

NEST SITE SELECTION PATTERNS OF DABBING DUCKS IN RESPONSE  
TO VARIATION IN PREDATION PRESSURE: AN EXPERIMENTAL STUDY

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## ABSTRACT

Nesting success is an important vital rate affecting the reproductive fitness of birds, and predation typically is the single most important factor affecting nesting success. Presumably, birds should nest in locations that maximize nest survival. If specific nest characteristics increase the probability that a nest will hatch, natural (phenotypic) selection could favour use of sites with these features, producing nonrandom patterns of nest site use. Alternatively, birds that are highly selective in nest site choices might be at a disadvantage if predators learn to forage preferentially in these locations and improve their efficiency in depredate nests; in this case, random nesting patterns could be favoured. Finally, it has been hypothesized that predation pressure can influence nest site selection patterns of entire bird communities. If predators develop a search image to hunt for bird nests, then nests that are most similar to each other, irrespective of species, should sustain higher mortality. To evaluate these hypotheses, I quantified nest site selection patterns of multiple species of ground-nesting dabbling ducks in areas where predation pressure was normally high, and compared these patterns to those on areas where predation was relaxed. Predation pressure was experimentally reduced by removing common predators of duck nests and females (mainly red foxes, coyotes, skunks and raccoons) on some study areas and not on others (controls). Predator removal and natural causes produced a 10-fold difference in duck nesting across study sites, allowing for investigation of effects of predation pressure on nest site selection of ducks.

Coarse scale habitat selection patterns were similar to results reported in previous studies; blue-winged teal and northern shoveler were found more often in native grassland than in other habitat types, while gadwall and mallard nests occurred more frequently in shrub patches when compared with other habitat patches. A difference in nest site characteristics was observed between hatched and depredated nests for gadwall and northern shoveler but not for blue-winged teal and mallard. However, in all species, the nest site selection patterns were non-random. Thus, the process of nest predation did not shape patterns of nest site choice.

Contrary to predictions, inter-specific overlap in nest site features was not related to predation pressure: nests that overlapped most with features of other species did not suffer higher predation, nor did inter-specific overlap in nest characteristics decrease during the nesting season. These findings were inconsistent with the hypothesis that community-level patterns of nest site use are differentiated as a result of predation pressure. Long-term work on nest site use by individually marked females of numerous ground-nesting bird species would be informative, as would experimental studies of other hypotheses about factors affecting nest site choices in birds.

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And now, as did the Ramones, so do I: I wanna be sedated.....

Dedicated to my old friend, mentor, and hunting partner George Sotnikow. He taught me to revere the animals we eat and had an effect on me that he didn't realize at the time, but I sure did and won't forget. He was one of the great ones.



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## **CHAPTER 1: GENERAL INTRODUCTION**

### **1.1 NESTING SUCCESS AND NEST SITE SELECTION**

Birds presumably choose nest locations based on criteria that influence reproductive success and/or survival of the nesting adults. Nest placement may have implications for nest-site microclimate which in turn may influence temperature, water loss from eggs, or thermal costs to incubating females, all of which could affect survival of the eggs and female (With and Webb 1993; Gloutney and Clark 1997). Parasite avoidance may also influence nest site placement, as parasites may be associated with specific nesting locations or features, possibly impairing health of females or their offspring (Brown and Brown 1986). Choice of nest site has far-reaching implications for reproductive success and survival, and female attributes or tactics that reduce the probability of predators finding the nest should be favoured (see Martin 1993, Martin 1998, McKee et al. 1998).

Martin (1988, 1993, 1995, 1996, 1998) investigated nest site selection in songbirds and hypothesized that the specific mechanisms of nest site selection could evolve in response to nest predation. Nest predation is the primary cause of nest failure in many groups of birds (e.g., Ricklefs 1969), including ducks (Klett et al. 1986, Sargeant et al. 1993, Greenwood et al. 1995). If choice of nest sites have a genetic basis, natural selection could favour characteristics of nest site placement that reduce predation risk, thereby increasing fitness of individuals that possess such characteristics.

Martin's studies of songbirds revealed that predation rate increased as density of nests and similarity of nest site characteristics increases. Predator species

develop a search image for profitable prey (e.g., nests), so if nests occur in relatively high density, predators will learn to hunt in such areas, and subsequently concentrate hunting effort in associated habitats (Martin 1988). If nests of different species have similar characteristics, predators that develop refined search images could become more efficient in finding nests. Since clutches of duck eggs represent a substantial nutritional reward, regardless of duck species, predator pressure might affect entire nesting communities, because an increase in overlap of duck nest site characteristics, both inter- and intra-specifically, could lead to decreased nesting success through refinement of predator search image and, hence, enhanced predator foraging efficiency.

Conversely, predators may be less efficient at finding nests with very different site attributes due to slower or even a lack of search image development. Martin's (1988, 1993, 1996) work led to the development and initial testing of this idea: predation rate on songbird nests decreased as density of nests that shared similar features decreased (i.e., overlap of nest site characteristics decreased). Martin argued that the mechanism underlying this process was an impaired ability by predators to develop a search image for nests, resulting in reduced success at foraging by predators.

Since a high degree of overlap in nest site characteristics could have direct fitness costs, predation pressure should create an increase in the partitioning of nest site characteristics, favouring greater differentiation in inter-specific and intra-specific nest site characteristics. Other things being equal, high predation pressure should result in a high degree of inter-specific and intra-specific nest site



partitioning (low degree of overlap of nest site characteristics). If ducks can respond to predation pressure within the same nesting season by altering nesting behaviour on subsequent re-nests (as suggested by Clark and Shutler 1999), overlap of nest site characteristics should decrease throughout the nesting season. This could occur as a product of predation (i.e., only dissimilar nests remain after predation) or as an adaptive response on the part of re-nesting female ducks.

Several studies have investigated differences in nest site characteristics between successful and destroyed nests (i.e., the process of selection) or differences between nest and random sites (i.e., pattern of selection; reviewed by Clark and Shutler [1999]), but few studies have linked pattern and process. Thus, other study objectives were to (1) compare successful and destroyed nests to allow prediction of the pattern of nest site selection; and (2) subsequently compare predicted patterns with observed patterns of nest site use. This will provide valuable insights into whether predation actually produces or reinforces patterns of nest site selection.

As mentioned above, predation pressure was experimentally manipulated in this study by removing predators from some study sites and leaving other sites as controls. Martin's hypothesis predicts that inter-specific overlap in nest characteristics will be directly related to predation pressure, as indexed by daily mortality rate of nests, such that areas of high predation rates will have lower nest site overlap. Furthermore, if female ducks can learn from failed nesting attempts and respond adaptively to nest predation, similarity of nest site characteristics should decrease throughout the nesting season and this trend should be most pronounced in areas with greater nest predation pressure.

The study was conducted on multiple, independent study sites, with each site having large samples of nests of several duck species. To my knowledge, this was the first experimental investigation of the effects of predation pressure on nest site selection by ducks.

## **1.2 THESIS ORGANIZATION**

The thesis is composed of two parts. The first part (Chapter 2) investigates effects of nest predation on the intra-specific patterns of nest site use by dabbling ducks. Specifically, nest site characteristics of successful (hatched) nests were compared to those of unsuccessful nests. Differences in nest characteristics from each group were then compared to predicted patterns, allowing evaluation of whether predation pressure could produce patterns of nest site use.

The second part of the thesis (Chapter 3) investigates whether predation pressure can influence patterns of nest site selection within an entire community of nesting ducks. I follow the rationale and methods used by Martin (1996) to test the generality of his hypothesis about the potential role of nest predation in structuring nest choices in a diverse bird community.

The thesis concludes (Chapter 4) with a general discussion about results obtained from this work, their relevance to ducks and to studies of avian nest site selection. I also suggest avenues for further work on this and related topics.

## **CHAPTER 2. NEST PREDATION AND INTRA-SPECIFIC PATTERNS OF NEST SITE USE IN DABBLING DUCKS**

### **2.1 INTRODUCTION**

An animal's choice of nest site can be influenced by numerous constraints, but predators represent the single most important cause of nest failure in many taxa (see Spencer and Thompson 2003), including most bird species (e.g. Ricklefs 1969). Natural selection could favour choice of nest characteristics or other behavioral responses that reduce predation risk, increasing fitness of individuals that possess these characteristics, but it is unclear whether a genetic basis exists for nest choices or if nest site choices are learned. Non-random patterns of nest use are commonly found, and many studies report differences between successful and depredated nests, creating potential for phenotypic and evolutionary responses (Jones 2001). However, most studies fail to determine whether mechanisms exist where predation pressure could produce patterns of nest site use (for exceptions see Martin 1998, Clark and Shutler 1999, Traylor et al. 2004). Here, I address this deficiency by evaluating patterns of nest site use in four species of dabbling ducks on areas with a five-fold difference in predation pressure (as indexed by nest survival); to my knowledge, this is the first experimental study conducted with large samples of nests on multiple, independent study sites.

Nest predation is the primary cause of nest failure in ducks (Klett et al. 1986, Sargeant et al. 1993, Greenwood et al. 1995), so it is reasonable to hypothesize that predation pressure could shape nest site selection patterns (e.g. Krasowski and Nudds 1986). Females are most vulnerable to predators when nesting, more so than

at any other phase of the life cycle, and with average annual adult survival  $<0.60$  in most species, most female ducks typically survive only one or two breeding seasons. Thus, several conditions could favour optimal nest site placement by female ducks, regardless of the precise behavioral or genetic mechanism.

My objective was to test whether predation could produce patterns of nest site use in ducks. If predation creates nest use patterns, I predicted that: (1) microhabitat nest site features that distinguish successful from depredated nests would also be those that best segregated nests from random sites; (2) ability to segregate hatched and destroyed nests would be better in areas with lower than higher nest survival; and, therefore, (3) nest site selection patterns (i.e., differences between nests and random sites) would be most pronounced in areas with lower nest survival.

## **2.2 STUDY AREA**

Work was conducted near the towns of Ceylon (529353E, 5478067N) and Ogema in southeastern Saskatchewan, *ca.* 75 km southwest of Weyburn. Primary land use is cultivation of cereal and oil seed crops, and livestock production. Much of the area is cultivated annually although some small (typically  $< 140$  ha) parcels of native grassland pasture and hay production areas are present. The area is typified by rolling hills with a high density of semi-permanent, seasonal and ephemeral wetlands. The study area lies within the grassland ecoregion of Saskatchewan where native vegetation communities are typically grassland or grassland-short shrub communities. Common native plant species in the area include grasses (*Agropyron* spp., *Bouteloua* spp., *Festuca* spp., *Hordeum* spp., *Koeleria* spp., *Poa* spp., *Stipa* spp.), shrubs such as western snowberry (*Symphoricarpos occidentalis*),

rose (*Rosa* spp.), and silverberry (*Elaeagnus commutata*), as well as various forbs. Naturally-occurring trees are rare, with most trees occurring as planted shelterbelts.

### 2.3 METHODS

Nine sites were studied once during 1999 – 2001 (each site studied for one nesting season only), each site consisting of a 41 km<sup>2</sup> contiguous area separated by >6.3 km from other study sites to reduce possible effects of predator removal on adjacent non-removal sites. Coarse-scale habitat composition was quantified by overlaying 100 randomly assigned points on an aerial photo mosaic map (1:20000 scale) of each site (400 total in each of 2000 and 2001), and assessing habitat type. Habitat assignments were verified with ground visits.

Predator removal by trapping was conducted from 10 March (i.e., well before ducks started nesting) to 15 July each year. In 1999, one professional trapper alternated trapping efforts between two sites, and targeted raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*) on one site and removing raccoons, skunks, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) on the other. In 2000 and 2001, raccoons, skunks, coyotes and red foxes were removed from two sites each year; however, one professional trapper trapped only one site, spending consecutive trapping days on the same site. Some non-target species (badger [*Taxidea taxus*], mink [*Mustela vison*], Franklin's ground squirrel [*Citellus franklini*]) were caught accidentally and destroyed. Predators were caught using any legal means including trapping via body grip traps, foot hold traps, live traps, power snares, and shooting. Poison was not used. All trapping was conducted under Saskatchewan Environment and Resource Management (SERM) special permits S99-H25-012 (1999), S00-

H2E-05 (2000), and S01-H2E-40 (2001). Nest searching and other field research activities were conducted under University of Saskatchewan Animal Care protocols 20000025 and 20010055 on behalf of the Canadian Council on Animal Care, and under Canadian Wildlife Service scientific permits CWS00-S004 and CWS01-S003.

In 1999, a total of ~130 mammals were captured on two predator removal sites. Cumulative numbers of predators captured on each site rose rapidly from mid-April to mid-June, and then increased more gradually until late June before leveling off (Appendix B, Figure B1). In 2000 and 2001, >200 mammals were removed annually on predator removal sites. Cumulative number of captures rose steadily from mid-March to mid-July and did not appear to level off (Figures B2 and B3).

Detailed information recorded in 2000 and 2001 indicated that raccoons and skunks accounted for >60% of predators captured on each site. Totals of 76 raccoons and 145 skunks were captured during 41,211 trap-nights in 2000, compared with 68 and 80, respectively, during 39,360 trap-nights in 2001. In these two years, 51 red foxes, 51 badgers and 34 coyotes were removed.

Overall, duck nest success was unrelated to predator control in 1999: estimates were very similar and confidence intervals overlapped on all three sites (Table 2.1). However, in 2000 and especially in 2001, duck nest success was much higher on predator removal sites, in some cases 2-3 times higher than on controls. With few exceptions, species-specific success estimates were consistent with those using all species combined, so females of all species had higher success in predator-reduced environments. This observation also provides some support for combining species into low, medium and high nest success groups for DFA (Figure 2.1).

**Table 2.1 Mayfield nesting success estimates for study sites near Ceylon, Saskatchewan, in 1999-2001. Shown for each species are number of nests found, daily survival rate (DSR), nesting success and lower and upper 95% confidence interval estimates (CI) for nesting success. DSR was not estimated when fewer than 10 nests of a species was found on a site.**

1999 Site A (Removal)					
Species <sup>a</sup>	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	1	-	-	-	-
AMWI	16	0.943	0.14	0.04	0.45
BWTE	53	0.949	0.17	0.09	0.30
GADW	68	0.969	0.33	0.22	0.48
LESC	5	-	-	-	-
MALL	51	0.943	0.13	0.06	0.26
NOPI	4	-	-	-	-
NSHO	22	0.970	0.36	0.19	0.64
Total	220	0.957	0.22	0.17	0.29
1999 Site B (Control)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	2	-	-	-	-
AMWI	9	-	-	-	-
BWTE	57	0.969	0.34	0.22	0.50
GADW	55	0.969	0.33	0.22	0.51
LESC	2	-	-	-	-
MALL	49	0.959	0.23	0.13	0.39
NOPI	10	0.932	0.11	0.01	0.93
NSHO	34	0.950	0.17	0.08	0.36
Total	218	0.962	0.27	0.21	0.34

Table 2.1 Continued...

1999 Site C (Removal)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	9	-	-	-	-
AMWI	15	0.971	0.37	0.18	0.78
BWTE	41	0.972	0.38	0.24	0.58
GADW	89	0.975	0.41	0.30	0.55
LESC	3	-	-	-	-
MALL	96	0.961	0.25	0.17	0.37
NOPI	21	0.972	0.40	0.21	0.76
NSHO	25	0.958	0.23	0.10	0.51
Total	299	0.968	0.33	0.28	0.40
2000 Site D (Removal)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	3	-	-	-	-
AMWI	6	-	-	-	-
BWTE	63	0.955	0.21	0.12	0.35
GADW	38	0.952	0.18	0.09	0.37
LESC	7	-	-	-	-
MALL	59	0.947	0.15	0.08	0.29
NOPI	4	-	-	-	-
NSHO	16	0.926	0.07	0.02	0.30
Total	196	0.950	0.18	0.13	0.24



Table 2.1 Continued...

2000 Site E (Removal)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	1	-	-	-	-
AMWI	1	-	-	-	-a
BWTE	64	0.974	0.40	0.28	0.58
GADW	40	0.983	0.55	0.38	0.80
LESC	1	-	-	-	-
MALL	57	0.963	0.27	0.16	0.45
NOPI	13	0.971	0.40	0.15	0.99
NSHO	30	0.967	0.32	0.15	0.65
Total	207	0.973	0.39	0.31	0.49
2000 Site F (Control)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	3	-	-	-	-
AMWI	10	0.935	0.11	0.02	0.56
BWTE	61	0.960	0.25	0.16	0.40
GADW	32	0.951	0.17	0.08	0.38
LESC	3	-	-	-	-
MALL	63	0.937	0.10	0.05	0.21
NOPI	11	0.973	0.42	0.17	0.99
NSHO	23	0.936	0.10	0.03	0.31
Total	206	0.950	0.18	0.13	0.24

Table 2.1 Continued...

2000 Site G (Control)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	2	-	-	-	-
AMWI	11	0.923	0.07	0.01	0.40
BWTE	61	0.922	0.06	0.03	0.14
GADW	43	0.923	0.06	0.02	0.16
LESC	1	-	-	-	-
MALL	64	0.909	0.04	0.01	0.09
NOPI	7	-	-	-	-
NSHO	20	0.925	0.07	0.02	0.25
Total	209	0.920	0.06	0.04	0.09
2001 Site H (Removal)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	0	-	-	-	-
AMWI	7	-	-	-	-
BWTE	35	0.994	0.82	0.68	1.00
GADW	57	0.993	0.80	0.67	0.95
LESC	6	-	-	-	-
MALL	104	0.992	0.75	0.64	0.87
NOPI	27	0.987	0.65	0.46	0.92
NSHO	28	0.988	0.67	0.49	0.93
Total	264	0.992	0.75	0.68	0.82

Table 2.1 Continued

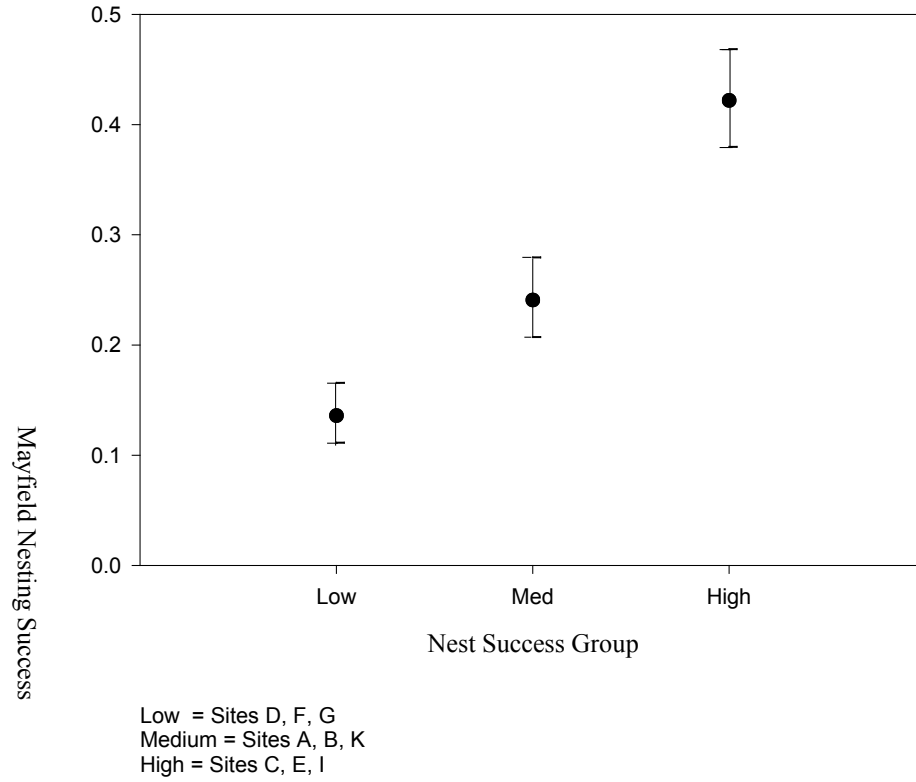
2001 Site I (Removal)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	0	-	-	-	-
AMWI	2	-	-	-	-
BWTE	38	0.987	0.64	0.47	0.86
GADW	52	0.994	0.80	0.66	0.96
LESC	3	-	-	-	-
MALL	72	0.977	0.45	0.33	0.61
NOPI	14	0.967	0.35	0.14	0.81
NSHO	32	0.989	0.68	0.51	0.91
Total	213	0.985	0.60	0.52	0.68
2001 Site J (Control)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	0	-	-	-	-
AMWI	5	-	-	-	-
BWTE	53	0.955	0.21	0.13	0.36
GADW	75	0.980	0.50	0.38	0.65
LESC	4	-	-	-	-
MALL	29	0.942	0.12	0.05	0.31
NOPI	13	0.957	0.24	0.08	0.70
NSHO	27	0.958	0.24	0.12	0.47
Total	206	0.965	0.30	0.24	0.37

Table 2.1 Continued

2001 Site K (Control)					
Species	Number of nests	DSR	Nesting success	Lower CI	Upper CI
AGWT	0	-	-	-	-
AMWI	4	-	-	-	-
BWTE	36	0.970	0.35	0.22	0.57
GADW	39	0.955	0.20	0.10	0.38
LESC	2	-	-	-	-
MALL	42	0.943	0.13	0.06	0.27
NOPI	28	0.952	0.21	0.09	0.47
NSHO	26	0.940	0.12	0.04	0.32
Total	177	0.953	0.20	0.14	0.27

<sup>a</sup> Species acronyms are AGWT (American green-winged teal), AMWI (American wigeon), BWTE (blue-winged teal), GADW (gadwall), LESL (lesser scaup), MALL (mallard), NOPI (northern pintail), NSHO (northern shoveler).

**Figure 2.1 Mayfield nesting success and 95% confidence intervals of pooled study sites near Ceylon, SK 1999-2001.**  
**Groups were used for comparing nest site selection patterns across a gradient of nesting success.**



Following methods described in Klett et al. (1986), nests were located by towing a 75 meter chain between two all-terrain vehicles. Female ducks were identified to species by plumage when flushed from the nest, or by using a combination of size and color of eggs, and/or contour feathers at nests (Klett et al. 1986). Nests were marked using a white lathe (1m x 5cm x 0.8cm) placed 20 meters from the nest in alternating cardinal directions. Lathes were marked with the nest number. A one meter tall willow cane was also placed one meter from the nest to aid nest checks. Incubation stage of eggs was determined by field candling (Weller 1956).

Nests were re-visited every seven to 10 days until fate was determined, recording number of eggs and incubation stage. Nests were considered successful if at least one egg hatched as determined by counts of intact membranes: other possible fates included abandoned, abandoned due to human disturbance, or depredated (Klett et al. 1986). Nests were considered abandoned due to human disturbance when it was clear that the female had not returned after the last visit (i.e., stage of incubation was unchanged and eggs were cold or wet). These nests were visited once more to confirm abandonment and, when abandoned, excluded from nest success analyses.

Nest searching crews consisted of two observers working in pairs on each site from early May until early to mid-July. Nest searching was conducted between 0800 and 1400 to increase the probability of encountering females on nests

(Gloutney et al. 1993). Searches were organized so that temporal overlap occurred across all sites during the nesting season. Within sites, all suitable nesting cover (excluding growing crops and crop stubble) on entire quarter sections was searched at least twice. The number of quarter sections searched per site depended on weather, but included > 25% (16 quarter sections) of the site. When time and weather permitted, larger areas of each site were searched.

Vegetation measurements were taken within 20 centimeters of the nest bowl at all nests (on three sites in 1999, four sites in 2000, and two sites in 2001), following methods used in other studies (see Bowman and Harris 1980, Livezey 1981, Crabtree et al. 1989, Guyn and Clark 1997, Pasitschniak-Arts et al. 1998, Clark and Shutler 1999). All site measurements were recorded at hatched or depredated nests only during the final nest check and, for each nest, at a randomly selected site within 200 meters of the nest (Appendix A). Each year, observers (four per year) measured an equal proportion of nests on each site to reduce systematic observer bias. All nests (and random sites) on removal and non-removal (control) sites were measured.

Nesting success was calculated for each species when >9 nests of that species were found on a study site using Mayfield's method (see Johnson 1979). Estimates of daily survival rate for each species were raised to the average number of days, by species, from the start of egg-laying until hatching.

Sites were initially grouped based on similarity of nest success estimates (Johnson 1979) as judged by overlapping 95% confidence intervals (CI); sites with common nest success (see Table 2.1) were then pooled into three groups with no overlap in 95% CI, representing low, moderate and high nest success rates.

## 2.4 STATISTICAL ANALYSES

All analyses were performed using SPSS. Patch-level nest choices were assessed by comparing the relative habitat distributions of blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), mallard (*Anas platyrhynchos*), and northern shoveler (*Anas clypeata*) nests with random sites using a contingency table analysis. Other species of ducks were excluded due to small sample sizes. Habitat patches were wetland margin, hay, native grassland, shrub patch, and road ditch.

Vegetation data were plotted and tested for normality to investigate distribution patterns and outliers, and variables were transformed when this improved normality. Distance to water and distance to edge were log-transformed; all other variables could not be normalized and were left in the original scale. Because variables did not vary with measurement date or year, no adjustments were made for temporal variation.

Principal Components Analysis (PCA) was initially conducted on vegetation variables (Gauch 1984), and PCA indicated that there was little data structure (i.e., variables contributed independently to total variance), with eigenvalues  $>0.70$  for five of six components. Principal component one explained only 28.5 % of the total variance and the remaining components explained from 19% to 9% of the total variation each. Thus, since PCA could not collapse the data in multivariate space, original variables were included in further analyses.



#### **2.4.1 Discriminating hatched from destroyed nests**

Discriminant function analyses (DFA) were conducted separately for blue-winged teal, gadwall, mallard, and northern shoveler to determine whether hatched nests could be distinguished from nests destroyed by predators, based on associated vegetation. DFA was first conducted on nests from non-removal sites only. Then, DFA was conducted on the entire data set, by species, to determine whether successful classification of hatched and destroyed nests varied among sites grouped by nest predation intensity. Since DFA scores were derived from the same analysis, chance-corrected classification success and variance of DFA scores could be compared directly among nest success groups (low, medium, and high nest success). Differences in the variance of DFA scores among groups were determined with tests for homogeneity of variance. As well, two-sample Kolmogorov-Smirnov tests were conducted to test for differences in the distribution of DF1 scores between nest success groups by species. Finally, analysis of variance tests (using Tukey's post hoc test) were used to test for differences in DFA scores between nest success groups for each species.

#### **2.4.2 Discriminating nests from random sites**

DFA was conducted separately for blue-winged teal, gadwall, mallard, and northern shoveler to evaluate whether nests could be distinguished from their matched random sites using site characteristics. DFA was conducted first on nonremoval sites only to determine how nest sites (of each species) differed from corresponding random sites in an un-manipulated environment. DFA was then conducted on the entire data set to identify broad patterns of nest site selection, overall and by nest success group (low, medium, and high nest success).

## 2.5 RESULTS

### 2.5.1 Patch-level habitat selection

Land use was dominated by agricultural activities, with >75% of land devoted to crop, grazed pasture, and hay lands (Table 2.2). Nest site selection patterns at the habitat patch level were determined by conducting a species x patch type contingency table analysis (Table 2.3). Blue-winged teal and northern shoveler nests occurred in native grassland more often than all other patch types (60% and 50%, respectively) whereas mallard and gadwall nests were found most often in shrub patches (41% and 50%, respectively). In general, nesting ducks used road ditches in proportion to availability whereas nests were found in wetland margins in lower proportion to the availability of wetland margins. Ducks made limited use of hay land, possibly because it was unsuitable until later in the nesting season.

A habitat patch type x nest success group contingency table analysis was conducted for each species to determine if coarse-scale habitat selection differs between nests under varying degrees of predation pressure (nest success group). Patch level nest site selection did not differ by nest success group for blue-winged teal ( $\chi^2 = 15.61$ ,  $df = 12$ ,  $P = 0.21$ ), mallard ( $\chi^2 = 16.40$ ,  $df = 10$ ,  $P = 0.09$ ) or northern shoveler ( $\chi^2 = 11.42$ ,  $df = 8$ ,  $P = 0.18$ ). There was, however, a difference in coarse-scale habitat selection between nest success group for gadwall ( $\chi^2 = 29.57$ ,  $df = 12$ ,  $P = 0.003$ ). Gadwall nests were found less often in native grassland in the higher predation pressure area (17%) than in medium (25%) or low (27%) predation areas.

**Table 2.2. Overall habitat composition (%) of study sites located near Ceylon, Saskatchewan, in 2000 and 2001 based on distribution of 400 randomly selected locations per year (100 per site per year).**

	2000	2001
Crop	51.5	49
Grass	16.3	17.5
Wetland margin	13.7	10.5
Hay	9.5	9.5
Shrub	1.5	3.8
Ditch	5.5	4
Water	2	5.6

**Table 2.3 Overall habitat patch type distribution of duck nests and random sites found near Ceylon SK (1999-2001). Numbers indicate the percentage of nests of each species that was found in a specific habitat type.**

Species (nests) or Random sites	Patch Type				
	Wetland Margin	Hay	Native Grassland	Shrub Patch	Road Ditch
Blue-winged teal (455)	20	4	60	6	10
Northern shoveler (218)	18	7	50	16	9
Gadwall (434)	8	7	24	50	11
Mallard (541)	10	3	30	41	16
Random (1648)	30	9	43	6	12

### **2.5.2 General patterns of nest site selection**

Using nests found on nonremoval sites, DFA provided good segregation of hatched and destroyed gadwall (Wilk's lambda = 0.977,  $P = 0.004$ ) and northern shoveler (Wilk's lambda = 0.826,  $P = 0.012$ ) nests, but not blue winged teal (Wilk's lambda = 0.957,  $P = 0.211$ ) and mallard (Wilk's lambda = 0.954,  $P = 0.173$ ) nests. Hatched gadwall nests were in taller vegetation and were closer to water than depredated nests (Table 2.4). Successful shoveler nests were placed in taller vegetation but with less shrub than depredated nests (Table 2.4).

Ability to discriminate hatched from destroyed nests was similar between nest success groups (low, medium, high) for blue-winged teal, with classification success between 0.54 (medium) and 0.58 (high), and was better than chance for all groups (Table 2.5). Classification success for gadwall was also similar between nest success groups, with success varying between 0.54 (low) and 0.60 (high); classification success was better than chance for low and medium nest success groups, but not for the high nest success group. Classification success for mallard and northern shoveler tended to decrease with increasing nest success, but classification success was no better than chance for any nest success group in these two species (Table 2.5).

When differences in variance of DF1 scores were compared between nest success groups, no statistical difference was obtained for blue-winged teal (Levene Statistic = 2.11, d.f. = 2, ,  $P = 0.12$ ), gadwall (Levene Statistic = 0.56, d.f. = 2, ,  $P = 0.57$ ), mallard (Levene Statistic = 1.18, d.f. = 2, ,  $P = 0.31$ ), or northern shoveler

(Levene Statistic = 0.31, d.f. = 2, , P = 0.731). Variance of DF1 scores tended to decrease with increasing nest success for all species except gadwall (Table 2.5), but not significantly so.

Results of Kolmogorov-Smirnov tests indicated that there was no difference in distribution of DF1 scores between nest success groups for any species except blue-winged teal, where there was a difference in distribution between high and low nest success groups and intermediate and high nest success groups (Table 2.6). Blue-wing nests tended to be loaded more negatively on DF1 on the high nest success sites, suggesting that they tended to be found in shorter vegetation with less overhead concealment on areas where predation was relaxed.

**Table 2.4 Standardized Canonical Discriminant Function Coefficients for each nest site variable for each species for DF1. Discriminant Function Analysis was conducted to discriminate hatched from depredated nests found near Ceylon, SK (1999-2001).**

	Blue-winged teal	Gadwall	Mallard	Northern shoveler
Maximum height of live vegetation	-.618	-.684	-.599	-.697
Percent shrub	.219	-.006	.472	.487
Percent live vegetation	.439	.170	.017	.384
Concealment	.644	.280	-.144	.061
Distance to water	.033	.465	.514	.261
Distance to habitat patch edge	.226	.018	.052	-.338

**Table 2.5 Classification success for hatched and destroyed nests by nest success group for nests found near Ceylon, SK (1999-2001). Classification success was determined by DFA and compared to classification success expected by chance (with associated Z statistic and P values). Also shown is variance of DF1 scores.**

Species	Nest success group	N	Classification Success	Chance classification	Z statistic	P	Variance of DF1 scores
Blue-winged teal	Low	163	0.58	0.51	1.79	0.037	1.25
	Medium	164	0.54	0.50	1.15	0.125	0.98
	High	91	0.57	0.48	1.79	0.023	0.72
Gadwall	Low	98	0.54	0.46	1.63	0.051	0.95
	Medium	230	0.57	0.52	1.61	0.054	1.08
	High	89	0.60	0.59	0.09	0.464	1.10
Mallard	Low	147	0.73	0.72	0.03	0.488	1.04
	Medium	222	0.63	0.59	1.39	0.082	1.10
	High	111	0.38	0.36	0.48	0.315	0.80
Northern shoveler	Low	53	0.79	0.73	1.00	0.161	1.12
	Medium	93	0.58	0.53	1.02	0.153	1.13
	High	56	0.34	0.33	0.02	0.436	0.92



**Table 2.6 Results of Kolmogorov-Smirnov two independent sample tests of the distribution of DF1 scores between nesting success groups by species for nests found near Ceylon, SK (1999-2001). Shown are K-S Z statistic for each analysis and the P-value of the test.**

Species	Nest success group comparison	K-S Z	P (two-tailed)
Blue-winged teal	Low-Medium	1.233	0.095
	Low-High	1.727	0.005
	Medium-High	2.377	<0.001
Gadwall	Low-Medium	1.172	0.128
	Low-High	0.885	0.414
	Medium-High	1.072	0.201
Mallard	Low-Medium	0.974	0.299
	Low-High	0.772	0.590
	Medium-High	0.744	0.638
Northern shoveler	Low-Medium	0.700	0.712
	Low-High	1.035	0.234
	Medium-High	0.957	0.319

Results of analysis of variance conducted to investigate differences in DF1 scores for each species by nest success group indicate that there was no difference in DF1 scores between nest success groups for gadwall (ANOVA,  $F = 1.736$ ,  $df = 2$ ,  $P = 0.178$ ), mallard (ANOVA,  $F = 0.45$ ,  $df = 2$ ,  $P = 0.956$ ), or northern shoveler (ANOVA,  $F = 2.250$ ,  $df = 2$ ,  $P = 0.109$ ). DF1 scores for blue-winged teal differed between the high and low nest success groups (Tukey's post hoc multiple comparison test,  $P = 0.001$ ), and intermediate and high nest success groups (Tukey's post hoc multiple comparison test,  $P < 0.001$ ). Results of this test supported the results of the two sample K-S tests where nests on the high nest success sites tended to be found in shorter vegetation with less overhead concealment when compared with nests from the other nest success groups.

### **2.5.3 Discriminating nests from random sites**

Blue-winged teal nests were distinguished from random sites (Wilk's lambda = 0.84,  $df = 6$ ,  $P < 0.001$ ) on control sites, with concealment being the only variable that was strongly correlated (correlation greater than 0.40) with DF1. Blue-winged teal nests had more overhead concealment than associated random sites. Regarding the difference between nests and random sites of gadwall, percent shrub, overhead concealment, and maximum height of live vegetation were strongly correlated (Wilk's lambda = 0.77,  $df = 6$ ,  $P < 0.001$ ) with DF1 (canonical correlation = 0.48) (Table 2.7). Gadwall nests had more shrub, more overhead concealment, and taller live vegetation than associated random sites (Table 2.7).

Percent shrub, overhead concealment, and maximum height of live vegetation were strongly correlated with DF1 in the analysis involving mallard nests and

random sites on control sites (canonical correlation = 0.44; Wilk's lambda = 0.80, df = 6, P<0.001). Mallard nests had more shrub, more overhead concealment, and taller live vegetation than associated random sites (Table 2.7).

With regard to northern shoveler nests versus random sites, the canonical correlation was 0.31 (Wilk's lambda = 0.91, df = 6, P = 0.003). Overhead concealment and maximum height of live vegetation were strongly correlated with DF1. Northern shoveler nests had more overhead concealment, and taller vegetation than associated random sites (Table 2.7).

When data from all nine sites are pooled, the same variables described discrimination between nest sites and random sites by species (i.e., differences between nests and random sites (of a species) were the same). Classification success remained relatively constant across the three nest success groups, ranging from 0.59 to 0.80 correct classification of nests and random sites (Table 2.8).

**Table 2.7 Standardized Canonical Discriminant Function Coefficients for each nest site variable for each species for DF1. Discriminant Function Analysis was conducted to discriminate nests from associated random sites for nests found near Ceylon, SK (1999-2001).**

	Blue-winged teal	Gadwall	Mallard	Northern shoveler
Maximum height of live vegetation	0.139	0.503	0.532	-0.244
Percent shrub	0.155	0.750	0.711	-0.109
Percent live vegetation	0.047	0.039	-0.083	0.073
Concealment	1.038	-0.370	-0.343	0.883
Distance to water	-0.017	0.048	-0.026	0.073
Distance to habitat patch edge	0.072	-0.073	-0.003	-0.112

**Table 2.8 Classification success by species of DFA discriminating nests from random sites across a nesting success gradient (low to high) for nests found near Ceylon, SK (1999-2001).**

Species	Nest Success Group	% Correctly Classified
Blue-winged teal	Low	70
	Medium	59
	High	69
Gadwall	Low	80
	Medium	71
	High	74
Mallard	Low	73
	Medium	72
	High	72
Northern shoveler	Low	67
	Medium	60
	High	70

## 2.6 DISCUSSION

Blue-winged teal and northern shoveler nests were most commonly found in native grassland patches while gadwall and mallard nests were most commonly found in shrub patches. All species nested in wetland margins less often than would be expected by availability. These broad patterns of nest site selection at the habitat patch level followed patterns observed in other studies of nest site selection by these species (see Gloutney and Clark 1997, Clark and Shutler 1999).

If predation pressure is driving nest site selection and nesting birds respond to this pressure, it is expected that nesting birds will choose “optimal” sites that enhance survival probability. Thus, differences in nest site characteristics between successful and depredated nests were expected. Also, if nesting birds are responding adaptively to predation pressure the same nest site characteristics that describe the difference between successful and failed nests would also describe the difference between nests and random sites (see Traylor et al. 2004) as birds are trying to nest or their nests survive longer in “optimal” sites. This could result if birds actively choose nest sites that are less likely to be found by a predator or nests that are found are superior sites because they have already survived sufficiently long to be detected (i.e., they remain after predation has eliminated “easily found” nests).

My first prediction was that site features that distinguished successful from depredated nests would also be those that best segregated nests from random sites. There was a difference in nest site characteristics between hatched and depredated gadwall (successful nests were in taller vegetation and closer to water than depredated nests) and shoveler (successful nests were in taller vegetation and less

shrub than depredated nests) nests. Hatched and depredated nests of blue-winged teal and mallard could not be distinguished but, contrary to expectations, female teal and mallard nested non-randomly rather than randomly with respect to site-vegetative characteristics.

Gadwall nests had more shrub, more overhead concealment and taller vegetation than random sites and northern shoveler nests had more overhead concealment and were located in taller vegetation than random sites. Thus, the scenario where non-random nest site selection may occur in response to a nest survival advantage occurs in only two of the four species (gadwall and northern shoveler) where vegetation characteristics that describe the difference between hatched and destroyed nests also describe the difference between nests and random sites. Interestingly, nests of all species had more overhead concealment than random sites and all species except blue-winged teal nested in taller vegetation than expected based on random sampling, but these choices had no consistent effect on nest survival.

If there are survival advantages to certain nest site characteristics, it is expected that nests that possess these characteristics will survive and nests that lack these characteristics will be found more quickly by predators and destroyed. Thus, there will be more similarity between successful and destroyed nests in areas of low predation pressure because “sub-optimal” nests should survive longer in areas of lower predation pressure. Thus, I predicted that segregation of hatched and destroyed nests would be better in areas with lower than higher nest survival. However, classification success was remarkably similar across the gradient of nest

success (predation pressure) for all species. In addition, variance of DF1 scores (i.e., the difference between hatched and depredated nests in multivariate space) did not differ by nest success group (predation pressure). Therefore, there was no evidence that nest site use was more variable when predation was relaxed.

If birds can respond to perceived high predation pressure, birds should place nests non-randomly in available habitat to maximize survival probability. Thus, I also predicted that nest site selection patterns (differences between nests and random sites) would be most pronounced in areas with lower nest survival (i.e., higher predation pressure). Classification success between nests and random sites did not differ between nest success groups (from low to high predation pressure) for any species. Thus, there is no evidence that relative predation pressure influences the non-random nest site selection pattern.

The data presented herein indicate that predation may be influencing nest site selection patterns for gadwall and northern shoveler only. Nest site selection patterns for these two species are consistent with a scenario where non-random nest site selection patterns may be influenced by predation pressure; however, the pattern reported here does not support the idea that nest site selection patterns are adaptive.

Interestingly, all species exhibited non-random nest site selection patterns, with nests (when compared to random sites) having more overhead concealment for all species, and nests of all species except blue-winged teal were found in taller vegetation than random sites. While other studies have found evidence of predation as a selective force influencing nest site selection patterns (see review in Traylor et al. 2004), my data fail to support the predictions. Further investigation into the



effects of predation and other biotic and abiotic factors must be completed to improve our understanding of this complex system.

## **CHAPTER 3 THE INFLUENCE OF PREDATION PRESSURE ON PATTERNS OF COMMUNITY NEST SITE SELECTION BY DUCKS**

### **3.1 INTRODUCTION**

Studies of nest site selection by songbirds have revealed that predation rate increases as nest density and similarity of nest site characteristics increase (Martin 1996, 1998). Many predators develop a search image for profitable prey such as bird nests (see Nams 1997, Lariviere and Messier 1998), so if nests occur at relatively high density, predators will learn to hunt in such areas, and subsequently concentrate hunting effort in these habitats (Martin 1988). If nests of different species have similar characteristics, predators that refine their search images could become progressively more efficient at finding nests. While Martin assessed effects of predation pressure using nesting songbird communities, these principles should be applicable to other bird communities as well. For instance, predation could affect entire communities of ground-nesting ducks, because an increase in inter-specific overlap of nest site characteristics could reduce nesting success through enhanced predator foraging efficiency as predators' search images improve. By contrast, predators may be less efficient at finding nests with very different site attributes due to slower or even a lack of search image development. Martin's (1988, 1993, 1996) work supports this idea: predation rate on songbird nests decreased as density of similar nests decreased, and overlap of nest site characteristics decreased. However, despite the general importance of these findings to habitat selection theory, there have been remarkably few independent

tests of Martin's ideas (Marini 1997) and some results have not been consistent with Martin's hypothesis (e.g., Rangen et al. 2001).

Since a high degree of overlap in nest site characteristics could have direct fitness costs, predation pressure should create greater partitioning of nest site characteristics, favouring greater differentiation in inter-specific and intra-specific nest site characteristics. Other things being equal, nesting areas under high predation pressure should exhibit a high degree of inter-specific and intra-specific nest site partitioning (low degree of overlap of nest site characteristics). The latter prediction was not supported by work reported in Chapter 2: here, I focus on inter-specific patterns of nest site use. If ducks can respond to predation pressure within the same nesting season by altering nesting behaviour on subsequent re-nests, as suggested by Clark and Shutler (1999), overlap of nest site characteristics should decrease throughout the nesting season. This could occur as a product of predation (i.e., only dissimilar nests remain after predation) or as an adaptive response by re-nesting female ducks.

I present results of an experimental study examining duck nest site selection across study sites representing a ten-fold difference in nesting success. Martin's hypothesis about predation-induced nest site selection was tested by evaluating several predictions. First, I determined which variables contributed to inter-specific differences in nest site characteristics. If predation pressure produces nest site selection patterns, there must be survival advantages for nests that differ most from characteristics of nests of other species. Therefore, nest sites which overlap most will have lower daily survival rate than nests that are less similar to nests of other

species. If nesting birds can respond to predation pressure by altering patterns of nest site selection, or if predation pressure creates the pattern, I predicted that inter-specific nest site partitioning would be strongest (i.e., indicating less nest site overlap) in areas with high predation pressure, and inter-specific overlap in nest site features should decrease throughout the nesting season.

### **3.2 STUDY AREA AND GENERAL FIELD METHODS**

Study area, predator trapping, and general field methods were described in Chapter 2. Results of trapping effort, together with site and species-specific nesting success estimates, were also reported in Chapter 2; these findings also formed the basis for grouping study sites into areas of low, moderate and high predation pressure for some analyses described below.

### **3.3 STATISTICAL ANALYSES**

All analyses were performed using SPSS. Data transformations are described in Chapter 2.

Principal Components Analysis (PCA) was initially conducted on vegetation variables (Gauch 1984), and indicated that there was little data structure (i.e., variables contribute independently to total variance), with eigenvalues  $>0.70$  for five of six components. Principle component one explained only 28.5 % of the total variance and the remaining components explained from 19% to 9% of the total variation each. Thus, since PCA could not collapse the data in multivariate space, original variables were included in further analyses. All analyses were conducted on a constrained data set to include nests initiated during the period when all species of ducks were nesting, thus only including nests exposed to similar abiotic and

predator conditions. For these analyses, the period when all species were initiating nests extended from 19 May (day 140) to 23 June (day 175).

### **3.3.1 Inter-specific nest site selection patterns**

In general, I followed an approach that was similar to that described by Martin (1994). Discriminant Function Analysis (DFA) was conducted on nest vegetation microhabitat variables to investigate inter-specific nest site selection patterns. Discriminant Function (DF) scores were calculated for each nest and Analysis of Variance (ANOVA) was conducted to test for differences in DF scores between species, with Tukey's test being used for post hoc multiple comparison tests between species.

Contingency table analysis was conducted to test for differences in nest site selection at the habitat patch scale (a more broad scale) between species with similar nest site microhabitat characteristics (blue-winged-teal versus northern shoveler, and gadwall versus mallard).

Kolmogorov-Smirnov (K-S) tests were conducted to test for differences in nest initiation date each year between species with similar nest site characteristics (blue-winged-teal versus northern shoveler, and gadwall versus mallard). These tests were conducted to investigate whether species with similar nest site microhabitat characteristics are segregating nests temporally.

### **3.3.2 Daily survival rate and nest site overlap (inter-specific and intra-specific)**

Mayfield nest success estimates were calculated separately, following Johnson (1979), for nests that were correctly assigned to species (low degree of inter-specific nest site overlap) and nests that were incorrectly classified to species

(high degree of inter-specific nest site overlap) by DFA. The first analysis consisted of all species pooled in the analysis to look for inter-specific differences between correctly and incorrectly classified nests; this increased the number of exposure days for each of the groups on each study site and improved the precision of daily survival rate estimates (Mayfield 1975). Mayfield nesting success and associated 95% confidence intervals were calculated for misclassified nests and correctly classified nests and estimates were compared between the groups to test for differences in nest success estimates between successfully classified and misclassified nests (to species).

A second intra-specific analysis was conducted on species with adequate sample size (blue-winged teal, gadwall, and mallard) only, pooling nests of each species across study sites to derive DF1 scores. Nesting success estimates and associated 95% confidence intervals were compared between correctly and misclassified nests of each species. While northern shoveler nests were relatively abundant on study sites, they were not analyzed because no shoveler nests were correctly classified to species, precluding a comparison of correctly classified and misclassified nests. All other species were excluded due to small sample size.

### **3.3.3 Inter-specific nest site partitioning and predation pressure**

A contingency table analysis was conducted for species with large sample size (blue-winged teal, gadwall, mallard, and northern shoveler) to test whether the patch-level nest site selection differed between species according to nesting success group (low, medium, high: see Figure 2.1).

Second, predicted (from DFA) species designation was compared to actual species of each nest using a contingency table analysis to calculate the percent of nests correctly classified to species for each site. Percent correct classification by study site was chance-corrected (Titus et al. 1984), and plotted according to Mayfield nesting success to look for trends in classification success across the gradient of predation pressure.

#### **3.3.4 Temporal change in nest site characteristic overlap**

DFA classification assignments for each nest (0 = incorrectly classified to species, 1 = correctly classified to species) were analyzed with logistic regression to test whether inter-specific nest site overlap (i.e., correct classification to species) changed over the nesting season.

## 3.4 RESULTS

### 3.4.1 Inter-specific nest site selection patterns

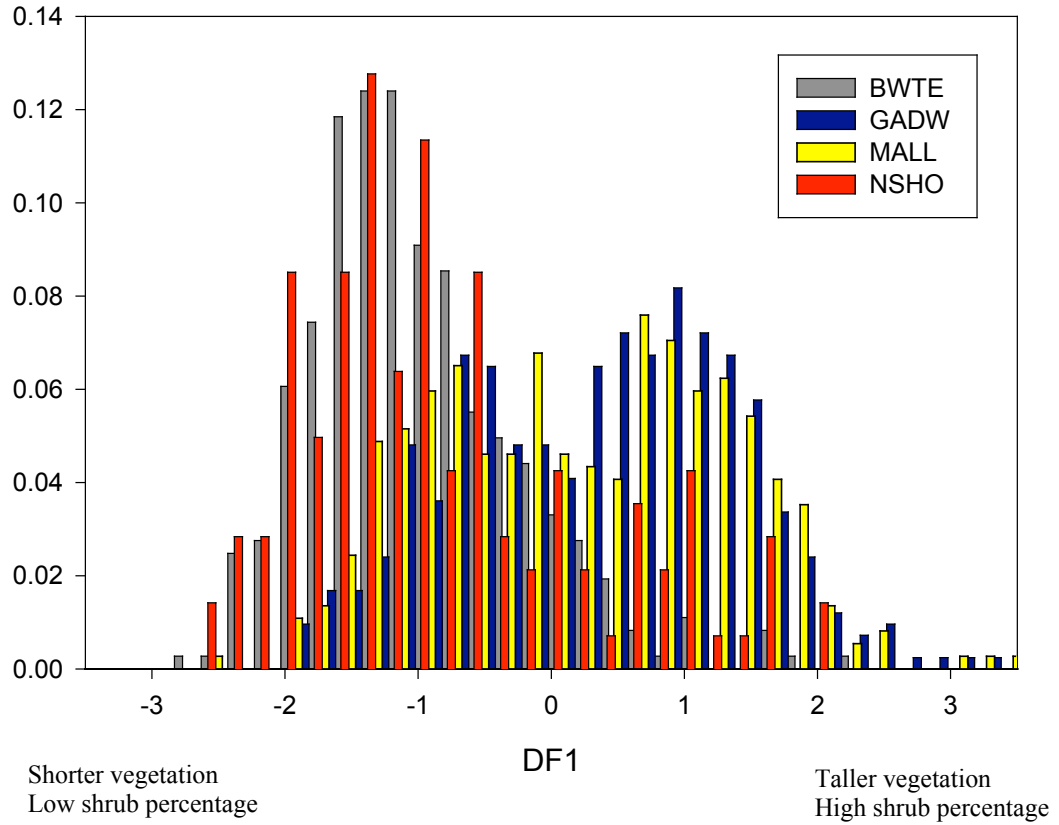
The first discriminant function (DF1) accounted for 94.6% of variance in the data when all species and study sites were pooled. The canonical correlation for DF1 was 0.553 (Wilk's lambda = 0.668,  $P < 0.001$ ). The remaining six DFs each accounted for  $< 2.5\%$  of variance, and were non-significant. Percent shrub and maximum height of live vegetation were positively correlated with DF1 (0.737 and 0.495, respectively: see Table 3.1). Green-winged teal, blue-winged teal, lesser scaup, and northern shoveler were negatively associated with DF1, while American wigeon (*Anas americana*), gadwall, mallard, and northern pintail were positively related to DF1. Thus, DFA produced separation of species based on a gradient in which green-winged teal, blue-winged teal, lesser scaup, and northern shoveler nests were located in sites with less shrub and shorter vegetation whereas American wigeon, gadwall, mallard, and northern pintail nests had more shrub and taller vegetation (Figures 3.1 and 3.2). When DF1 scores were plotted for these species, two distinct groups of species were apparent based on the loading on DF1. Specifically, with regard to species with  $>100$  nests, blue-winged teal and northern shoveler DF1 scores cluster together, while gadwall and mallard DF1 scores cluster together.

Contingency table analysis of macro-habitat characteristics (habitat patch type) indicated no difference in patch type nest site selection between blue-winged teal versus northern shoveler ( $\chi^2 = 3.67$ , d.f. = 5,  $P = 0.59$ ) or gadwall versus mallard ( $\chi^2 = 8.33$ , d.f. = 5,  $P = 0.14$ ).

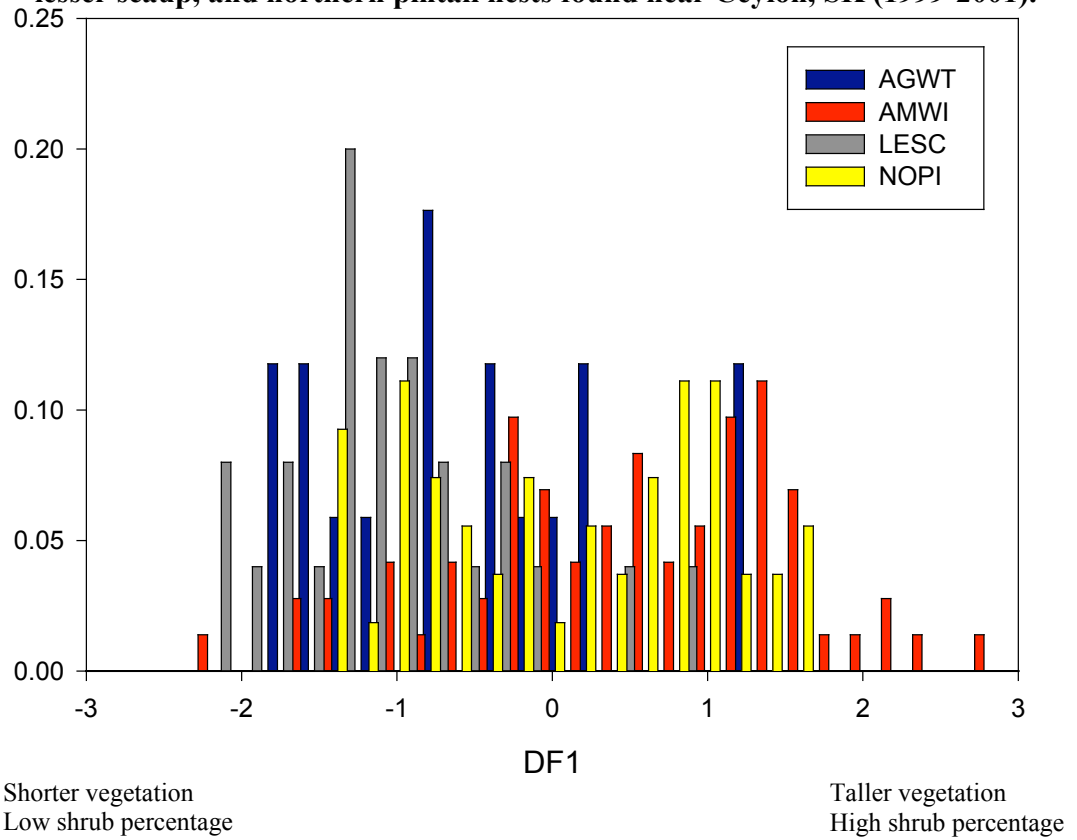


Results of the K-S tests on nest initiation date indicated that the distribution of blue-winged teal nest initiation dates was later than that of northern shoveler in 1999 (K-S  $Z = 1.51$ ,  $P = 0.02$ ) but not different in 2000 (K-S  $Z = 1.05$ ,  $P = 0.22$ ) or 2001 (K-S  $Z = 1.31$ ,  $P = 0.07$ ). K-S tests indicated that gadwall nest initiation dates were later than those of mallard in 1999 (K-S  $Z = 1.63$ ,  $P = 0.01$ ), 2000 (K-S  $Z = 2.20$ ,  $P < 0.01$ ), and 2001 (K-S  $Z = 2.45$ ,  $P < 0.01$ ).

**Figure 3.1. Histogram of discriminant function scores (DF1) (proportion of observations) for blue-winged teal, gadwall, mallard and northern shoveler nests found near Ceylon SK (1999-2001).**



**Figure 3.2. Histogram of discriminant function scores (DF1) (proportion of observations) for Green-wing teal, American wigeon, lesser scaup, and northern pintail nests found near Ceylon, SK (1999-2001).**



ANOVA was conducted on the DF1 scores for blue-winged teal-shoveler vs. gadwall-mallard . Comparison of DF1 scores indicated that teal nests were located in shorter vegetation with less shrub than shoveler nests (Tukey's multiple comparison test,  $\alpha = 0.05$ ;  $P = 0.001$ ), while there was no difference between gadwall and mallard (Tukey's test,  $P = 0.92$ ).

### **3.4.2 Daily survival rate and nest site overlap (inter-specifically and intra-specifically)**

Of 1463 nests in the analysis (all species), 681 nests were correctly classified to species. A total of 9397 exposure days was obtained for correctly classified nests and 10409 exposure days for misclassified nests. Pooled nesting success and 95% CI for nests correctly classified to species (i.e., nests with less inter-specific site overlap) was 27% (23% - 31%). Pooled nesting success and 95% CI for nests that were misclassified (i.e., nests with higher inter-specific site overlap) was 24% (21% - 28%). Since the 95% confidence intervals overlap, there is no difference in nesting success between nests that were correctly classified to species and nests that are misclassified to species.

Nesting success did not differ between correctly versus incorrectly classified blue-winged teal nests, while correctly classified gadwall nests had higher nesting success and mallard nests that were correctly classified to species had lower nesting success (Table 3.2). Thus, no consistent pattern was evident.

**Table 3.1 Standardized Canonical Discriminant Function Coefficients of DF1 for the analysis of the inter-specific differences in nest site selection for duck nests found near Ceylon, SK (1999-2001).**

Variable	Standardized Canonical Discriminant Function Coefficient
Maximum height of live vegetation	.654
Percent shrub	.836
Percent live vegetation	-.075
Concealment	.076
Distance to water	.268
Distance to habitat edge	-.029

**Table 3.2 Nesting success, 95% confidence intervals, and exposure days for correctly classified and misclassified (to species) blue-winged teal, gadwall, and mallard nests.**

Species	Classification	Exposure days	DSR	nesting success	Lower CI	Upper CI
Blue-winged teal	Incorrect	1090	0.963	0.28	0.19	0.42
Blue-winged teal	Correct	4197	0.962	0.27	0.22	0.33
Gadwall	Incorrect	2590	0.962	0.26	0.20	0.34
Gadwall	Correct	3575	0.975	0.41	0.34	0.50
Mallard	Incorrect	2942	0.959	0.24	0.18	0.31
Mallard	Correct	1448	0.936	0.10	0.06	0.16

### **3.4.3 Inter-specific nest site partitioning and predation pressure**

Classification success to species obtained from DFA was calculated for each study site, representing a difference in ranging from 6% to 60% (Table 3.3).

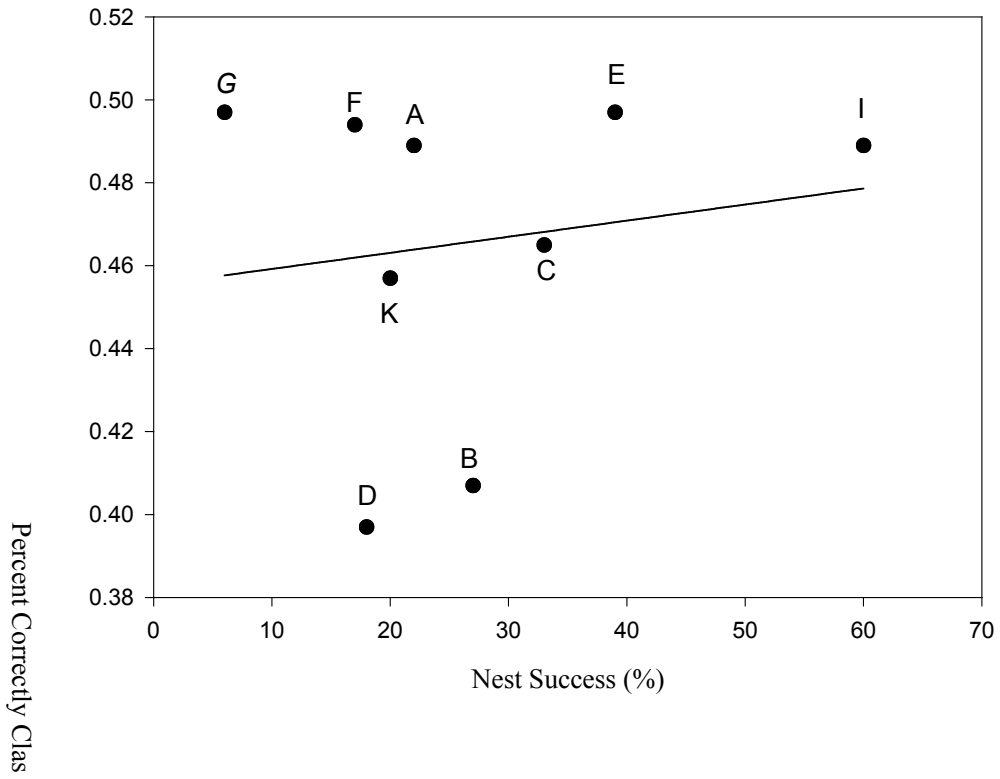
Classification success on all study sites except sites F ( $Z = 1.25$ ,  $P = 0.10$ ; low nest success group) and K ( $Z = 0.95$ ,  $P = 0.17$ ; medium nest success group) was better than expected by chance. Percentages of nests correctly classified to species were also plotted versus Mayfield nesting success estimates, with each nesting success estimate representing one study site (Figure 3.3). Correct designation to species did not improve with increasing nesting success ( $R^2 = 0.024$ ,  $F = 0.18$ ,  $df = 8$ ,  $P = 0.69$ ).

**Table 3.3 Success rate for designating duck nests to correct species obtained by using DFA compared with classification success expected by chance for study sites near Ceylon, Saskatchewan (1999-2001). Also shown are Z statistic and P-value.**

Study Site	N	Observed classification success	Classification success expected by chance	Z	P
A	184	0.49	0.37	3.208	0.001
B	177	0.41	0.32	2.502	0.006
C	213	0.47	0.36	3.272	0.001
D	146	0.40	0.28	3.117	0.001
E	145	0.50	0.40	2.346	0.010
F	158	0.49	0.44	1.255	0.106
G	177	0.50	0.39	3.019	0.001
I	133	0.49	0.41	1.829	0.034
K	129	0.46	0.42	0.948	0.174



**Figure 3.3 Percent of nests correctly classified to species versus Mayfield nesting success estimate for nests found near Ceylon, SK (1999-2001). Letters indicate study site (also see Table 3.3)**



The contingency table analysis of patch level nest site selection for blue-winged teal, gadwall, mallard, and northern shoveler indicated a difference between species in patch type selection for all three nest success groups. Chi square tests were significant for low ( $\chi^2 = 99.23$ , d.f. = 12,  $P < 0.001$ ), medium ( $\chi^2 = 98.41$ , d.f. = 12,  $P < 0.001$ ), and high ( $\chi^2 = 79.94$ , d.f. = 12,  $P < 0.001$ ) nest success groups. General patterns of nest site selection at the patch level did not differ between nest success groups (i.e., the between -species differences in patch level nest site selection were consistent across the gradient).

#### **3.4.4 Temporal change in overlap of nest site characteristics among species**

Logistic regression (overall model  $\chi^2 = 502.7$ , d.f. = 16,  $P < 0.001$ ) showed that likelihood of correctly classifying nests to species based on vegetation features did not vary with initiation date (Wald's  $\chi^2 = 0.43$ , d.f. = 1,  $P = 0.51$ ) or study site (Wald's  $\chi^2 = 14.97$ , d.f. = 8,  $P = 0.06$ ), but was related to species (Wald's  $\chi^2 = 254.5$ , d.f. = 7,  $P < 0.001$ ).

Likelihood of correctly classifying nests to species varied by species for blue-winged teal (Wald's  $\chi^2 = 134.84$ , d.f. = 1,  $P < 0.001$ ), gadwall (Wald's  $\chi^2 = 67.87$ , d.f. = 1,  $P < 0.001$ ), and mallard (Wald's  $\chi^2 = 36.22$ , d.f. = 1,  $P < 0.001$ ) only.

### 3.5 DISCUSSION

Until this study, Martin's (1996, 1998) innovative work on factors affecting nest site selection by birds had not been tested experimentally using natural nests. My study examined nest site selection by multiple ground-nesting duck species under varying levels of predation, creating ideal conditions for testing Martin's hypothesis; however, I failed to substantiate any *a priori* predictions about processes underlying nest site selection. Likewise, Rangen et al. (2001) failed to find support for predictions arising from this hypothesis; however, their study relied on artificial songbird nests which may not reliably indicate natural processes.

Inter-specific nest site selection patterns at the patch level were consistent with patterns identified in other studies (see Gloutney and Clark 1997, Clark and Shutler 1999). Two main "guilds" were evident in choices of nest site location. Green-winged teal, blue-winged teal, lesser scaup, and northern shoveler females tended to nest in shorter vegetation with less shrub cover than did female American wigeon, gadwall, mallard, and northern pintail.

In species with large sample size, blue-winged teal and northern shoveler nests tended to be similar to one another, while gadwall and mallard nests tended to be similar. Blue-winged teal nests were distinguished from shoveler nests by the height of vegetation and shrub component of the nests. Blue-winged teal nests tended to be located in shorter vegetation with less shrub than northern shoveler nests. Gadwall and mallard nest sites were very similar in nest site characteristics, however, mallards tend to initiate nests earlier than gadwalls. Importantly, inter-

specific differences in nest site characteristics allowed testing for differences in nest site selection patterns between species in relation to predation pressure.

If predators use specific cues to search for nests, Martin's theories of community response to the predation pressure would predict that nesting birds should differentiate their nests inter-specifically to depress search image development. Development of such a pattern would require that there be survival advantages for nests that are less similar to other nests (both inter-specifically and intra-specifically). Thus, it seems reasonable to predict that nests with a low degree of nest site overlap with other nests should have higher nesting success (see Marini 1997). Inter-specifically, this predicted pattern is not supported by the data. Intra-specifically, there is no difference in nesting success between nests that overlap other nests and nests that are different from other nests for blue-winged teal, while for gadwall nests that do not overlap with other nests have higher nesting success, and mallard nests that overlap with other nests have higher nesting success. There is no consistent trend intra-specifically between survival advantages and overlap in nest site characteristics.

Martin's theories would predict that predation pressure causes an increase in partitioning of nest site characteristics, so inter-specific classification success should increase with increasing predation pressure (i.e., lower nesting success), because there should be an increase in nest site partitioning between species at high levels of predation pressure (i.e., more difference in nest site characteristics between species). My results showed that the percent of nests correctly classified to species (degree of inter-specific nest site overlap) does not follow a trend of increasing classification

success with increasing predation pressure. There was no trend evident in the classification success versus predation pressure, with all study sites (representing a ten-fold difference in nesting success) having an inter-specific classification success between 40% and 50%. Coarse-level nest site selection (at the patch level) also shows no difference in overlap of inter-specific nest site selection at the patch level between different intensities of predation pressure.

Comparisons of species with similar nest site selection patterns (blue-winged teal versus northern shoveler and gadwall versus mallard) indicated that there is no difference between the species in terms of patch scale nest site selection. There was, however, a trend of segregation of nest sites temporally for gadwall-mallard in all years and blue-winged teal - northern shoveler in one year of the study. Thus, species with similar nest site microhabitat characteristics may be able to reduce predation risk by nesting at different times., a hypothesis that is untested.

Finally, Martin's theories predict that if nesting ducks can respond adaptively to predation pressure throughout the nesting season, the degree of overlap in nest site characteristics should decrease (indicating an increase in the degree of inter-specific nest site partitioning) throughout the nesting season so that birds can counteract effects of predator search image development. My data showed that there was no change in the degree of inter-specific nest site overlap throughout the nesting season; therefore, nesting ducks are not changing nest site selection patterns adaptively in response to predation pressure.

Possibly, the disparity between results of my investigation of nest site selection of ducks and results of Martin's investigations into the nest site selection

of songbirds may be described in the context of the ecological differences between study systems. Notably, Martin's work used forest songbirds as the study community. I speculate that the habitat where Martin's study occurred (high altitude, mixed conifer drainages) is more ecologically stable (with a relatively consistent predator community) than the agricultural landscape of my study. The Prairie Pothole Region of North America has undergone considerable change in the past century. Native prairie habitats have been converted to agricultural fields, wetlands have been drained, and importantly, the predator community has changed dramatically as a result of the changes in the prairie landscape (Sargeant et al. 1993). Specialist predators such as prairie wolves, grizzly bears, and swift foxes that occurred at relatively low densities have been replaced by high densities of generalist mesocarnivores such as striped skunk, raccoon, red fox, and coyote (Sargeant et al 1993). It seems plausible that the phenotypic nest site selection patterns that were observed in this study evolved in a different ecological environment (i.e., under predation pressure from a different suite of predators), and are not optimal for the current situation (Schlaepfer et al. 2002).

Alternatively, nest site selection of upland nesting ducks may be influenced by some factor other than predation pressure. Nest site selection of upland nesting ducks has been shown to be non-random in this study as well as many others (see Clark and Shutler 1999); however, this non-random pattern may be related more strongly to some factor that I did not investigate.

## CHAPTER 4 SYNTHESIS

The literature is replete with papers on nest site selection in birds, but very few have explicitly tested for processes underlying patterns of nest site use and few of these have manipulated factors hypothesized to affect nest placement (Clark and Shutler 1999, Jones 2001). Therefore, my study was unique in investigating experimentally how predation pressure influences nest site selection patterns of an entire duck nesting community, both intra-specifically and inter-specifically. Some studies of nest site selection propose that predation pressure can produce nest site selection patterns (e.g., Martin 1998, Clark and Shutler 1999). This hypothesis suggests that nesting birds should try to segregate nest site attributes from other species, and assumes that predators develop refined search images for nests. If predation pressure influences nest site selection of entire nesting communities of birds (as suggested by Martin 1996), I predicted that overlap of nest site characteristics would decrease with increasing predation pressure, intra and inter-specifically. In addition, I predicted that overlap of nest site characteristics would decrease during the nesting season. My results showed that nest site selection patterns of ground nesting ducks are non-random, but observed patterns did not closely match predicted patterns.

Intra-specifically, I predicted that nest site features that distinguish successful from depredated nests would also be variables that distinguished nests from random sites. Support for this prediction was mixed, being observed in gadwall and northern shoveler but not in blue-winged teal or mallard. In addition, if specific nest site

characteristics are advantageous, or birds segregate nest site characteristics to avoid predation pressure, it was predicted that the ability to segregate successful from depredated nests would be best in areas with high predation pressure, because either birds are segregating nest site characteristics in response to predation pressure, or only nests possessing advantageous characteristics would survive under higher predation pressure. Likewise, if predators favour non-random nest placement, I predicted that the ability to distinguish between nests and random sites would be most pronounced on high predation sites. However, neither pattern was observed, despite a 10-fold nesting success gradient across study sites.

Based on Martin's (1996) hypothesis, if there is a survival advantage to a decrease in the overlap of nest site characteristics, I predicted that there should be a difference in daily survival rate between nests that were most similar to nests of other species versus nests that possessed very different site characteristics. This prediction was not upheld; in four duck species, no difference in daily survival rate was found between nests of high and low overlap with nests of congeners. I also predicted that there would be increased partitioning of nest site characteristics in areas with high predation pressure however this trend was not observed. In addition, if birds are responding adaptively to predation pressure, there should be an increase in nest site partitioning throughout the nesting season. This pattern was not observed.

In general, few predictions about the role of predators in shaping nest site use patterns of ducks obtained support. I employed a strong experimental design, with large sample size and site replication, creating conditions that would favour



discovering patterns if they existed. Also, since there is strong evidence to suggest that predation pressure influences nesting communities of songbirds (Martin 1998), it is entirely plausible that the process may occur in ground nesting ducks, but at a different scale from that used in my study.

Results of this study are interesting when taken in context with other recent studies of the effects of predation pressure on nest site selection of birds. My findings are consistent with those reported by Rangen et. al (2001) for a study of predation pressure on nest success of artificial boreal songbird nests; they found that predation rate was not higher on plots composed of similar artificial nests versus plots with more varied nest characteristics and placement. Contrary to predictions, they also found no increase in variability of nest site characteristics of successful nests when predation pressure increased. In general, results of their study failed to support Martin's (1996) hypothesis. One critical point to consider is that their study used artificial nests which may have influenced predation rates.

Results from my study also differ from several of Clark and Shutler (1999), who found consistent evidence of directional selection on nest site characteristics for blue-winged teal and gadwall (hatched nests differed from depredated nests). Thus, their study and that of Traylor et al. (2004) on white-winged scoters (*Melanitta fusca*) supported the theory that predation pressure could provide a mechanism for nest site selection in ducks.

Why were my results contrary to Martin's (1996) studies of songbirds and somewhat different from Clark and Shutler's (1999) results on the same species of nesting ducks? One explanation is that methodological differences between studies

account for the different results. It is possible that the nest site variables that were measured during my study were less important in terms of predator avoidance (i.e., measured variables do not influence nest success). Thus, if the variables that are important in terms of the probability of a predator finding a nest were not measured, there would likely be no measured difference between hatched and destroyed nests (as was the case with this study) indicating a lack of selective forces even if predation is indeed important as a selective force.

Another possible explanation involves constraints placed on random site measurement. Since random sites were constrained to areas within 200 meters of a nest site, it is possible that measurements are not representative of available habitat. My results indicate non-random habitat selection in all four species at this scale, but these may not fully reveal habitat selection patterns of greater relevance to predation processes, and could possibly confuse patterns and relationships between the pattern of nest site selection and the natural selection process as driven by predation pressure.

Other possible explanations of the disparity between my results and the results of other studies involve spatio-temporal constraints. This study measured phenotypic nest site selection patterns of unmarked individuals on study sites that were studied for only one year. Thus, temporal evaluation of individual female responses to breeding success or failure was not possible. In addition, predation pressure was reduced while the birds were nesting, so it is possible that nest site selection decisions were made before relative predation pressure was depressed

sufficiently, so the measured predation pressure was not the same as when birds were choosing nest sites.

Aside from possible methodological differences that may account for the lack of support for Martin's theories, I postulate the following: since there is observed non-random nest site selection in ducks, and predation of nests strongly influences recruitment (and thus fitness), it seems reasonable that nesting ducks should try to decrease predation rate on nests. I suggest that the phenotypic patterns of nest site selection that were observed during this study were not appropriate for the current ecological situation. There is much evidence that the predator community on the prairies has changed substantially in the last century, with a switch from specialized predators such as grizzly bears and swift foxes to more generalist (and more numerous) mesocarnivores such as striped skunk, raccoon, and red fox. It seems possible that the nest site selection patterns of ducks evolved in a different ecological environment (most notably a different predator community), and may not be appropriate for the current ecological situation. Thus, we do not observe the predicted patterns of predation pressure influenced nest site selection patterns.

Future studies of the effects of predation pressure on the nest site selection patterns of nesting birds could follow a more robust study design by trying to eliminate some of the possible systematic bias that occurred in this study. Future studies should be conducted in areas where the predator community has been relatively stable over time. This would reduce the possibility that the phenotypic selection patterns evolved under a different predation scenario. Studies of nest site

selection of ground nesting ducks in the boreal forest would be a possible solution; however, nest searching logistics would hamper this. Studies of boreal forest songbirds would be ideal candidates. Experimental removal of predators would still need to be conducted to ensure variation in predation pressure. This should be done on multiple study sites over multiple years to investigate temporal variation.

Adaptive responses of nesting birds within a nesting season could be measured by radio marking females prior to the nesting season and following nest site selection throughout the nesting season on subsequent re-nests. Also, if natural selection is to occur on the nest site selection patterns, there must be a genetic basis for the nest site selection. Thus, genetic studies could be used to measure genotypic nest site selection patterns as this would give support to the idea that nest site selection patterns are genetic and thus can be influenced by natural selection. Then, it would be necessary to evaluate whether predation pressure influences the phenotypic expression of nest site selection patterns.

Further studies with strong experimental design and large sample sizes are required to gain final insight into the influence of predation pressure on nest site selection of nesting birds. Until these types of studies are conducted, it will be difficult to adequately assess the generality of Martin's ideas or other processes shaping nest site selection in birds.

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## APPENDICES

### Appendix A: Vegetation Measurements

The following measurements were taken at nests and random sites, with all measurements at the nest bowl being taken within 20 cm of the nest bowl:

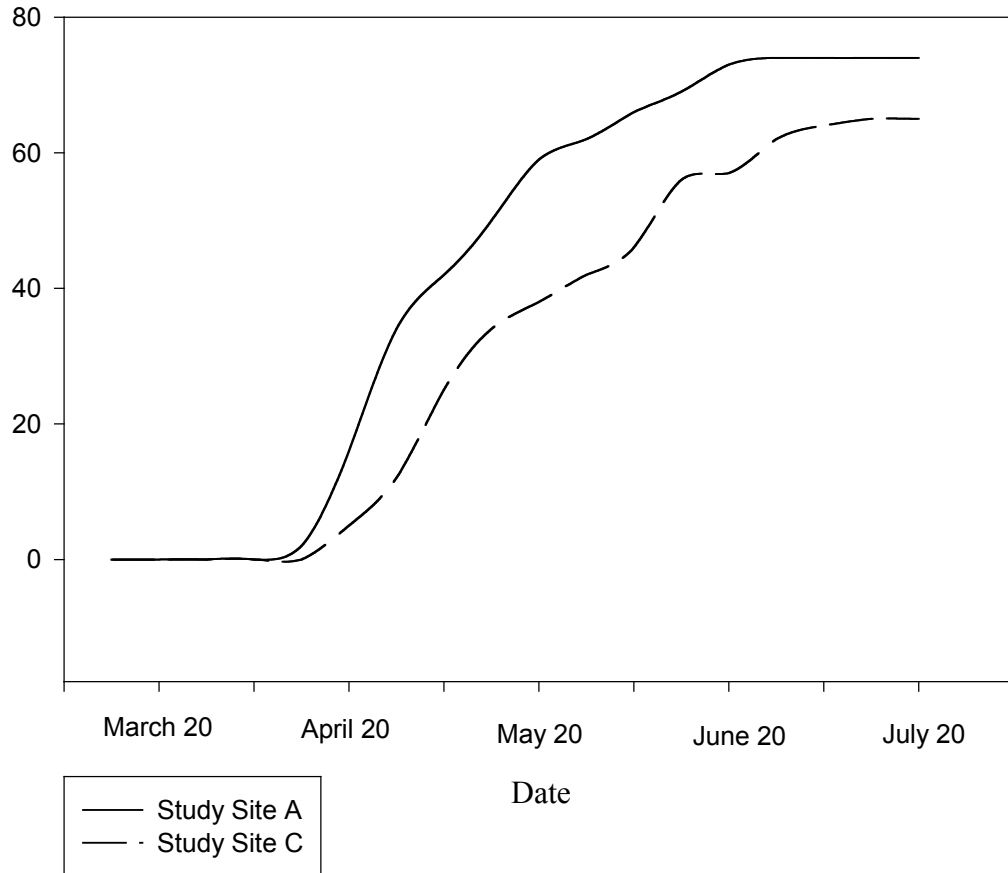
1. Maximum height of live vegetation.
2. Maximum height of dead vegetation.
3. Maximum height of understory vegetation. Understory vegetation is any vegetation that occurs as a sub-canopy layer beneath the tallest vegetation canopy.
4. Percent of vegetation cover composed of grass. This is a subjective estimate placed into five categories (0-21 %, 21-40 %, 41-60 %, 61-80 %, 81-100 %).
5. Percent of vegetation composed of shrub. This is a subjective estimate placed into five categories (0-21 %, 21-40 %, 41-60 %, 61-80 %, 81-100 %).
6. Percent living vegetation. This is a subjective estimate placed into five categories (0-21 %, 21-40 %, 41-60 %, 61-80 %, 81-100 %).
7. Distance to nearest water. This measurement is taken by pacing standardized meter paces to the nearest wetland. The distance is taken at the closest straight-line distance to the point where the observer's boot sole gets wet. Distances greater than 200 m are designated as such and not measured past 200 m.



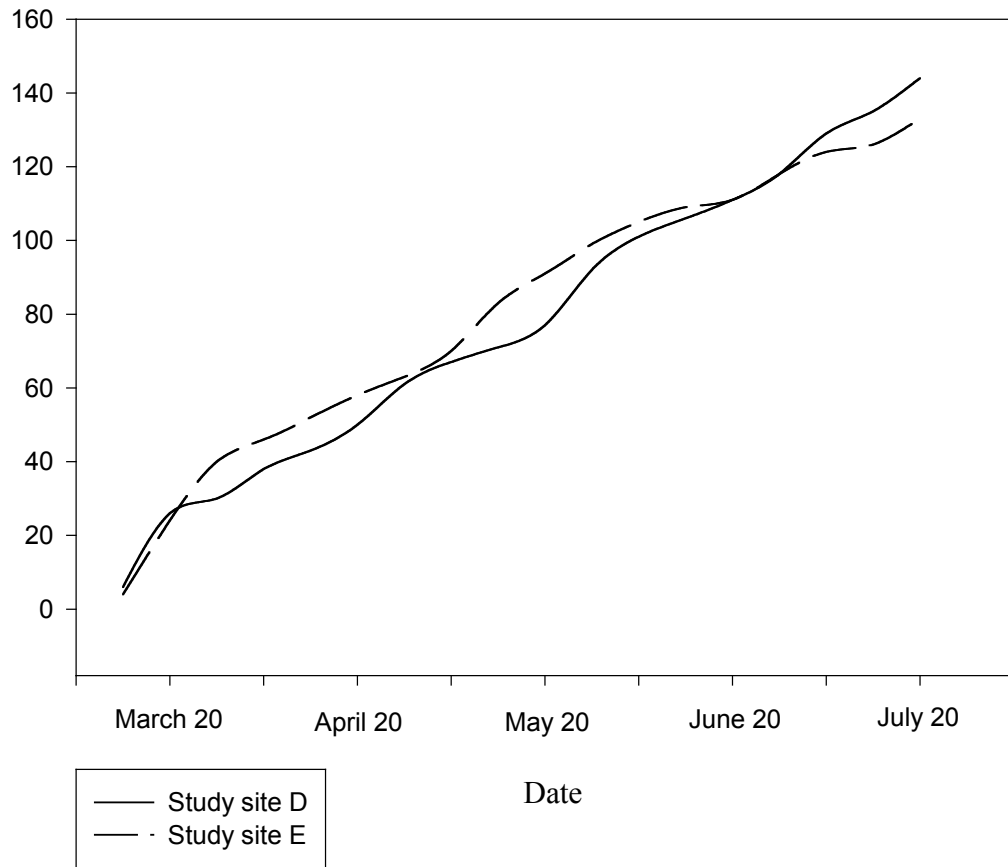
8. Distance to nearest habitat edge. Using standardized paces, the observer paces straight line to the nearest point where there is a visible change in the plant community surrounding the nest bowl. This edge may be a striking physical feature such as a road, or may be subtle such as the interface between a snowberry patch and native grassland.
9. Concealment index. This measurement is taken by placing a black disc with five white  $6.5\text{cm}^2$  squares painted on it into the nest bowl. The concealment index is the sum percentage of the white squares visible when viewed from 1m directly above the nest bowl.
10. Habitat patch type. Habitat patch type is the general habitat type that the nest bowl is located in, assigned to the following categories: Wetland Edge; Planted Cover (including hay or dense nesting cover); Native Grassland; Shrub; Tree; Roadside Ditch; Abandoned Farmyard.

## Appendix B Cumulative catch figures

**Figure B.1 Cumulative number of predators removed over time from study sites near Ceylon Saskatchewan (1999)**



**Figure B.2 Cumulative number of predators removed over time from study sites near Ceylon Saskatchewan (2000)**



**Figure B.3 Cumulative number of predators removed over time from study sites near Ceylon Saskatchewan (2001)**

