WILSON'S PHALAROPE NEST SUCCESS IS NOT INFLUENCED BY VEGETATION CONCEALMENT[1]

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Abstract. I examined vegetation characteristics at nests of Wilson's Phalaropes (*Phalaropus tricolor*) to evaluate the null hypothesis that nest success was independent of concealment from predators. During 1983 and 1984, 28% (*n* = 25) and 18% (*n* = 60) of phalarope clutches successfully hatched chicks; both years predation caused most (60%) clutch failures. No relationship obtained between nesting success and vegetation density, height and heterogeneity, but plant communities differed between successful and depredated nests in 1983. These results do not support the hypothesis that clutch concealment deters predation; rather they suggest that other, perhaps multiple, factors should be examined as forces shaping nest-site selection of ground-nesting birds.

Key words: Nesting success; predation; Wilson's Phalarope; Phalaropus tricolor; concealment.

INTRODUCTION

Numerous studies of nest-site selection in ground-nesting birds have demonstrated that vegetation structure at nests often differs from surrounding habitat. In many cases, nests of waterfowl (see Clark and Nudds 1991) and shorebirds (Colwell and Oring 1990) are located in denser, taller vegetation when compared with surrounding habitat. These patterns usually are interpreted as evidence for the importance of predation in nest-site selection, with authors arguing that birds select habitats that afford greater concealment from predators. If concealment is an important component of nest-site selection, then nests differing in vegetation density should exhibit varying rates of predation.

Both observational and experimental studies have yielded varying support for the relationship between concealment and predation. Success of dabbling duck (e.g., Livezey 1981) and Spruce Grouse (*Canachites canadensis*; Keppie and Herzog 1978) nests was positively associated with concealment. However, other studies of waterfowl (e.g., Krasowski and Nudds 1986) and gallinaceous birds (e.g., Storaas and Wegge 1987) demonstrated no relationship between vegetative cover and nest fate. Moreover, experimental studies have produced both positive (Sugden and

Beyersbergen 1987) and negative support (O'Reilly and Hannon 1989) for the concealment-nest success hypothesis.

Wilson's Phalarope (*Phalaropus tricolor*) breeds in wetland habitats of North America (American Ornithologists' Union 1983), where annual reproductive success varies greatly (17–56% nest success) and most (41%; *n* = 386) clutch failures result from mammalian or avian predation (Colwell and Oring 1988). Nests of nonterritorial phalaropes were hyperdispersed (Colwell and Oring 1988), a pattern commonly observed in waterfowl and argued to be a mechanism by which predation is reduced (McKinney 1965, but see Andrén 1991). In this paper, I examine the fate and survival of Wilson's Phalarope clutches in association with characteristics of nest site vegetation. Phalaropes nest on the ground in vegetation that is denser, taller, and more homogeneous than random sites (Colwell and Oring 1990). As a result, I predicted that successful nests would have denser, taller, more homogeneous vegetation (offering greater concealment) than depredated nests.

METHODS

I studied phalaropes from 1982–1987 at two wetlands near Last Mountain Lake National Wildlife Area in south-central Saskatchewan (51°10'N; 110°2'W). This paper examines data collected in 1983 and 1984. During 1983 I worked on a 40-ha site situated within a provincial pasture; cattle were not present during the field season. In 1984 I worked on a 100-ha area within a private pas-

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ture, which received heavy grazing pressure (approximately 45 cattle) throughout most of the nesting season. During both years, I kept detailed reproductive histories for uniquely color-marked phalaropes, including date of clutch initiation and clutch fate (Colwell and Oring 1988). Based on the intensive nature of this study, I am confident that my assistants and I found nearly all nests initiated within the study sites.

To approximate habitat characteristics at the time of nest-site selection, vegetation was measured at the time of clutch completion or immediately after I located a completed (4 egg) clutch. I found most clutches (1983, 72% [n = 25] and 1984, 60% [n = 60]) prior to clutch completion. At each nest, I summarized vegetation structure using a point-intercept method based on the average of eight nest-cup samples. Each sample consisted of the total number of vegetation contacts with a 5 mm diameter metal rod dropped vertically through the vegetation. From these data, I derived six measures of vegetation structure: (1) *density* equals the number of vegetation contacts over the height of the rod, (2) *first dm density* is the number of contacts in the first dm interval above ground, (3) *height* represents the highest (cm) point where vegetation contacts the rod, (4) *horizontal heterogeneity* is the coefficient of variation for density, and (5) *vertical heterogeneity* is the coefficient of variation for height. In addition, I recorded the presence of plant species in a 0.25 m² quadrat encompassing the nest. For details of vegetation sampling see Colwell and Oring (1990).

I portrayed plant communities at nests by ordinating samples (nests) by species (plants) using Detrended Correspondence Analysis (DCA, Hill 1979, Colwell and Oring 1990). DCA is an ordination technique based on reciprocal averaging (Gauch 1982), which organizes nests based on similarities in plant species composition. Nests with similar plant communities have more similar axis scores than nests with different flora.

I compared the structure of vegetation at successful nests (hatched at least one chick) with nests whose clutches were lost to predators. I excluded other unsuccessful (abandoned) nests from analyses for two reasons. First, the nest concealment hypothesis makes no prediction regarding vegetation at abandoned nests; and, second, depredated and abandoned nests were very similar in vegetation. Finally, I excluded nests from analyses if cattle or humans caused clutch

failure. I did not conduct between-year comparisons of vegetation because of annual differences in: (1) observers (n = 2), (2) study areas, (3) grazing intensity, and (4) plant phenology associated with wet (1983) and dry (1984) seasons. I analyzed untransformed data with t-tests and I used nonparametric tests (Mann-Whitney U-test) to compare axis scores of the ordination (SAS 1985).

RESULTS

Reproductive success. Phalaropes experienced low nesting success both years mostly owing to predation (Colwell and Oring 1988). In 1983, 28% (n = 25) of clutches hatched, whereas in 1984 18% (n = 60) of clutches hatched. In both years, predators caused failure at 60% of nests. The average period (days after the first egg was laid) that clutches survived did not differ between years (1983, $\bar{x}$ = 13.6 ± 8.8; 1984, $\bar{x}$ = 12.4 ± 8.3; t = 0.53, P = 0.61). In 1983, successful clutches were initiated later in the season than depredated clutches (z = 2.19, P = 0.03). Moreover, clutches initiated later in 1983 tended to survive longer (r = 0.42, n = 22, P = 0.05). However, neither of these patterns obtained in 1984: nest fate was not associated with initiation date (successful vs. depredated, z = 0.29, P = 0.77), nor was clutch survival associated with initiation date (r = 0.002, n = 41, P = 0.99).

Nest site characteristics and nest fate. Phalarope nest success was not associated with concealment at nests (Fig. 1; t-test, P > 0.10, years analyzed separately). Additionally, the number of days that clutches survived generally did not correlate with vegetation structure (Pearson correlation, P > 0.05), although in 1984 clutches with more horizontally homogeneous vegetation survived longer (r = 0.37, n = 41, P = 0.02).

Axes 1 and 2 of the ordination explained 78% and 39%, respectively, of variation in plant species composition at 1983 nests, whereas axes explained 38% and 24% of variation in flora in 1984 (Fig. 2). In 1983, plant communities differed between successful and depredated nests (axis 1 scores, z = 3.36, P = 0.0008; axis 2 scores, z = 0.64, P = 0.53), but this relationship did not obtain in 1984 (axis 1 scores, z = 0.49, P = 0.62; axis 2 scores, z = 0.86, P = 0.39).

DISCUSSION

Colwell and Oring (1990) showed that nest-sites of Wilson's Phalarope have denser and taller vegetation when compared with random locations.
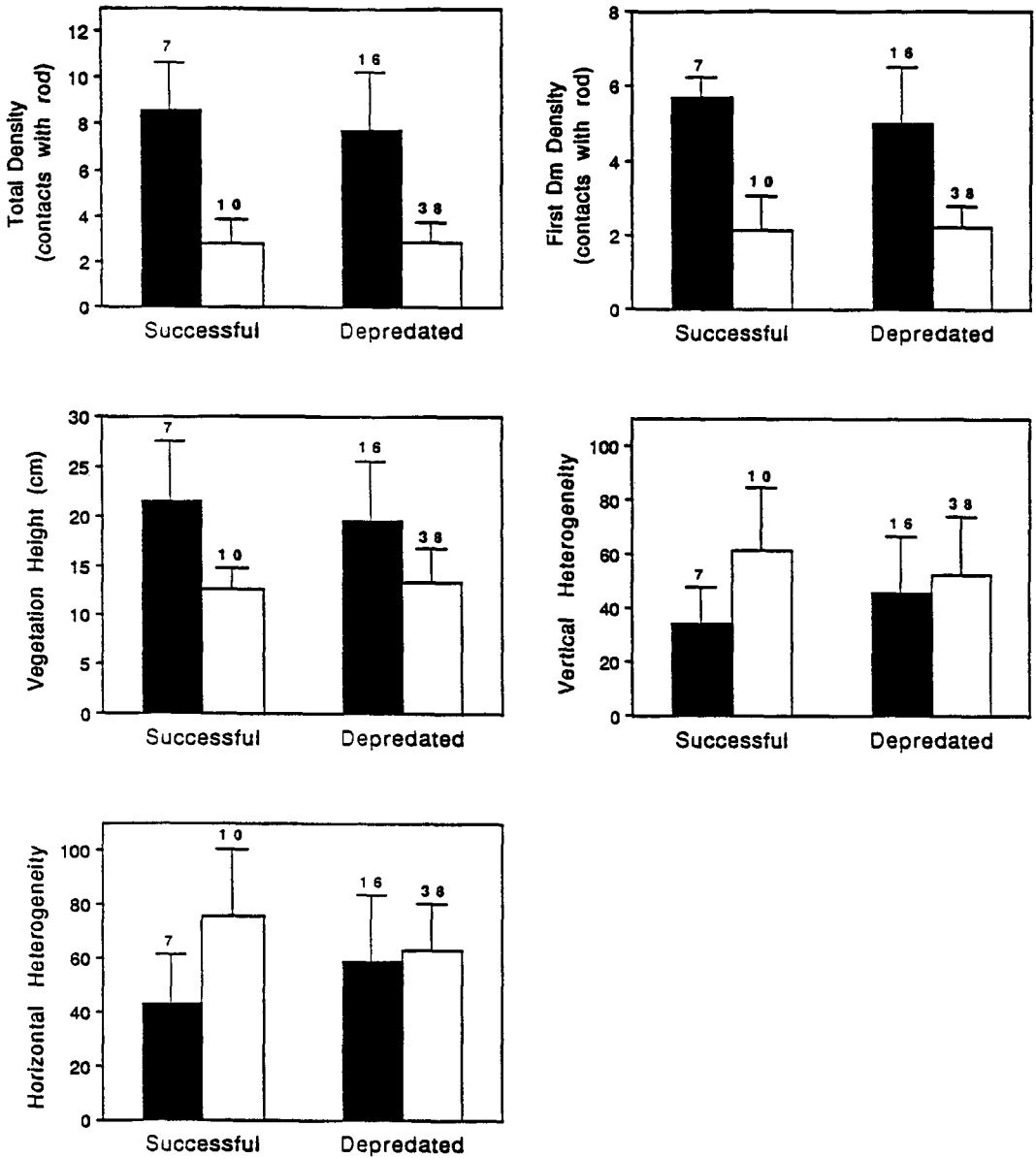
FIGURE 1.   Comparison of vegetation structure at successful and depredated Wilson's Phalarope nests during 1983 (closed histograms) and 1984 (open histograms). Values are presented as $\bar{x} \pm$ SD with sample sizes shown above histograms.

Moreover, the same nonrandom patterns hold when nest-cup vegetation is compared with habitat measured 0.5 m from the cup (Colwell and Oring 1990). One interpretation of these observations is that phalaropes nest in vegetation that offers greater concealment from predators. However, when phalarope nest fate is examined in association with vegetation characteristics, there is little indication that greater concealment (density and height) or homogeneity of vegetation is correlated with nesting success (Fig. 1). Flora did, however, differ between successful and depredated nests in 1983 (Fig. 2).

Several non-mutually exclusive explanations exist for the absence of a relationship between concealment and nest fate, including: (1) types
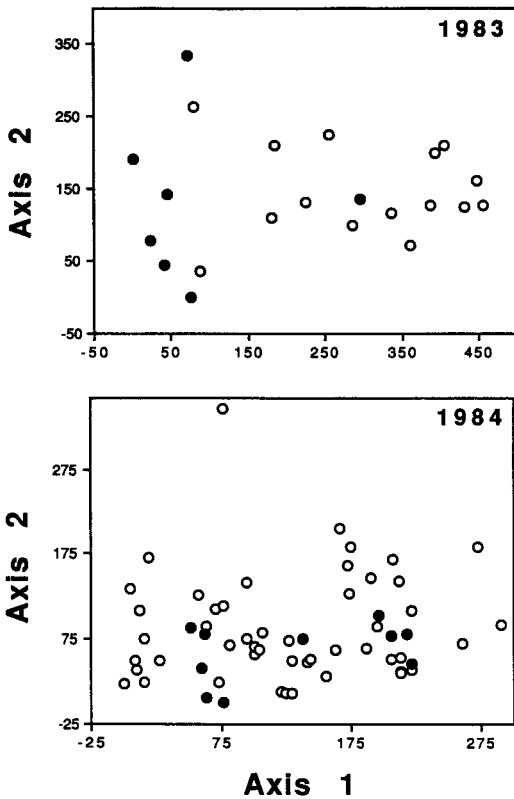
FIGURE 2. Successful (closed circles) and depredated (open circles) Wilson's Phalarope nests associated with plant communities analyzed by Detrended Correspondence Analysis.

of predators responsible for clutch failure (Clark and Nudds 1991), (2) the influence of nest density on the functional response of predators (Sugden and Beyersbergen 1987) and temporal variation in the abundance of alternate prey, (3) investigator influence on clutch fate (Krasowski and Nudds 1986), (4) selection for nest-site vegetation with benefits other than (or additional to) concealment from predators (Walsberg 1985), and (5) characteristics of incubating birds (e.g., age, nutritional condition, incubation behavior).

With regard to types of predator, it is commonly argued that the effect of concealment varies with predator community. In a review of studies of ground-nesting waterfowl, Clark and Nudds (1991) suggested that the importance of concealment was linked to type of predator. Concealment was important where avian predators (e.g., American Crow, *Corvus brachyrhynchos*; Sugden and Beyersbergen 1986, 1987) were dominant. By contrast, concealment offered less

protection from mammals. This dichotomy presumably results from differences in foraging techniques employed by birds (visual) and mammals (olfaction) to detect clutches.

In this study, the absence of an effect of concealment on nest success is consonant with the view that mammals caused most nest losses. During six years of study of phalaropes in Saskatchewan, 17–56% of phalarope nests successfully hatched chicks and most failed attempts resulted from predation (Colwell and Oring 1988). During 1984 a striped skunk (*Mephitis mephitis*), which denned within the study area boundaries, ate one clutch and probably many more (Colwell and Oring 1988). Additionally, the following potential mammalian predators occurred (in order of frequency of observation) within the study areas: Richardson's Ground Squirrel (*Citellus richardsoni*), Badger (*Taxidea taxus*), Franklin's Ground Squirrel (*Spermophilus franklinii*), Coyote (*Canis latrans*) and Mink (*Mustela vison*). During this study, I observed Ring-billed Gulls (*Larus delawarensis*) and American Crows taking phalarope clutches (Colwell and Oring 1988). My observations are anecdotal, however, and I am unable to characterize these two years with regard to the importance of avian and mammalian predation to overall clutch losses.

For phalaropes, the risk of clutch loss varies seasonally, with predation risk highest early in the nesting season (Colwell and Oring 1988) when nest densities are low. The common assumption that vegetation growth increases clutch concealment may explain why nests initiated later in the 1983 season tended to survive longer and had a greater likelihood of being successful. This argument, however, is countered by the observation that nest concealment generally declines seasonally (Colwell and Oring 1990) and that there was no relationship between clutch initiation date and number of days survived in 1984.

The absence of a relationship between concealment and nest success also may be influenced by the functional response of predators encountering varying densities of nests (Sugden and Beyersbergen 1986, 1987). Sugden and Beyersbergen (1986, 1987) demonstrated that American Crow predation on artificial duck nests was density dependent, with predation rates increasing at nest densities greater than one nest per ha and reaching an asymptote at densities of six nests per ha. At high nest densities, concealment did not deter crows. Moreover, maximum protection afforded

by nesting cover would be achieved at low densities or in dense cover that would inhibit crows from searching for nests on the ground (Sugden and Beyersbergen 1986, 1987).

Within the confines of the study areas, densities for all shorebirds nests (0.90 and 0.95 nests per ha in 1983 and 1984, respectively; Colwell 1986) approximated the lower density limits suggested by Sugden and Beyersbergen (1987) to evoke density dependent predation by crows. But an unknown number of ground-nesting passerines and waterfowl also nested within the study area, pushing nest densities higher. Finally, local nest densities undoubtedly were greater still because most nests occurred within 100 m of the wetland (Colwell and Oring 1990). Together, these observations suggest that an absence of an effect of concealment on nesting success may have obtained because predators focused their hunting behavior on this site and took most nests. This idea requires formal testing but a recent analysis (Andrén 1991) suggests that nest density may not be as important as the spatial distribution of clutches.

Predation rates may have been magnified by activities of observers (Krasowski and Nudds 1987), masking any effects of concealment. During this study, observers found most nests early in the nesting cycle, and marked nest locations by placing dried cow dung (which was abundant within the pastures) several meters from the nest. We visited nests regularly and captured many incubating males. Among the six years I studied phalaropes, predation caused the greatest losses (60% of nests) during the two years when I measured vegetation. Thus, increased observer activity associated with measuring nest-site vegetation may have influenced nesting success.

Finally, it is possible that vegetation structure at nests may be related to selective factors other than concealment from predators. As noted by Walsberg (1985), placement of nests in dense vegetation is probably the most common pattern of nest-site selection, which has advantages additional to concealment from predators. Specifically, nests placed in dense vegetation may gain from: (1) being shielded from wind, (2) experiencing less nocturnal radiation loss, (3) exhibiting reduced diurnal heat gain from solar radiation, and (4) enhanced humidity (Walsberg 1985). These features of nest microclimate may benefit incubating adults, as well as influence embryo viability. For Wilson's Phalaropes, it is possible

that vegetation that offers greater concealment from predators also confers a favorable environment for incubation. Male phalaropes alone provide parental care for eggs and young, under sometimes hot thermal regimes (Colwell, pers. obs.).

Although many ground-nesting birds nest in vegetation providing greater concealment from predators compared to surrounding habitat, evaluation of the hypothesis that concealment deters predators has yielded mixed results (see Clark and Nudds 1991). Increased understanding of the role predation (and other environmental factors) plays in nest-site selection processes of ground-nesting birds will require detailed behavioral observations of individuals at the time nest sites are chosen, careful measurement of nest-site characteristics, as well as a detailed understanding of the behavior and ecology of predators.

ACKNOWLEDGMENTS

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