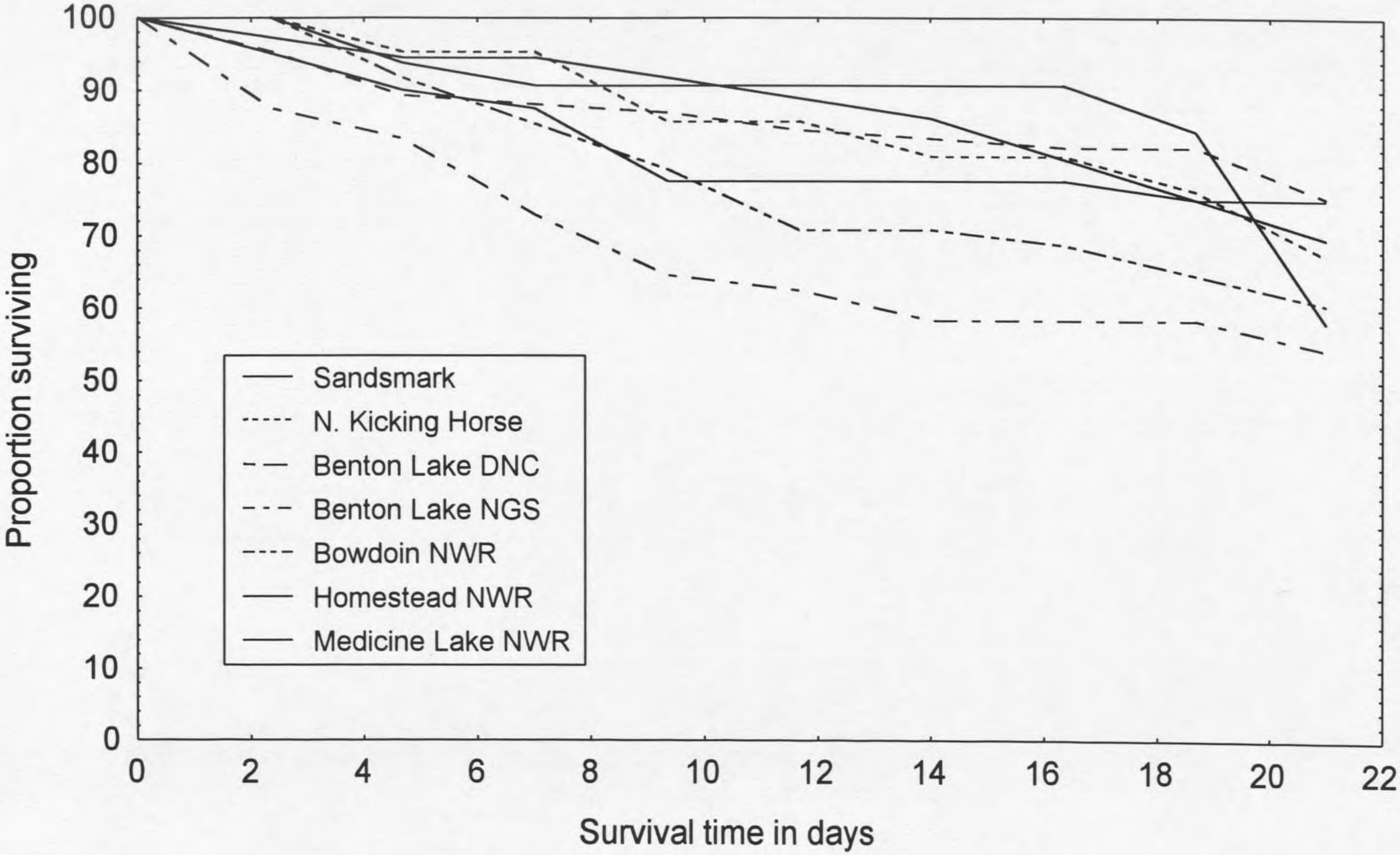

Figure 9. Kaplan-Meier survivorship curves of artificial nests placed on 7 research sites across northern Montana, 1994.