

AVIAN HABITAT SELECTION: PATTERN FROM PROCESS IN NEST-SITE USE BY DUCKS?

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Abstract. Patterns of habitat use in animals presumably have evolved in response to diverse selective processes, so we first examined whether the theory of natural selection formed the conceptual framework for published studies ($N = 270$) of nest-site selection by birds. Most (61%) studies of nest-site selection tested for pattern arising from natural selection (whether used nest habitat differed from available nesting habitat), many (54%) tested for evidence of the process of natural selection (whether unsuccessful nests differed from successful nests), some (10%) tested whether the process of natural selection caused subsequent adaptation, but remarkably few conceptually linked these elements or used the theory of natural selection as the rationale for their questions.

We then tested for evidence of natural (phenotypic) selection with data for six species of ducks. At nests, we used six variables to describe vegetation structure/nest position and categorized patch types (pond edge, native grass, planted cover, shrubs, or trees) in which nests were found; nest fates (abandoned, depredated, or successful) were also determined. For Blue-winged Teal (*Anas discors*), Northern Shoveler (*A. clypeata*), and Mallard (*A. platyrhynchos*), there were significant patterns of nonrandom nest-site placement within a gradient of vegetation structure/nest position. For Blue-winged Teal and Gadwall (*A. strepera*), nest success varied within these gradients in a way that could exert directional selection. Several tests for adaptive nest-site choice were conducted. Nest fate did not influence fidelity of females to patch types. However, Mallards with previously unsuccessful nests dispersed farther than females with previously successful nests. Nonetheless, neither fidelity to patch type nor dispersal distance influenced subsequent nest success. In the long term (over 8 yr), there was a weak tendency within species for nest density to be higher among patch types where relative nest success was higher. In the short term (from year t to year $t + 1$), this pattern was not observed in a vegetation-structure/nest-position gradient for any species. The strongest evidence of adaptive response to nest fate was higher nest density on an island where nest success was relatively high.

Key words: adaptation; breeding dispersal; ducks; habitat selection; islands; nest-site selection; predation; vegetation structure.

INTRODUCTION

Organisms are typically not distributed randomly among habitats, and it is generally assumed that non-random distribution patterns result from natural selection (Southwood 1977). Interspecific differences in habitat selection are often ascribed to variation in morphology or physiology (Cody 1985, Morse 1985, Sherry and Holmes 1985, Martin 1995). However, variation in fitness, which is implicit in these studies (Fretwell and Lucas 1970, Fretwell 1972, Kirsch 1996), is seldom explicit in tests of habitat selection. A further deficiency in much of the habitat selection literature is evidence of adaptation to spatial variation in fitness (cf. Gavin 1991). Here, we illustrate these deficiencies with a review of studies about nest-site selection in

birds, although our findings and approach could easily be extended to other aspects of habitat selection in a wide variety of animals. We then illustrate how the theoretical framework for habitat selection (Rosenzweig 1981, 1985, 1996) can be used to predict nest-site selection by ducks.

Avian survival and reproductive performance can depend on nest-site choices (Burger 1985, Dow and Fredga 1985, Martin 1992, Badyaev 1995), forming a basis for evolution of nest-site preferences. Natural selection could result in nest-site preferences that are genetic, imprinted, or learned (Klopfer 1963, Hildén 1965, Cink 1976, Sonnerud 1985). Regardless, natural selection could contribute to species' current patterns of nest-site distribution, given certain conditions (see Endler 1986:4–14). The *process* of natural selection is often evaluated as part of habitat selection studies, but it may be more subtle than *patterns* in habitat use that emerge over evolutionary time. Hence, with respect to nest-site selection, researchers typically ask first about

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pattern (Wiens 1989), i.e., how available habitat differs from nest habitat. However, patterns of habitat use may not accurately indicate species' optimal choices if, for example, some individuals have not learned to identify, or are prevented from occupying, appropriate sites (Wiens and Rotenberry 1981, Van Horne 1983, Sollerud 1985, Pulliam 1988). Therefore, a crucial second step in studying nest-site selection is to ask whether, and how, unsuccessful and successful nest sites differ.

The process of natural selection can occur when there are habitat differences between unsuccessful and successful nests, and this may ultimately shape observed patterns of nest-site distribution (Martin 1998). Differences between unsuccessful and successful nests may be more subtle than those between nonnest and nest habitat, because short-term selection typically produces less distinct patterns than long-term selection (Dawkins 1986). Moreover, short-term selective pressures such as predation can oscillate unpredictably, both temporally and spatially (Wiens 1985, Burger 1987, Crabtree et al. 1989, Filliater et al. 1994, Hogstad 1995). Thus, characteristics of successful nest sites can vary over time and space (Austin 1976, van Riper 1984), and nest-site selection may reflect long-term optima that are neutral or maladaptive in the short term. Although this poses difficulties for finding evidence of the process of natural selection, putative differences between unsuccessful and successful nest sites (and between nonnest and nest sites) are often identified, especially with a sufficiently large array of habitat measures (Filliater et al. 1994). However, temporal and spatial variation in selection could invalidate presumed differences between unsuccessful and successful nest sites.

Because putative characteristics of successful nest sites may be inaccurate or have uncertain biological meaning, a crucial third step in studying nest-site selection is to test whether those characteristics predict preferences for nest sites. In other words, to complete the evidence for natural selection, one needs to validate conclusions about nest-site choice, and show adaptive response to spatial variation in fitness (Endler 1986). This prediction is seldom tested in studies of habitat selection. Predictions can be fine-tuned according to the kind of selection occurring (see Endler 1986 for details); in all cases, adaptive responses are manifested by a subsequent increase in nest density in parts of habitat gradients that have above-average nest success rates. Stabilizing selection implies greater nest failure at extremes of a habitat gradient (Fig. 1A). Under stabilizing selection, unsuccessful nest sites and successful nest sites should have the same mean traits, but traits of unsuccessful nest sites should have greater variation than those of successful nest sites. Directional selection implies proportionately higher nest failure at one end of a habitat gradient (Fig. 1B). Under directional selection, trait means should differ between unsuccessful and successful nest sites, but there need not

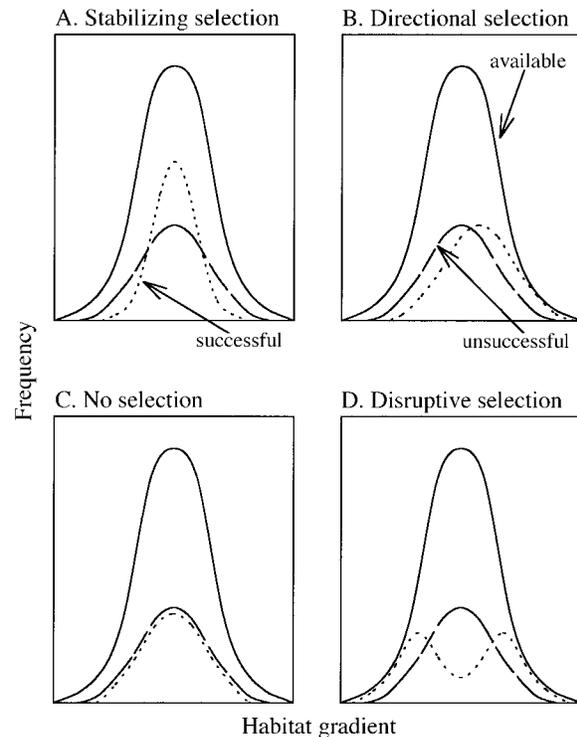


FIG. 1. A hypothetical habitat gradient showing nest habitat available to a species (everything below the solid line), and the frequency with which individuals in that gradient have unsuccessful nest sites (everything below the line with long dashes) and successful nest sites (everything below the dotted line).

be differences in variation of traits. No selection implies an equal proportion of failure in all parts of a habitat gradient. If there is no selection, unsuccessful nest sites will be indistinguishable from successful nest sites, in terms of mean or variation of traits (Fig. 1C). Disruptive selection (Fig. 1D) implies higher nest failure somewhere between the extremes of a habitat gradient. This will result in greater variation in successful than unsuccessful nest sites; means would be the same only if success was equivalent in both tails of the gradient. In the long term, a pattern equivalent to that from stabilizing or no selection could arise from temporal (shifting directional selection) or spatial variation in directional selection (collectively, oscillating selection); hence temporal and spatial scale are important in defining selection (Wiens 1985).

In looking for evidence of adaptive nest-site choice, we make a distinction between a specific area (proximity to precise geographic coordinates) and habitat (potentially several independent geographic coordinates), usually considered together under the label of habitat selection. We do so because predators are the most important selective force affecting nest success (Ricklefs 1969, Martin 1995), and choice of an area may be associated with staying out of home ranges of individual predators (Stenseth and Lidicker 1992),



PLATE 1. This nasal-marked female Gadwall (*Anas strepera*) was photographed during late incubation at a nest site in planted cover on St. Denis National Wildlife Area. Photo courtesy of Mark L. Gloutney.

whereas choice of a habitat may be associated with concealment from, or diversion of, predators. We define nest sites as a combination of area and habitat.

Two processes could result in adaptive site preferences, both of which could be genetic, imprinted, or learned (note that Endler [1986] argues that only genetically based preferences constitute strong evidence of natural selection). One is fidelity to habitats or areas in which fitness was previously high. Fidelity to habitats is seldom considered in studies of nest-site selection (but see Lokemoen et al. 1990, Badyaev and Faust 1996). Fidelity to areas is examined more often, usually in terms of internest dispersal distance (breeding dispersal, sensu Greenwood 1980). Longer breeding dispersal by failed nesters (e.g., Nolan 1978, Greenwood 1980, Dow and Fredga 1985, Blancher and Robertson 1985, but see Sonerud 1985) is frequently interpreted as adaptive avoidance of sites (or mates) associated with nest failure.

Attraction to better sites is a second process that would be indicative of adaptive site preferences, and would be reflected in higher density where fitness was previously high. Attraction and fidelity are not synonymous because birds may move from formerly occupied to new habitats, exhibiting infidelity to the former and attraction to the latter. More intense competition for better sites would also suggest adaptive site preferences (Dow and Fredga 1985), but competition for nest sites probably does not occur among ground-nesting ducks, except perhaps at exceptional densities (Lokemoen et al. 1984). Hence, we assume an ideal free distribution of duck nests in this study (Fretwell and Lucas 1970, Fretwell 1972).

We first reviewed the literature to determine the rationale for published studies of nest-site selection by birds. We then tested for evidence of natural selection in 14 yr of data for six species of duck (five *Anas* spp. and one *Aythya* sp.). We tested whether: (1) random sites differed from nest sites, evidence consistent with

long-term natural (phenotypic) selection; and (2) unsuccessful nest sites differed from successful nest sites, providing evidence consistent with ongoing natural selection. For evidence of adaptive response to natural selection, we tested whether: (3) nest fate influenced fidelity of marked females to sites (areas and habitats); (4) fidelity influenced subsequent nest success; and (5) attraction to sites was greater where previous nest success was relatively high.

METHODS

Literature search

We first reviewed our own collections of reprints on avian nest-site selection, and subsequently surveyed the last 10 yr (1986–1995) of the *Auk*, the *Condor*, the *Ibis*, the *Journal of Wildlife Management*, and the *Wilson Bulletin*. This protocol provided representative rather than complete data. Multispecies studies counted as one observation, and we used authors' interpretation of their results. For each study, we determined whether investigators had collected data to address any of the following questions: (1) Did nonnest sites differ from nest sites? (2) Did unsuccessful nest sites differ from successful nest sites? and (3) Was there evidence of adaptive preferences for successful nest habitats or areas?

Field data

Field work was supervised by Clark on the 385-ha St. Denis National Wildlife Area (NWA), 40 km east of Saskatoon, Saskatchewan, Canada. The NWA contained >100 wetland basins that varied in size and permanency (Woo et al. 1993). Land use on the NWA consisted of annually tilled cropland (~37% of area), natural and planted cover (~53%), and wetlands (~10%) (details in Sugden and Beyersbergen 1985). The NWA consists of a diverse suite of habitats available to nesting ducks, including wetland margins, na-

tive grasses, shrub land, groves of aspen (*Populus tremuloides*), mixes of two or more of these categories, and planted cover (mixes of brome grass, *Bromus* sp., and alfalfa, *Medicago sativa*). Thus, female ducks could choose from a large variety of habitats for nesting.

From early May to mid-July, 1983–1997, duck nests were found (by scaring females from nests) in herbaceous cover by pulling heavy ropes or cable-chain devices between two vehicles (usually all-terrain cycles), and by searching shrub–woodland cover while walking and beating vegetation with bamboo canes. Three or four nest searches were completed each year. For each nest (defined as a bowl containing one or more eggs), we recorded species (Blue-winged Teal, *Anas discors*; Northern Shoveler, *A. clypeata*; American Wigeon, *A. americana*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; or Lesser Scaup, *Aythya affinis*) and clutch size, estimated incubation stage, and subsequently determined nest fate (hatched, depredated, abandoned) following criteria in Klett et al. (1986). Searches were conducted from 0700 to 1500 (Gloutney et al. 1993). To mimic normal nest departures by females, we covered eggs with nest material following visits (Götmark 1992).

Following hatch or predation, from 1984 to 1990 (beginning in 1986 for Gadwall), vegetation structure/nest position was characterized at all but Lesser Scaup nests. This included four characteristics of nest sites that were measured within a 20-cm radius of the nest bowl: percentage of vegetation composed of grass (Percent Grass), average maximum height of vegetation (Vegetation Height), percentage of living vegetation (Percent Living), and vertical Cover (average percentage of each of five 6.5-cm² squares on a cardboard disc that were occluded in the vertical plane when viewed from 1 m above the nest bowl). Vegetation structure/nest position also included distance in meters from the nest site to the nearest different vegetation patch (Distance to Edge) and distance to the nearest flooded wetland (Distance to Water). From 1983 to 1997, we also categorized patch types in which nests were found (including those of Lesser Scaup) as wetland edge, planted cover, native grass, shrub, or tree.

On the same days as measurements were taken at nest sites, measurements were also recorded at random, nonnest sites (one random site for each nest) during the period when nest sites were being measured. Random sites were selected by plotting random coordinates ($\approx 5 \times 5$ m grid) overlaid on a map of the study area. Random sites in cropland were not used because nesting ducks avoid this habitat on our study area (R. G. Clark, unpublished data). At random coordinates, an observer tossed a rock over one shoulder, and where it landed recorded the same variables as for nests.

In addition to a categorical comparison of successful and unsuccessful nests, we also analyzed whether nest characteristics influenced the length of time that nests

survived. We assumed that one egg was laid per day, and that predation events occurred two-fifths of the interval between nest visits (Mayfield 1975, Johnson 1979). Hence, for depredated nests, “nest duration” was the number of eggs, plus the number of days of incubation, plus the interval between nest visits multiplied by 0.4; for hatched nests, it was clutch size plus incubation period. Because results of nest duration analyses were similar to those obtained by categorical comparison of successful and unsuccessful nests, duration results are not mentioned further.

Data on breeding dispersal were collected between 1983 and 1997 for all species (beginning in 1986 for Gadwall). To reduce nest abandonment while monitoring breeding dispersal, we waited until later stages of incubation to capture and mark females (using standard leg bands and nasal tags) on their nests. Because few unsuccessful females reach late incubation, this protocol was biased to marking females of successful nests. These data were used to test whether known individuals’ fidelity to areas or patch types was affected by nest fate.

Because abandonment (21% of 917 nests) may have been caused by our activities (Gloutney et al. 1993), and because this kind of abandonment may not be indicative of normal selection pressures, most analyses included only depredated and successful nests. However, abandoned nests were included in tests for adaptive nesting response to previous habitat-related patterns of nest fate because ducks chose these “response” sites independent of our disturbance. For these reasons, and because some variables were not recorded for some nests or in some years (see above), sample sizes vary among tests. Except where indicated, tests made use of data for both unmarked and marked ducks.

Analyses

Statistical analyses were performed with SAS (1989, 1990). Because vegetation structure/nest position variables were not normally distributed, we determined optimal transformations (assessed by comparing magnitude of Shapiro-Wilks’ test statistics) for variables prior to using them in analyses (arcsine square-root transformations for Percent Grass, Percent Living, and Cover; square-root transformations for Vegetation Height; and log transformations for Distance to Edge and Distance to Water). Although some variables were still not normally distributed after transformation, we judged that remaining departures from normality were not sufficiently large to substantially violate assumptions for parametric analyses (all Shapiro-Wilks’ test statistics greater than 0.88 for transformed variables).

We first tested for multicollinearity among the six vegetation structure/nest position variables using principal components analysis. For each species and for random sites, the first principal component explained less variation (maximum 30%) than could occur by chance (40%) (Frontier 1976, Legendre and Legendre

1983, Jackson 1993), implying that the original variables were orthogonal. Hence, we used the original variables in a discriminant function analysis (DFA). We chose DFA to collapse the six vegetation structure/nest position variables into one synergistic (Krasowski and Nudds 1986) axis that maximized differences between random sites and nest sites, and to maximize differences between unsuccessful and successful nests. The first set of DFAs tested, for each species, whether random sites differed from nest sites (i.e., combining depredated and successful nest sites). Similarly, the second set of DFAs tested whether depredated nest sites differed from successful nest sites (i.e., excluding random sites). For all DFAs, since we were interested in habitat differences among sites, to control for effects of season on vegetation variables, we saved residuals from an analysis of covariance, with site descriptors as dependent variables and Julian date as the explanatory variable. To remove year effects and to combine data for all years, we created, within years, standard normal deviates for residuals of each site descriptor. This gave us six descriptors, corrected for effects of date and year, that were then used in DFAs. To compensate for unequal sample sizes among groups, we set prior classification probabilities proportional to initial sample sizes for each site type (PRIORS PROPORTIONAL in SAS). Because DFA in SAS does not correct for the probability that some sites will be classified correctly just by chance, we used chance-corrections to determine probability values for discriminations (Titus et al. 1984). Chance-corrected values are the proportion of correctly classified observations that exceeded what might have been obtained by chance. For all DFAs, variables with loadings of <0.40 were deemed unimportant to discriminations (Cooley and Lohnes 1985).

We compared fidelity to patch types of failed and successful nesters using contingency tables, and breeding dispersal distances of failed and successful nesters using Kolmogorov-Smirnov tests. To test whether site fidelity influenced subsequent nest fate, we used logistic regression, with fate as dependent variable, and fidelity to patch type (yes or no), dispersal distance, and their interaction as explanatory variables. The three preceding tests relied on data for marked individuals only.

To test whether relatively high nest success was associated with higher nest density, we first computed relative use of patch types using number of nests within a patch type divided by total number of nests, minus total area of a patch type divided by total area of vegetation searched. Number of nests within a patch type was corrected for patch-specific detection biases following Miller and Johnson (1978), wherein nests that were depredated before searches occurred can be estimated from the observed Mayfield (1975) success rate. We then computed nest daily survival rates, using Johnson's (1979) modification of the Mayfield method (Mayfield 1975), both within and across patch types.

To be included, we required a minimum combined sum of 100 exposure days for a species' nests within a given patch type.

Similarly, for each species, we tested whether vegetation structure/nest position of nest sites in year $t + 1$ shifted to parts of the gradient where nests were more successful in year t . We used depredated and successful nests from year t as predictor nests, and within this DFA we used all nests (abandoned, depredated, or successful) from year $t + 1$ as test nests (options TESTDATA and TESTOUT in SAS). This procedure created discriminant functions (DFs) using predictor data, and then calculated how test data would be classified based on criteria from predictor DFs. We excluded nests from the last half of year $t + 1$ to control for the possibility that within-year renesting was responding to within-year patterns of nest fate (i.e., using only early nests in year $t + 1$, since they are expected to most closely reflect year t nest fates). DFA assigned a mean canonical score of 0 to year t predictor nests, and distinguished depredated and successful nests by the sign of their mean canonical scores. The preceding approach was repeated for each of the six sequential pairs of years for which data were available (1984–1985, 1985–1986, etc.) and for each species, providing that sample sizes were sufficient ($N \geq 3$ for each of depredated, successful, and test nests).

RESULTS

Literature search

Of 309 studies that we found, 258 (83%) were from the five focal journals in which systematic searches were done. Of the 309 studies, 39 (13%) used artificial nests to test whether characteristics of unsuccessful differed from successful nest sites, and 36 (95%) obtained affirmative answers. Because results with artificial nests may not represent natural success patterns (Major and Kendal 1996, Guyn and Clark 1997), they were excluded from further analysis. Of the 270 remaining studies, 166 (61%) compared nonnest with nest sites (i.e., determined pattern), 148 (54%) compared characteristics of unsuccessful and successful nest sites (i.e., looked at process), and only 27 (10%) considered evidence of adaptive preferences for successful nest sites. In 68 (26%) studies, both pattern and process were evaluated, although often not in the context of natural selection. A greater proportion of studies obtained evidence of pattern (98%, 162/166) than of process (82%, 122/148) or of adaptive nest-site selection (85%, 23/27). No question was asked more or less frequently with time (pooling studies to give similar interval totals; $N = 22$ for 1956–1975, $N = 19$ for 1976–1982, $N = 25$ for 1983–1985, N ranging from 14 to 31 for each year thereafter; Spearman rank correlations; all $r_s < 0.04$, all $P > 0.90$).

Pattern and process in wild ducks

Numbers of nests that we found (Table 1) varied across years owing to yearly variations in numbers of

TABLE 1. Variables (mean \pm 1 SD) measured at depredated and successful nest sites of each species, and for random sites, from 1983 to 1993.

Species	D/S†	N‡	Vegetation				Distance to edge (m)	Distance to water (m)
			Grass (%)	Height (cm)	Living (%)	Cover (%)		
Blue-winged Teal	D	81	76 \pm 24	42 \pm 12	72 \pm 20	40 \pm 27	12 \pm 15	55 \pm 54
	S	52	78 \pm 24	47 \pm 14	79 \pm 18	37 \pm 25	15 \pm 18	57 \pm 73
Northern Shoveler	D	71	86 \pm 22	44 \pm 15	68 \pm 21	35 \pm 28	19 \pm 22	69 \pm 62
	S	31	78 \pm 29	50 \pm 17	78 \pm 17	31 \pm 19	15 \pm 16	90 \pm 100
American Wigeon	D	12	42 \pm 28	69 \pm 24	73 \pm 14	51 \pm 35	16 \pm 18	161 \pm 110
	S	22	39 \pm 39	60 \pm 20	72 \pm 26	61 \pm 31	21 \pm 29	125 \pm 147
Gadwall	D	30	56 \pm 38	62 \pm 18	73 \pm 19	44 \pm 32	17 \pm 24	118 \pm 83
	S	41	42 \pm 39	58 \pm 17	77 \pm 19	50 \pm 33	14 \pm 15	130 \pm 130
Mallard	D	129	49 \pm 38	59 \pm 21	62 \pm 28	39 \pm 29	22 \pm 23	108 \pm 98
	S	93	43 \pm 40	71 \pm 30	68 \pm 25	38 \pm 32	21 \pm 23	101 \pm 92
Random		848	72 \pm 31	49 \pm 23	61 \pm 24	20 \pm 22	18 \pm 20	115 \pm 115

† Depredated (D) or successful (S).
 ‡ N is minimum sample size for explanatory variables.

wetlands, breeding pairs, and nesting effort. The first set of DFAs revealed significant differences between nest sites and random sites for Blue-winged Teal, Northern Shoveler, and Mallard (Table 2, top parts of Figs. 2–6). In order of variables' importance to discrimination, Blue-winged Teal nest sites had more cover, and were closer to water than random sites (Fig. 2). Northern Shoveler nest sites were closer to water, had more cover, and more grass than random sites (Fig. 3). Despite apparent patterns, no significant distinctions emerged between random sites and either American Wigeon nest sites (Fig. 4) or Gadwall nest sites (Fig. 5), although results for Gadwall approached significance. Mallard nest sites had more cover, taller vegetation, and less grass than random sites (Fig. 6). In sum, we had strong evidence of nonrandom nest habitat use for teal, shoveler and Mallard, weak evidence for Gadwall, and none for wigeon (Tables 1 and 2).

The second set of DFAs detected significant differences between depredated and successful nests for Blue-winged Teal and Gadwall (Table 2, bottom parts of Figs. 2 and 5). Depredated Blue-winged Teal nest sites were closer to patch edges and had less living vegetation than did successful nests, whereas depredated Gadwall nest sites had more grass and were farther from patch edges than were successful nests. For Mallard and, to a lesser extent, Blue-winged Teal and Northern Shoveler, differences between depredated and successful nest sites were smaller than between random sites and nest sites (Figs. 2, 3, and 6; also compare percentage of correct classifications of first and second DFAs in Table 2), whereas a strong opposite pattern was found with wigeon and Gadwall. In sum, there was strong evidence for habitat-specific nonrandom predation (process) on nest sites of teal and Gadwall.

We inferred the type of natural selection acting on

TABLE 2. Loadings on discriminant functions of nest-site variables (those $>$ |0.40| are underlined).

Variable	Blue-winged Teal	Northern Shoveler	American Wigeon	Gadwall	Mallard
Random sites vs. nest sites					
Percent grass	0.19	<u>0.46</u>	<u>-0.57</u>	<u>-0.60</u>	<u>-0.63</u>
Percent living	0.24	<u>0.12</u>	<u>0.21</u>	<u>0.44</u>	<u>0.07</u>
Vegetation height	-0.15	-0.09	<u>0.50</u>	<u>0.63</u>	<u>0.64</u>
Cover	<u>0.73</u>	<u>0.50</u>	<u>0.92</u>	<u>0.84</u>	<u>0.78</u>
Distance to edge	-0.04	<u>0.08</u>	<u>0.09</u>	<u>0.11</u>	<u>0.26</u>
Distance to water	<u>-0.47</u>	<u>-0.51</u>	<u>0.08</u>	-0.04	-0.14
Percent improvement on chance discrimination†	28	20	8	14	34
Significance of discrimination (P)	<0.0001	0.01	0.30	0.09	<0.0001
Depredated vs. successful nest sites					
Percent grass	0.18	0.05	-0.08	<u>0.84</u>	-0.27
Percent living	<u>0.57</u>	<u>0.83</u>	0.08	-0.40	<u>0.72</u>
Vegetation height	<u>0.33</u>	<u>0.46</u>	<u>0.50</u>	0.31	<u>0.62</u>
Cover	-0.01	<u>0.06</u>	<u>-0.47</u>	-0.27	<u>0.46</u>
Distance to edge	<u>0.73</u>	-0.17	-0.01	<u>0.50</u>	<u>0.19</u>
Distance to water	<u>0.09</u>	<u>0.40</u>	<u>0.62</u>	-0.01	0.15
Percent improvement on chance discrimination†	24	18	24	44	9
Significance of discrimination (P)	0.01	0.11	0.13	0.0005	0.13

Note: Sample sizes are given in Table 1.
 † See *Methods: Analyses* and Titus et al. (1984).

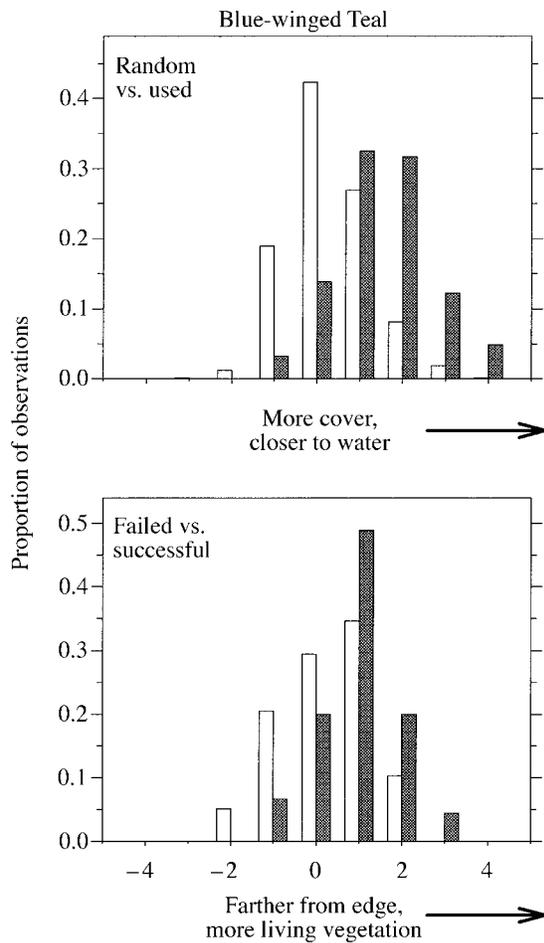


FIG. 2. Distribution of discriminant function scores from one analysis (top) comparing random sites (open bars) and nest sites (filled bars), and from a separate analysis (bottom) comparing failed (open bars) and successful (filled bars) nest sites of Blue-winged Teal. Nest-site variables noted below the abscissa are listed in order of decreasing importance in discriminant function analyses and are given only if they had loadings $>|0.40|$ (see Table 2) (Cooley and Lohnes 1985). Sample sizes are given in Table 1.

nest-site choice by comparing scores of depredated and successful nests from the second set of DFAs. Because these DFAs indicated significant patterns of nest success for Blue-winged Teal and Gadwall only, comparisons for the other species should be interpreted only as indicative of trends. Mean canonical scores of successful nests differed from unsuccessful nests for all species but American Wigeon (Table 3, bottom parts of Figs. 2–6), which could result in either directional or disruptive selection. For all species but Gadwall, variation was the same for scores of unsuccessful and successful nest sites (Table 3), which excludes disruptive selection for these species. Disruptive selection can also be excluded for Gadwall, because variation in scores should be higher for successful nests. Based on

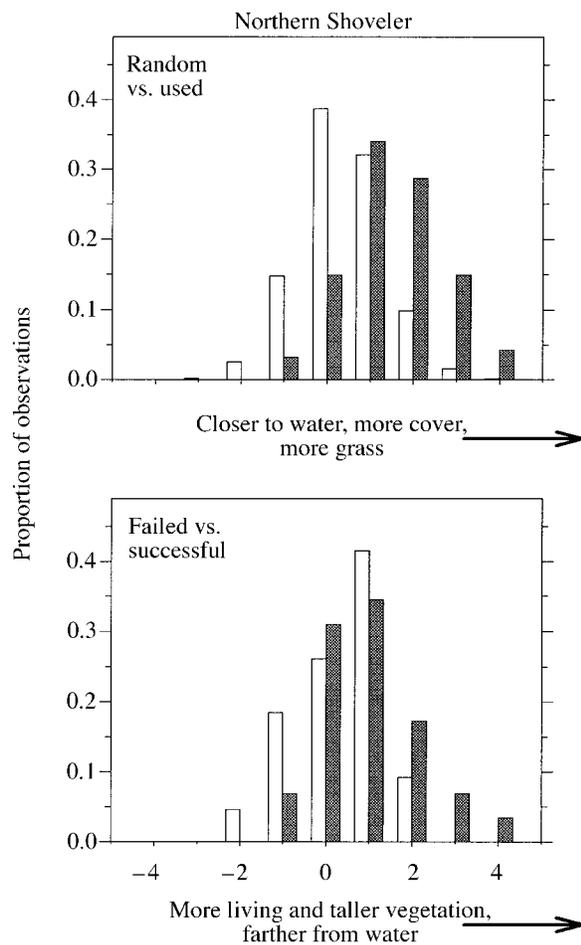


FIG. 3. Distribution of discriminant function scores from one analysis (top) comparing random sites (open bars) and nest sites (filled bars), and from a separate analysis (bottom) comparing failed (open bars) and successful (filled bars) nest sites of Northern Shoveler. See Fig. 2 for an explanation of the sequence of nest-site variables listed below the abscissa, and Table 1 for sample sizes.

the second set of DFAs (Table 2), directional selection was occurring on nest-site selection in Blue-winged Teal and Gadwall. Results of the DFAs for the other species were consistent with either stabilizing, disruptive, or no selection, although results in Table 3 indicate a trend toward directional selection for Northern Shoveler and Mallard.

Nest fate and fidelity, fidelity and nest fate

For the two species for which we had sufficient sample sizes, nest fate did not influence marked females' fidelity to patch types (Table 4). Although unsuccessful Mallards and Gadwalls dispersed farther than did successful birds (Table 4), neither fidelity to patch type nor fidelity to area influenced subsequent nest fate (Table 5). To illustrate, 24 of 27 Gadwalls that stayed in the same patch type and 9 of 11 that switched patch

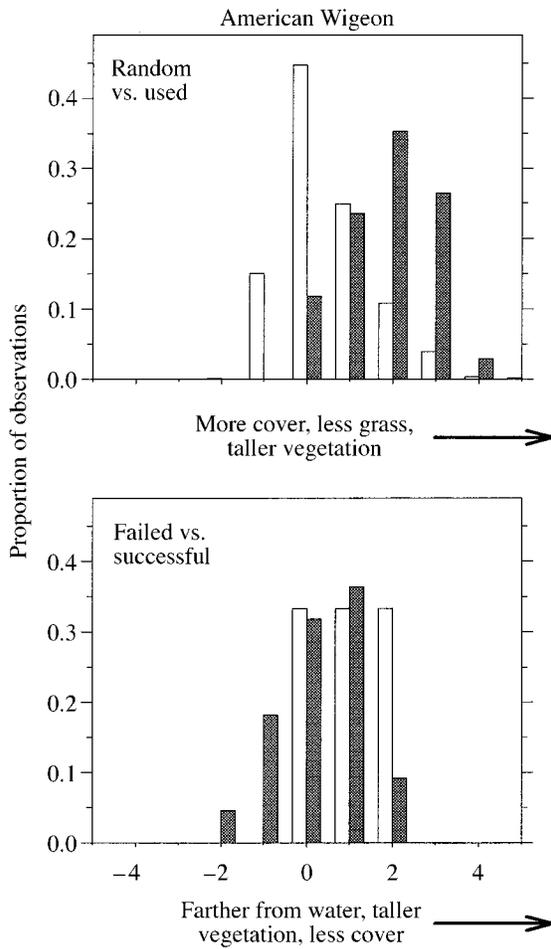


FIG. 4. Distribution of discriminant function scores from one analysis (top) comparing random sites (open bars) and nest sites (filled bars), and from a separate analysis (bottom) comparing failed (open bars) and successful (filled bars) nest sites of American Wigeon. See Fig. 2 for an explanation of the sequence of nest-site variables listed below the abscissa, and Table 1 for sample sizes.

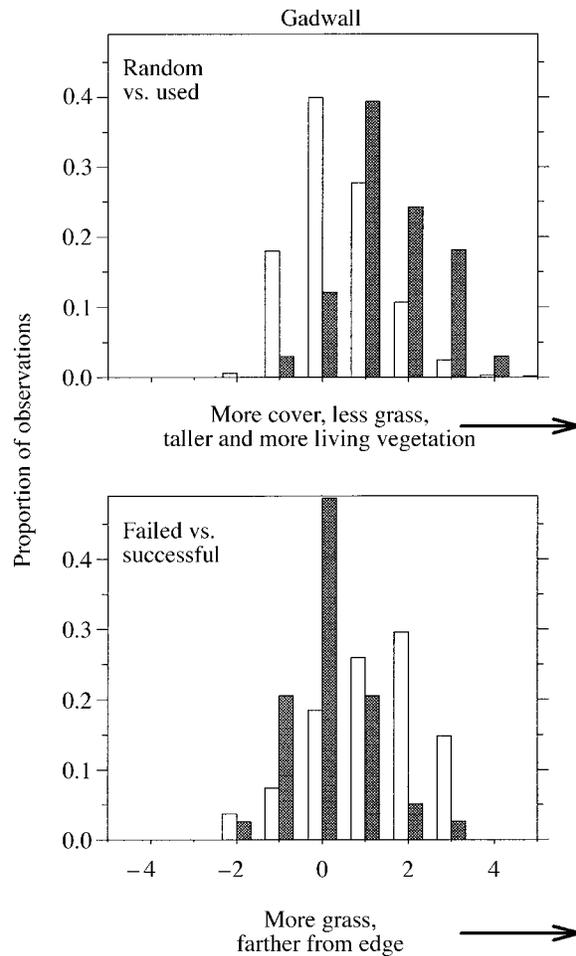


FIG. 5. Distribution of discriminant function scores from one analysis (top) comparing random sites (open bars) and nest sites (filled bars), and from a separate analysis comparing failed (open bars) and successful (filled bars) nest sites (bottom) of Gadwall. See Fig. 2 for an explanation of the sequence of nest-site variables listed below the abscissa, and Table 1 for sample sizes.

types were successful; comparable figures for Mallards were 49 of 59, and 16 of 20 (Fisher exact tests, $P > 0.61$). Thus, although we found some evidence that nest fate influenced fidelity, we found no evidence that fidelity was adaptive.

Nest fate and habitat attractiveness

We predicted that nest density would be higher in patch types that typically had higher than average daily survival rates. In 13 of 21 cases (pooling among species), use of patch type was adaptive relative to daily survival rates (Fig. 7), producing weak evidence, across species, that patch use conformed with the predicted pattern (binomial test, $P = 0.09$). Although we found no direct evidence that fidelity or infidelity to patch types was adaptive (see previous section), we tested, using marked individuals only, whether switching fe-

males were more likely to nest in patch types that had relatively higher daily survival rates. Eight of 16 Gadwall switched to patch types that had higher than average daily success rates, and 7 of 22 Mallards did the same. For each species, these proportions were significantly higher than expectation (binomial tests, $P < 0.03$), based on the proportion of patch types available in the study area. However, proportions were not significantly different from overall species' use of nest habitat (all $P > 0.30$). Hence we have no evidence that experience had a significant effect on preferences for patch type.

We predicted that in year $t + 1$, for each species, nest-site density would increase in the vegetation structure/nest position gradient where nest success was highest in year t . In 15 tests (3 each for Blue-winged Teal, Northern Shoveler, and Gadwall, 0 for American

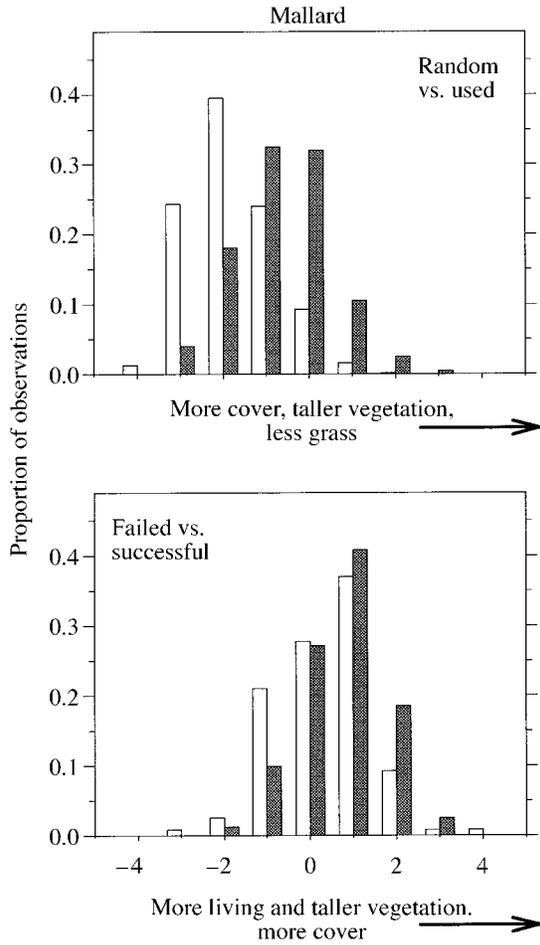


FIG. 6. Distribution of discriminant function scores from one analysis (top) comparing random sites (open bars) and nest sites (filled bars), and from a separate analysis (bottom) comparing failed (open bars) and successful (filled bars) nest sites of Mallard. See Fig. 2 for an explanation of the sequence of nest-site variables listed below the abscissa, and Table 1 for sample sizes.

Wigeon, 6 for Mallards; Fig. 8 shows Mallard results only), we found no significant shifts in mean canonical scores (*t* tests comparing test data with predictor data, all *P* > 0.09). Furthermore, shifts along the nest vegetation structure/nest position gradient were in the predicted direction in only 7 of 15 cases (pooling species,

TABLE 4. Fidelity of Gadwalls and Mallards to patch types (pond edge, planted cover, native grasses, shrubs, or trees) and areas (geographic coordinates) relative to previous nest fate.

Species	Previous nest fate		<i>P</i> †
	Unsuccessful	Successful	
Percent patch type fidelity			
Gadwall	88 (11)	67 (30)	0.40
Mallard	100 (8)	72 (71)	0.19
Median breeding dispersal distance (m)			
Gadwall	494 (8)	240 (30)	0.08
Range	128–1052	4–1244	
Mallard	226 (8)	28 (70)	0.03
Range	20–716	0–1064	

Note: Numbers in parentheses are sample sizes (*N*).
 † Fisher exact tests for fidelity to patch type, Kolmogorov-Smirnov two-sample test for dispersal distances.

binomial test, *P* = 0.50; Fig. 8). These results were not affected if we included cases only with samples sizes ≥5, or ≥10, for each of depredated, successful, and test nests (7/13 for ≥5, *P* = 0.71; 3/6 for ≥10, *P* = 0.66).

Because of the former result, we examined whether there was any consistency in vegetation structure/nest position that predicted nest fate by identifying variables that contributed heavily to the discriminant functions. We found a great deal of year-to-year variability in site characteristics that distinguished between unsuccessful and successful nests (Table 6). Hence, successful nest-site features were not consistent, and probably not predictable within the range of vegetation structure used/nest position.

Our last analysis considered whether ducks preferentially used an island that was relatively free of predators. The study area includes 200 ha of suitable mainland nesting cover, plus a single 2-ha island within one large wetland. Between 1988 and 1994, 86 nests were found on the island, and these had an average daily survival rate of $0.99 \pm 0.016 \text{ d}^{-1}$ (mean \pm 1 SE). In contrast, 439 mainland nests had a daily survival rate of $0.95 \pm 0.004 \text{ d}^{-1}$. By virtue of higher nest density and more intense nest searching on the island, it was more difficult to miss nests than on the mainland. We corrected for this bias in nest detection following Miller and Johnson (1978; see *Methods: Analyses*). Differ-

TABLE 3. Comparisons of means and variances of scores from discriminant function analysis of depredated and successful nests.

Species	Means		Variances		Evidence consistent with selection that is:
	<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Blue-winged Teal	4.0	<0.0001	1.30	0.35	Directional
Northern Shoveler	2.9	0.006	-1.32	0.36	Directional
American Wigeon	-1.7	0.10	-1.25	0.72	Not occurring or weak directional
Gadwall	-3.7	0.001	2.12	0.03	Directional
Mallard	2.4	0.02	1.37	0.13	Directional

Note: Negative signs indicate that successful nest sites had higher values than depredated nest sites.

TABLE 5. Influence of fidelity to patch type (pond edge, planted cover, native grasses, shrubs, or trees) and area (geographic coordinates) on subsequent nest success of Gadwall and Mallard.

Species	Logistic regression χ^2 value			
	Intercept	Patch type fidelity (P)	Dispersal distance (D)	P \times D interaction
Gadwall	4.0*	0.7	0.5	0.1
Mallard	13.7**	0.2	2.7	0.5

Notes: Main effects were still not significant if interaction term was dropped from the model. Sample sizes are given in Table 4.

* $P < 0.05$, ** $P < 0.01$.

ences in daily survival translated into 70% nest success on the island, vs. 17% on the mainland. This gave a corrected nest density (pooling years) for American Wigeon of 0.6 nests/ha on the mainland vs. 6.5 on the island; comparable values for Gadwall were 2.4 vs. 11.5 nests/ha, for Mallard 3.4 vs. 24.5 nests/ha, and for Lesser Scaup 0.7 vs. 9.5 nests/ha (χ^2 tests, all $P < 0.0001$). Collectively, duck nest density on the island was roughly six times that of the mainland, and use of the island resulted in roughly a fourfold increase in nesting success.

DISCUSSION

A clear rationale for studying avian nest-site selection has not been explicit in much of this literature, a problem that we suspect extends to other aspects of habitat selection as well (also see Gavin 1991). Many researchers likely intuit that natural selection plays a role in nest-site selection, but because they do not clearly articulate a natural selection framework, their studies have not proceeded to the extent possible. Thus, we encourage researchers to first measure natural selection (i.e., the consequence of choosing to use a particular site), then predict and test for adaptive responses in habitat use (Badyaev and Faust 1996, Rosenzweig 1996, Stokes and Boersma 1998). In the short term, agreement between process and pattern would indicate ongoing selection; for instance, we found some consistency between process and pattern in nest-site use by Gadwall (Fig. 5) and Mallard (Fig. 6). On the other hand, lack of concordance might be explained in several ways, ranging from mundane methodological artifact (i.e., not measuring an important variable) to identifying new or other selective forces. The preceding approach could also assist conservation. For instance, a peripheral finding from our literature review was that studies on endangered or threatened species (Piping Plover, *Charadrius melodus*; Least Tern, *Sterna antillarum*; Spotted Owl, *Strix occidentalis*; Burrowing Owl, *Athene cunicularia*; and Red-cockaded Woodpecker, *Picoides borealis*) seldom do more than distinguish random sites from used nest sites. Of 21 studies on these species, 15 tested whether used nest habitat differed from available nest habitat, only 6 tested whether unsuccessful nest habitat differed from successful nest habitats, and none looked at adaptive use of successful habitat (G test com-

paring with the same proportions in studies of nonthreatened species, $P = 0.03$). Hence, nest-site research appears deficient where it can least afford to be. Although we recognize that there may be justifiable reasons for minimizing human impact on rarer species, as may sometimes be required in determining nest fates, we need also to consider the importance of identifying optimal, rather than simply used, nest habitat for these species (Wiens and Rotenberry 1981, Van Horne 1983, Sonerud 1985, Pulliam 1988).

The results of our field study provided evidence of both pattern and process in nest-site selection. The patterns entailed differences in characteristics of random sites and nest sites, arising from long-term selection. Cover was the most important variable in distinguishing random from nest sites for three species. Evidence for the process of natural selection entailed differences between unsuccessful and successful nest sites, suggesting ongoing natural selection. Although cover is the most frequently cited difference between unsuccessful and successful nest sites (Crabtree et al. 1989, Martin 1992), this was not always the case in this study (also see Clark and Nudds 1991, Götmark et al. 1995, Howlett and Stutchbury 1996). We did find that successful Blue-winged Teal nest sites were farther from patch edges, as has been reported for some species (Gates and Gysel 1978, Wilcove 1985, Andrén and Angelstam 1988, Martin 1992), but the reverse pattern was found with Gadwall (also see Pasitschniak-Arts et al., 1998). For three species, we found no differences between unsuccessful and successful nest sites. Such patterns of nest success could result if predators use search images to locate nests, resulting in natural selection favoring random nest placement (Martin 1988, Filliater et al. 1994).

Some of our results suggested adaptive nest-site preferences of ducks. These included longer dispersal by failed nesters, a tendency to higher nest density in vegetation patches with above-average nest success, and higher nest density on an island that also had above-average nest success. Other researchers have found that Mallards whose nests failed dispersed farther than those whose nests succeeded (Majewski and Beszterda 1990). However, although longer breeding dispersal is frequently assumed to be adaptive for failed nesters,

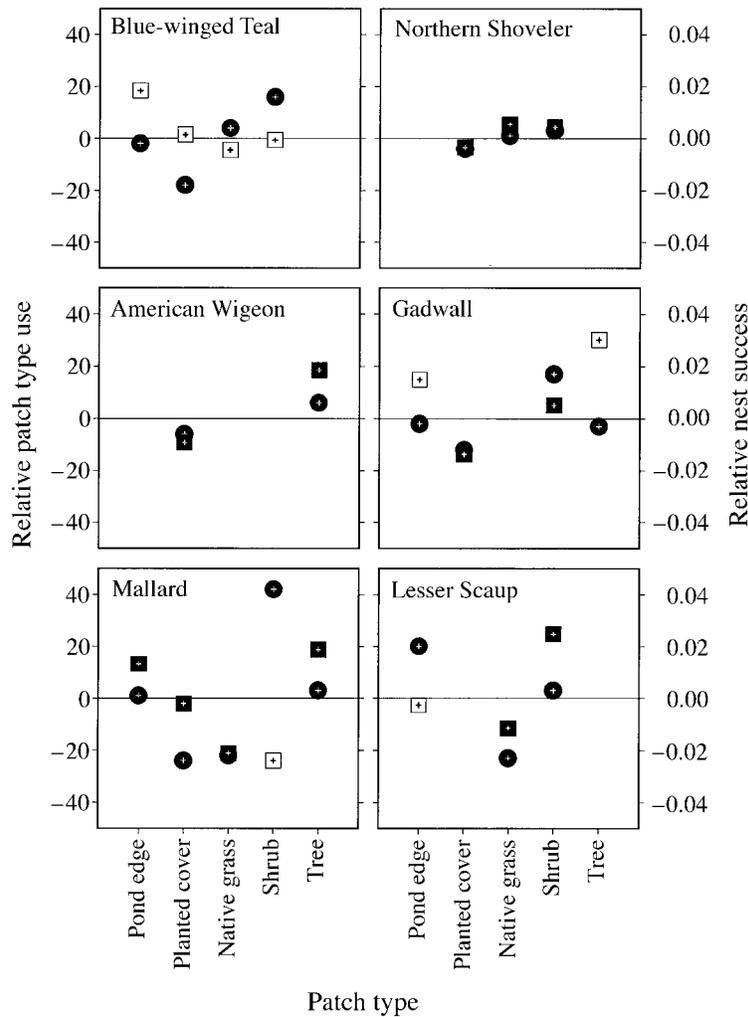


FIG. 7. Relative patch type use (circles) and relative nest success (squares). Use is calculated as the number of nests in a patch type divided by the total number of nests, minus the proportion of that habitat available in the study area, times 100. Relative nest success is calculated as the daily nest survival rate within a patch type minus the daily nest survival rate across patch types. Solid squares indicate points that are in agreement with the hypothesis (see *Methods*); open squares are points that are contrary to the hypothesis.

dispersal distance had no effect on subsequent nest success in this study (also see Newton and Marquiss 1982, Wiklund 1996, Lindberg and Sedinger 1997, Robinson and Oring 1997). Nonetheless, greater breeding dispersal by birds following breeding failure is common (von Haartman 1949 cited in Nolan 1978, Nolan 1978, Burger 1982, Shields 1984, Martin 1992, also see Delius 1965; waterfowl reviewed in Anderson et al. 1992), and several advantages to this behavior have been proposed. The first is mate-switching, which in some colonial seabirds can increase breeding success if the new mate has previous breeding experience (Coulson 1966, 1972, Mills 1973, Brooke 1978, Ollason and Dunnet 1978). However, male ducks of species in the present study probably have no influence on predation rates at nests, which is the principal cause of breeding failure. A second advantage of breeding dis-

persal is acquisition of a superior territory (Beletsky and Orrians 1987, Wiklund 1996). However, as indicated above, territoriality probably does not influence nest-site placement of ground-nesting ducks. A third advantage of breeding dispersal may be escape from predators (Stenseth and Lidicker 1992). However, many nest predators (e.g., skunk, *Mephitis mephitis*; raccoon, *Procyon lotor*; fox, *Vulpes vulpes*; American Crow, *Corvus brachyrhynchos*) have home ranges that occupy a large part of our study area, which would render neutral any benefits of dispersal distances of less than several kilometers. Moreover, ubiquity of these predators over much of the prairies would neutralize any benefits of dispersal distances within and beyond that range. Similar arguments could be made against dispersal as a way to avoid competitors (Stenseth and Lidicker 1992) because Mallard and Gadwall may nest

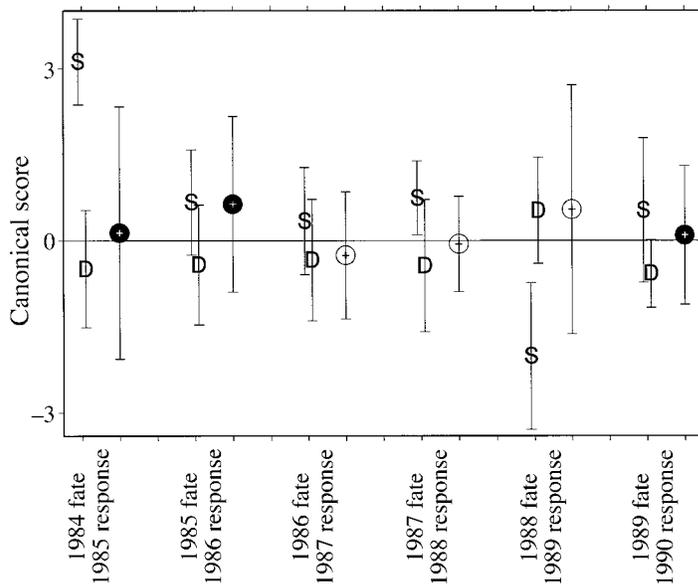


FIG. 8. Nesting responses of Mallards in year $t + 1$ to patterns of nest success in year t . S denotes the mean vegetation structure/nest position (canonical scores from a discriminant function analysis) of successful nests, and D denotes the mean vegetation structure/nest position of depredated nests. Circles represent mean Mallard vegetation structure/nest position scores (using the same canonical axis as the preceding S and D nests) in response to the previous year's pattern of nest fate. Error bars show ± 1 SD. The combined mean for S and D nests is 0. None of the mean responses was significantly different from 0. Solid circles indicate points that are in agreement with the prediction that nest-site density would increase in year $t + 1$ in the vegetation-structure/nest-position gradient where nest success was highest in year t ; open circles are points that are contrary to the prediction.

a long distance from wetlands (territories). Dispersal to avoid ectoparasites (Brown and Brown 1986, 1992) is also probably unimportant, because ducks in this study rarely use the same nest site. Hence, many proposed benefits of breeding dispersal may not apply to ducks. A disadvantage to breeding dispersal is lost fa-

miliarity with a site (Nolan 1978, Smith 1978, Pusey 1992, Shutler and Weatherhead 1994, Badyaev and Faust 1996), and area familiarity has been suggested as the most important cause of breeding area fidelity in female waterfowl (Rohwer and Anderson 1988, Anderson et al. 1992). Nonetheless, dispersal distances of

TABLE 6. Years in which nest vegetation structure/nest position variables differed (loadings of $>|0.40|$) on total canonical structure in DFAs) between depredated and successful nests.

Species	% Grass	Vegetation height	% Living vegetation	Vertical cover	Distance to patch edge	Distance to water
Blue-winged Teal		-1984b 1985a	1984c 1986b	1984a		
	1988c	-1988a			1986a 1987a 1988b	
Northern Shoveler		-1984b 1985c	-1985b -1986c	-1985d	1984c 1986a	1984a 1985a
	-1986b			1987a 1988c		
	1988d		-1988a <u>1990a</u>			1988b <u>1990b</u>
Gadwall	1986b -1987a 1988a	-1986d	1986c	1987b	1986a	
	1990b			1989b -1990a	-1989a	-1989c
					<u>1984a</u>	
Mallard	1986a <u>1988a</u>	1985b	1985a	1985c -1986b -1987c	1987b	1986c 1987a <u>1988b</u>
	-1990b	1989a 1990a	1989b	1990c	-1989c	-1990d

Notes: Letters following dates indicate relative sizes of loadings, with "a" being highest. Years are underlined if significant discrimination ($P < 0.005$ for chance-corrected discrimination [Titus et al. 1984]) was obtained. Negative values indicate that depredated nests had lower values on the canonical axis. Years are not included if there were insufficient data; there were insufficient data for all variables for American Wigeon.

females in this study exceeded average radii of vegetation patches (18 ± 20 m; mean ± 1 SD). Hence, some successful females subsequently nested in new patch types (also see Lokemoen et al. 1990), thereby losing nest habitat familiarity. However, dispersal distances were not so great as to prevent individuals from using the same foraging areas, so they retained some area familiarity. In sum, we have no evidence that breeding dispersal was adaptive, and dispersal distance, per se, may not always be adaptive for other bird (Newton and Marquis 1982, Badyaev and Faust 1996, Wiklund 1996, Robison and Oring 1997, Lindberg and Sedinger 1997) or mammal species either (Pusey 1992).

These results leave us with a paradox. Breeding dispersal by Mallards (and possibly Gadwalls) is greater for failed nesters, but we cannot ascribe an adaptive advantage to the behavior. This paradox deserves more attention, particularly in other taxa, such as mammals, where there has been little attention devoted to breeding dispersal relative to breeding success (F. Messier, J. A. Millar, and J. Virgl, *personal communications*). Although some studies of mammals document breeding success following dispersal (reviewed in Pusey 1992), this has not been considered in relation to previous breeding performance. A problem with examining this paradox is that the proper control cannot be performed, namely by preventing dispersal among failed breeders to determine how this influences their subsequent success (Newton and Marquiss 1982).

The second body of evidence for adaptive nest placement was that patch types with relatively high nest success tended to have greater relative use. In contrast, Lokemoen et al. (1990) found no tendency for females to have fidelity to patch types, but in their study there also was no difference in breeding success among patch types. Because we found variation in success among patch types, findings contrary to Lokemoen et al. are expected, and collectively each of these observations is consistent with adaptive nest-site preferences.

We did not find evidence of short-term adaptive response (fidelity) to directional selection on vegetation structure/nest position use for Blue-winged Teal and Gadwall, even though breeding area fidelity has been shown for these species in this study area (Arnold and Clark 1996). On the other hand, we found that predation pressures within this habitat gradient were not consistent from year to year, which would make it difficult to predict where optimal nest vegetation structure/nest position would occur (also see Wiens 1985, Martin 1988, 1992, Filliater et al. 1994, Badyaev and Faust 1996, Kirsch 1996). At any rate, results from these tests were not inconsistent with adaptive, long-term choice of nest sites. An alternative possibility for some of these tests is that we had insufficient sample sizes to detect adaptive shifts, but even with Mallards (where sample sizes were much greater) only three of six comparisons were in the predicted direction.

The most convincing evidence we had of adaptive

nest-site preferences was high nest density on an island where nest success was relatively high. High nest success on islands has frequently been reported for ducks and other species (Hammond and Mann 1956, Lokemoen et al. 1984). Possible mechanisms promoting higher density on islands include natal philopatry, site fidelity, attraction based on genetically programmed recognition of islands as predator-free havens, or dispersal of failed nesters from sinks to sources (Wiens and Rotenberry 1981, Pulliam 1988). Some preliminary data from marked individuals (R. G. Clark, *unpublished data*) support the first two possibilities, but do not allow us to assess the last two.

Interpretation of our results rests on a few assumptions that we cannot test directly. First, although we assumed that we measured nest-site variables relevant to female ducks, other site characteristics (e.g., patch level features or local predators) may be more important determinants of nest success. Hence, we may have missed patterns in nest-site preferences, or the patterns we observed could be causally linked to other site characteristics. Second, we compared how predation was related to nest-site characters, whereas factors such as thermal conditions may impose opposing constraints on nest-site choice (Ricklefs and Hainsworth 1969, Walsberg 1981, With and Webb 1993, Gloutney and Clark 1997). In addition, variation in female behavior (e.g., conspicuousness during approaches and departures) could influence nest success. Such variation in behaviors is evident from interspecific comparisons, wherein smaller, shorter lived species are more reluctant to flush from their nests (Forbes et al. 1994). Female age or condition might influence nest success (Blums et al. 1997), but the generality of a condition-dependent response is debated (Arnold et al. 1995). We have also assumed that the nests we found perfectly represented duck use of habitats; however, it would be necessary to follow birds marked with radio transmitters prior to nesting to test this assumption. Finally, we are unaware of evidence supporting the assumption that variation in nest choice behavior is controlled genetically.

We considered nest-site choice for each species separately. However, a female choosing a site may have to consider where other individuals are nesting, including those of other species. (It is not known with any certainty whether females do this.) This is because too much similarity in nest sites could make it too easy for generalist predators to find nests of all species (Martin 1988). Predators of duck nests typically are generalist foragers (Sargeant et al. 1993), to the extent that those identified on our study area are known to prey on nests of any duck species (Clark et al. 1991). Hence, a case could be made for analyzing all duck nest sites collectively. Such an approach would overlook species-specific factors that may shape nest-site selection, such as genetic (imprinting) inertia or thermoregulation (Gloutney and Clark 1997), but might reveal other in-

terspecific selection pressures. At any rate, our results indicate substantial interspecific variation in how nest sites differ from random sites, in factors affecting nest success, and in adaptive responses to selection.

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