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EFFECTS OF HEIGHT AND VEGETATION ON
SUCCESS OF BIRD NESTS IN MARITIME FORESTS

Sharon M. DeFalco

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**EFFECTS OF HEIGHT AND VEGETATION ON SUCCESS OF BIRD NESTS IN
MARITIME FORESTS**

A Thesis

Presented to

the College of Graduate Studies of
Georgia Southern University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
In the Department of Biology

by

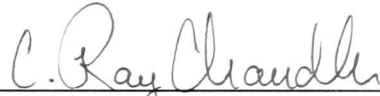
Sharon M. DeFalco

December 2000

December 7, 2000


To the Graduate School:

This thesis, entitled "Effects of Height and Vegetation on Success of Bird Nests in Maritime Forests" and written by Sharon M. DeFalco, is presented to the College of Graduate Studies of Georgia Southern University. I recommend that it be accepted in partial fulfillment of the requirements for the Master's Degree in Biology.

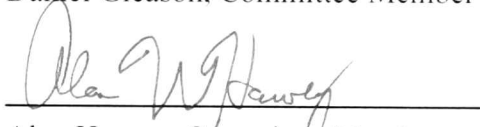


C. Ray Chandler, Supervising Committee Chair

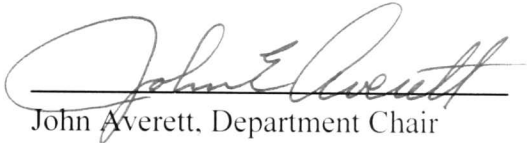
We have reviewed this thesis
and recommend its acceptance:



Daniel Gleason, Committee Member

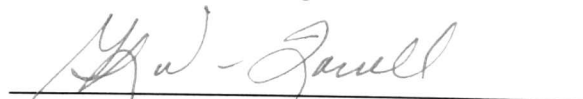


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ABSTRACT

EFFECTS OF HEIGHT AND VEGETATION ON SUCCESS OF BIRD NESTS IN MARITIME FORESTS

December 2000

SHARON M. DEFALCO

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Directed by: Professor C. Ray Chandler

Nest predation is an important source of mortality in songbirds and may contribute to declines in Neotropical migrants. I used artificial nests baited with fresh Japanese Quail and Zebra Finch eggs in conjunction with observations of natural nests to quantify the effects of nest height and vegetation on nest predation on St. Catherine's Island, a barrier island in southeast Georgia. Because of intense browsing by white-tailed deer, I predicted that lower, more exposed nests would be least successful. Artificial nests ($n = 389$) were placed in the field, and natural nests ($n = 49$) were observed, during April and May 1999 – 2000. Natural nests were more likely to be successful (77.6%; 38/49) than artificial nests (49.9%; 194/389). Nest success decreased with nest height in artificial nests, but height did not affect natural nests. Successful nests tended to have more vegetation cover horizontally within 1 m of the nest; this effect was most pronounced in artificial nests. The effects of vegetation were consistent across nest

heights. Patterns of egg loss suggest that most nest predation was by larger nest predators, but smaller predators (such as mice or small snakes) appeared important at lower nest heights. Overall, lower nests were not less successful on St. Catherine's Island, but vegetation cover was important to nest success. Deer browsing does not appear to be causing unusual mortality in songbird nests below 2 m, but passerines on St. Catherine's Island tended to select nest sites non-randomly to minimize detection by predators. Although shrub-nesting passerines were able to find suitable nest sites in this study, the effects of browsing on the habitat may limit the number of available nest sites, thus decreasing the overall population of Neotropical migrants on St. Catherine's Island. Because the majority of Neotropical migrants nest in the shrub layer and are more prone to the effects of nest predation, future research should assess the effects of populations of white-tailed deer on vegetation in southeastern maritime forests.

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Chapter I

Introduction

Populations of many species of passerine birds have been declining in the forests of eastern North America, with forest-dwelling Neotropical migrants suffering the most dramatic declines (Wilcove 1985, Askins et al. 1990, Martin 1992). As many as 75% of the Neotropical migrant species breeding in the eastern U.S. are in the midst of population declines that began in the 1970s (Askins et al. 1990). For example, populations of Painted Buntings (*Passerina ciris*), White-eyed Vireos (*Vireo griseus*), Common Yellowthroats (*Geothlypis trichas*), and Hooded Warblers (*Wilsonia citrina*) have decreased by as much as 2.8% per year (DeGraaf and Rappole 1995, Peterjohn et al. 1995). Many factors contribute to these declines, including loss or modification of habitat on the wintering and breeding grounds (Askins et al. 1990), brood parasitism (DeGraaf and Rappole 1995), and nest predation (Martin 1995, Ortega et al. 1998). Species-area effects, interspecific competition, (DeGraaf and Rappole 1995), and increasing severity of storms during migration (Butler 2000) have also been mentioned as possible reasons for population declines in Neotropical migrants.

Of the factors listed above, predation is a primary cause of nest failure in most birds (Ricklefs 1969, Martin 1995). It is believed that nesting habits of Neotropical migrants (low, open-cup nests, usually one or two broods per year) make populations of Neotropical migrants potentially more susceptible to the impacts of nest predation than populations of resident species (Askins et al. 1990, Peterjohn et al. 1995). Thus, any

factors that tend to increase nest predation may contribute to the declines in Neotropical migrants (Ortega et al. 1998). Many factors may play a role in escalating the incidence of nest predation (Hoi and Winkler 1994). For example, habitat fragmentation increases the exposure of forest-nesting birds to edges, along which mesopredators such as skunks and raccoons hunt for nests, and can increase population density of these nest predators (Hoi and Winkler 1994). Because many open-cup-nesting birds choose nest sites non-randomly to minimize discovery by predators (Martin 1992), habitat alterations that limit these choices also result in greater predation on nests (Martin 1992, Cresswell 1997). The density of vegetation around the nest, concealment of the nest, and the position and height of the nest may all be related to the risk of predation on small, open-cup nests (Martin 1993, Howlett and Stutchbury 1996). Thus, habitat modification in the form of decreasing understory vegetation via habitat management or intense browsing by ungulates has been implicated as a cause of increased nest predation in passerines (Wilcove 1985, Roper 1992, Major and Kendal 1996, Cresswell 1997).

St. Catherine's Island, Georgia, is a good example of an area in the southeastern United States that suffers from high populations of potential nest predators (particularly raccoons) and from habitat modifications that may contribute to exposure of songbird nests. White-tailed deer (*Odocoileus virginianus*) and wild hogs (*Sus scrofa*) are abundant on St. Catherine's Island (Royce Hayes, St. Catherine's Island Foundation, pers. comm.). Browsing by white-tailed deer has resulted in an open forest with little vegetation between ground level and a pronounced "browse line" at a height of approximately 2 m. Rooting by wild hogs has limited growth of saplings and herbaceous

vegetation in many areas. Several species of birds that have been declining in the southeast United States (DeGraaf and Rappole 1995), such as Painted Buntings, Hooded Warblers, and Eastern Towhees (*Pipilo erythrophthalmus*), nest in the forests that have been impacted by deer and hogs. Other shrub-nesting passerines nesting on St. Catherine's Island include Northern Cardinals (*Cardinalis cardinalis*) and White-eyed Vireos (*Vireo griseus*). That vegetation changes have affected nest success of songbirds on St. Catherine's Island is suggested by a preliminary study during the summer of 1998 on the mortality of nests of Neotropical migrants. In the 1998 study, I noted that the average nest heights of Northern Cardinals, Painted Buntings, and White-eyed Vireos were higher than published averages (Harrison 1978). This finding suggested that lack of understory vegetation may force birds to nest higher where vegetation is thicker and nest success higher. There have been no experimental tests of this hypothesis.

Little is known about nest predation in maritime forests of the southeastern United States, even though there has been a tremendous increase in human population in this area in recent years. Furthermore, data on the relationship between habitat change and nest predation are critical to understanding the ongoing declines in populations of Neotropical migrants. We need to know if nest height and understory cover contribute to decline in some populations of Neotropical migrants and other songbirds in maritime forests. Therefore, this study assessed the effects of nest height and vegetation on rates of predation on open-cup nesting birds. Specifically, I quantified variation in microhabitat and macrohabitat around artificial and natural passerine nests at various heights and quantified whether this variation was related to the fate of the nest.

Chapter II

Study Area and Methods

Study Area

St. Catherine's Island, a 5,665-ha barrier island, is located 3.5 km off the coast of southeast Georgia in Liberty County. The island consists of maritime forests, beaches, pastures, freshwater ponds and marshes, and surrounding saltwater marsh, ocean, and estuaries (Cohn 1990). Maritime forests of oak and pine, sand dunes, and beaches cover the northeastern portion of the island and extend south along the eastern coast. Small dirt roads are scattered throughout the island, and the only developed area, the Wildlife Conservation Society's species survival center, is located on the west side of the island adjacent to Walburg Creek (Fig. 1).

Until the 1940s, St. Catherine's Island was cultivated for rice and cotton, and logged extensively. Since then, most of the areas that were cleared were left to natural succession (Cohn 1990) and are currently dominated by slash pine (*Pinus elliotii*), loblolly pine (*P. taeda*), and longleaf pine (*P. palustris*). Areas not cleared for human purposes are still dominated by oaks, especially live oak (*Quercus virginiana*). The two sites chosen for this study (31° 40' 20" N, 81° 08' 40" W; 31° 38' 10" N, 81° 09' 30" W) were located in oak-dominated maritime forest along the eastern side of St. Catherine's Island. Occasional mixed and pine-dominated patches also existed within the study sites (Fig. 1).

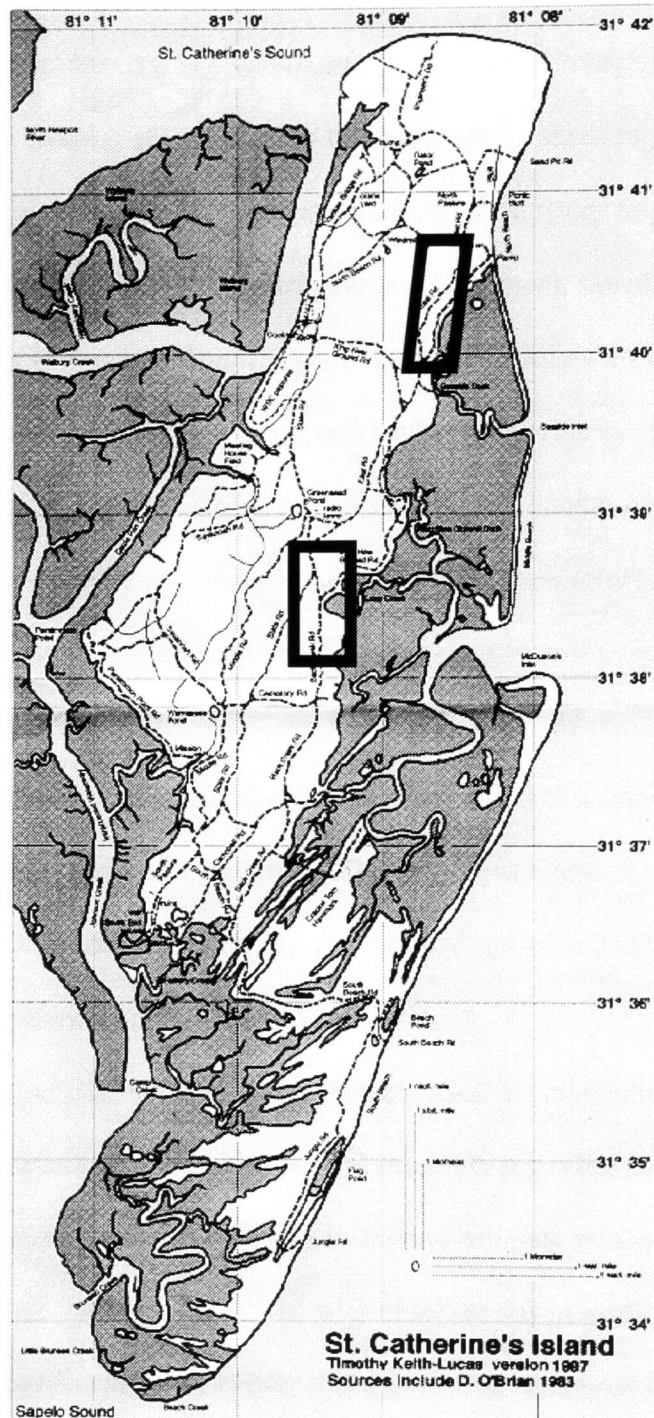


Figure 1. Map of St. Catherine's Island, Georgia, showing the location of the two sites used in this study.

Abundant tree species in the maritime forest include slash pine, longleaf pine, loblolly pine, live oak, sand live oak (*Q. geminata*), laurel oak (*Q. laurifolia*), southern magnolia (*Magnolia grandiflora*), pignut hickory (*Carya glabra*), small pignut hickory (*Carya ovalis*), and sweetgum (*Liquidambar styraciflua*). Understory vegetation includes cabbage palm (*Sabal palmetto*), dwarf palmetto (*S. minor*), sawtooth palmetto (*Serenoa repens*), red bay (*Persea borbonia*), sparkleberry (*Vaccinium arboretum*), yaupon (*Ilex vomitoria*), American holly (*I. opaca*), and bayberry (*Myrica cerifera*).

Fauna of St. Catherine's Island that may impact habitat or contribute to nest predation include wild hog (*Sus scrofa*), raccoon (*Procyon lotor*), white-tailed deer (*Odocoileus virginianus*), gray squirrel (*Sciurus carolinensis*), Norway rat (*Rattus norvegicus*), eastern woodrat (*Neotoma floridana*), mice (*Mus musculus*, *Peromyscus gossypinus*), Fish Crow (*Corvus ossifragus*), Boat-tailed Grackle (*Quiscalus major*), Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*), rat snake (*Elaphe obsoleta*), and black racer (*Coluber constrictor*). Brown-headed Cowbirds (*Molothrus ater*) are also common on St. Catherine's Island.

In this study, baited artificial nests were used in conjunction with natural nests to quantify nest predation rates in Neotropical migrants and other passerines on St. Catherine's Island. Artificial nests can be used to estimate trends in predation rates and are valuable when used in conjunction with observations on natural nests (Ortega et al. 1998, Wilson and Brittingham 1998). They have also been used extensively to estimate effects of habitat on predation rates on small, open-cup, natural bird nests (Bayne et al. 1997, Ortega et al. 1998, Wilson and Brittingham 1998, DeGraaf et al. 1999, Matessi and Bogliani 1999, Rangen et al. 1999, Knutson et al. 2000, Reitsma and Whelan 2000, Song

and Hannon 2000, Zanette and Jenkins 2000). Artificial nests provide larger sample sizes, more control, and increased efficiency of data collection in comparison to locating only natural, active nests (Ortega et al. 1998, Wilson and Brittingham 1998). However, appearance of artificial nests may differ from natural nests, which may lead to ambiguous and inaccurate estimates of predation rates as well as the types of predators found at different types of nests (Major and Kendal 1996, Wilson and Brittingham 1998). When artificial nests are carefully designed, however, they can provide more accurate estimates by having the same visual appearance as natural nests.

Artificial nests

Each artificial nest was framed with dark annealed steel wire to approximate the size (10x10x5 cm) and shape of small open-cup nests (Wilson and Brittingham 1998) typical of Northern Cardinals, Painted Buntings, and White-eyed Vireos. The nests were constructed with Spanish moss (*Tillandsia usneoides*) and grasses native to St. Catherine's Island to resemble the materials typically found in Northern Cardinal and Painted Bunting nests.

Twelve transect lines, each 500-m long, were placed parallel to each other 100 m apart throughout the study sites. Three transect lines made up the northern study site while the remaining nine transect lines made up the southern site (Fig. 1). I placed artificial nests at 50-m intervals along transects in sites typical of natural bird nests (hanging under the skirt of a tree, in thick brush, or on top of a forked branch). No two sites were used twice within or between years. The height of each artificial nest was selected at random from four height categories: ground (0-0.9 m), shrub (1

– 2.4 m), understory (2.5 – 3.5 m), and overstory (3.6 – 7 m). Ground nests were used to examine predation on the ground, shrub nests were elevated to examine predation at the browse line or just below it. Understory and overstory nests were located at least one meter above the browse line to examine predation at higher elevations. Most incubation periods for natural nests range from 12-15 days (Harrison 1978), so artificial nests were left in place for 15-day intervals. Because most passerines on St. Catherine’s Island have at least two broods per year, the artificial nests were set up in two time intervals within each year; one in April and one in May. These months coincided with the incubation period for most natural nests of small songbirds on the island. In order to get a relative timeline for predation, the contents of each artificial nest were checked for predation every 5 -7 days for a total of fifteen days. A nest was considered unsuccessful if one or more eggs were missing or broken.

Eggs

Each artificial nest was baited with one Japanese Quail (*Coturnix japonica*) egg (30x24 mm) and one Zebra Finch (*Poephila guttata*) egg (16x13 mm) to bracket the size of eggs found in natural nests and minimize bias towards predator size and type (Fig. 2). Larger fresh eggs (Japanese Quail, Northern Bobwhite [*Colinus virginianus*] and domestic chicken [*Gallus gallus*]) may be more conspicuous to visual predators than smaller ones (plasticine, ceramic, and Zebra Finch) (Major 1990), but small predators (mice, some snakes) are unable to break the shells of larger eggs (Roper 1992, Bayne et al. 1997). Fresh eggs were used because they may emit a scent to which some predators, such as snakes, may be attracted. Thus, the use of plasticine or ceramic eggs could lower



Figure 2. Comparison of eggs used in this study. Japanese Quail and Zebra Finch eggs were used to bait the artificial nests. Northern Cardinal, Painted Bunting, and White-eyed Vireo nests were located on St. Catherine's Island for comparison. Brown-headed Cowbird eggs occurred in a few parasitized natural nests.

the estimate of predation. To minimize the possibility of leaving human scent on eggs, nests, and trails to the artificial nests, rubber gloves and boots were worn when handling nest items (Seitz and Zegers 1993, Whelan et al. 1994). In April 1999, artificial nests were baited with only one Japanese Quail because the shipment of Zebra Finch eggs did not arrive.

Natural nests

In order to compare patterns of nest predation on artificial nests to that on natural nests, active nests of Northern Cardinals (n=19), White-eyed Vireos (n=27), Painted Buntings (n=1), and other similar-sized passerines (n=2) were located and monitored within the same habitat as the artificial nests (Major and Kendal 1996, Ortega et al. 1998). Success of natural nests was quantified up to the time of hatching to make them comparable to artificial. Because the date of onset of incubation was not known for all natural nests located, they were monitored every 3-5 days until hatching, then every 7 days until fledging or loss of chicks.

Vegetation characteristics

Vegetation structure and composition at each nest were estimated using James and Shugart (1970) vegetation plots (11.3-m radius) (Table I). The vegetation characteristics measured were separated into two categories: microhabitat and macrohabitat. Microhabitat characteristics were measured directly from the nest and described the position of the nest as well as the vegetation cover around the nest. Macrohabitat characteristics were measured within the 11.3-m radius plot centered on the

Table I. Vegetation characteristics measured at artificial and natural nests. St. Catherine's Island, Georgia.

| Variable | Definition |
|-----------------|---|
| Veg. Species | Species of tree or shrub in which the nest was found or placed. |
| Veg. Height | Height (m) of the tree or shrub in which the nest was found or placed. |
| Nest Height | Height (m) of the nest (nearest 0.1 m). |
| Nest-Can | Vertical distance (m) from the center of the nest to the canopy. |
| Nest-Edge | Horizontal distance (m) from the center of the nest to the closest edge of the tree or shrub in which the nest was found or placed. |
| Hor. Cover 0-1m | Sum of the number of times vegetation contacted a 1-m pole (hits) every 0.1m from 0-1m held horizontal from the center of the nest in the four cardinal directions. |
| Hor. Cover 1-3m | Sum of the number of times vegetation contacted a 3-m pole (hits) held horizontal from the center of the nest in the four cardinal directions. |
| Veg. Below | Number of times vegetation contacted a 1-m pole (hits) held vertical from the bottom of the nest. |
| Veg. Above | Number of times vegetation contacted a 1-m pole (hits) held vertical from the top of the nest. |
| Pine Saplings | Total number of pine saplings (waist high) in the 11.3-m radius plot (centered on the nest). |
| Basal Area | Cross-sectional area of trees > 2.5 cm DBH in 11.3-m plot. |
| Ground Cover | Percentage of the ground in the 11.3-m radius plot (centered on the nest) covered by grasses, pines, palmettos, and forbes. |
| Canopy Cover | Percentage of the 11.3-m radius plot (centered on the nest) covered by the canopy of pine or deciduous overstory trees. |

Table I (continued). Vegetation characteristics measured at artificial and natural nests.

St. Catherine's Island, Georgia.

| Variable | Definition |
|-----------------|--|
| Tot. Under | Total number of understory trees (2.5 cm<DBH<10 cm) in the 11.3-m radius plot (centered on the nest). |
| Dec.-Pine Under | Total number of pine understory trees subtracted from total number deciduous understory trees in the 11.3-m radius plot (centered on the nest). This index describes whether the habitat is dominated by deciduous or pine understory. |
| Tot. Overstory | Sum total of all overstory trees (DBH>10 cm) in the 11.3-m radius plot (centered on the nest). |
| Dec.-Pine Over | Total number of pine overstory trees subtracted from total number deciduous overstory trees in the 11.3-m radius plot (centered on the nest). This index describes whether the habitat is dominated by deciduous or pine overstory. |

nest and described the general habitat in which the nest was placed or found. Vegetation was quantified after fledging for natural nests and, at the most, three weeks after the end of each artificial nest trial.

Analysis

I quantified the relationship between nest success and categorical variables (nest type, height interval, month, year) using G-tests. I compared vegetation between successful and unsuccessful nests using Mann-Whitney tests (for univariate comparisons) and MANOVA (for multivariate comparisons). Canonical discriminant analysis was used to identify those vegetation variables that best discriminated successful and unsuccessful nests. ANCOVA was used to quantify whether canonical scores provided similar discrimination at all nest heights. Survival curves for artificial and natural nests were analyzed using the Kaplan-Meier method. Survival rates were evaluated as a function of height and vegetation characteristics, which were analyzed using MANOVA and ANOVA. All statistical procedures were performed in JMP (SAS Institute, 1998). Comparisons among artificial nests by month were made only in 2000 because the contents of artificial nests in April 1999 (one Japanese Quail egg) were not directly comparable to the contents in May 1999 (one Japanese Quail egg and one Zebra Finch egg).

Chapter III

Results

Do predation rates differ between natural and artificial nests?

I monitored 389 artificial and 49 natural nests during this study. Overall, 47% (206/438) were preyed upon. Natural nests were more successful than artificial nests ($G=14.2$, $df=1$, $P<0.001$); 49.9% (194/389) of artificial nests were successful while 77.6% (38/49) of natural nests were successful. The median survival time of incubating natural nests was 14 days while that of artificial nests was 12 days (Fig. 3). However, the tendency for natural nests to be more successful depended upon year. Success of artificial and natural nests was similar in 1999 (Fig. 4), but in 2000 natural nests were more successful than artificial nests.

Success of natural nests did not vary with month (April vs. May) in 1999 ($G=0.76$, $df=1$, $P=0.39$) or 2000 ($G=1.15$, $df=1$, $P=0.28$). In 1999, 85% (11/13) of natural nests were successful in April and 67% (4/6) were successful in May. In 2000, 82% (18/22) natural nests were successful in April and 62.5% (5/8) were successful in May. Artificial nests were significantly more successful in April than May in both 1999 ($G=64.94$, $df=1$, $P<0.001$) and 2000 ($G=14.25$, $df=1$, $P<0.001$). In 1999, 93% (93/101) of artificial nests were successful in April and 40% (36/91) were successful in May. In 2000, 45% (45/99) of artificial nests were successful in April and 21% (20/96) were successful in May.

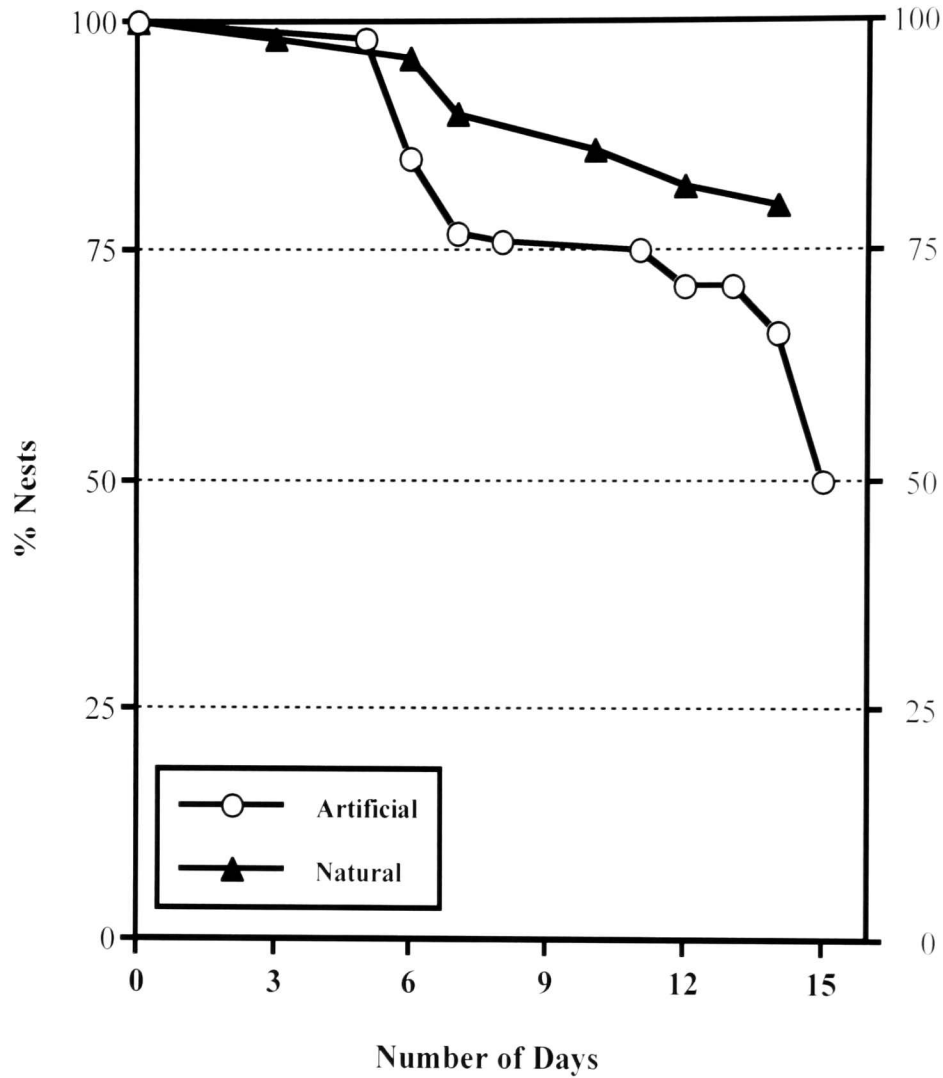


Figure 3. Success of artificial and natural nests over a 15-day incubation period.

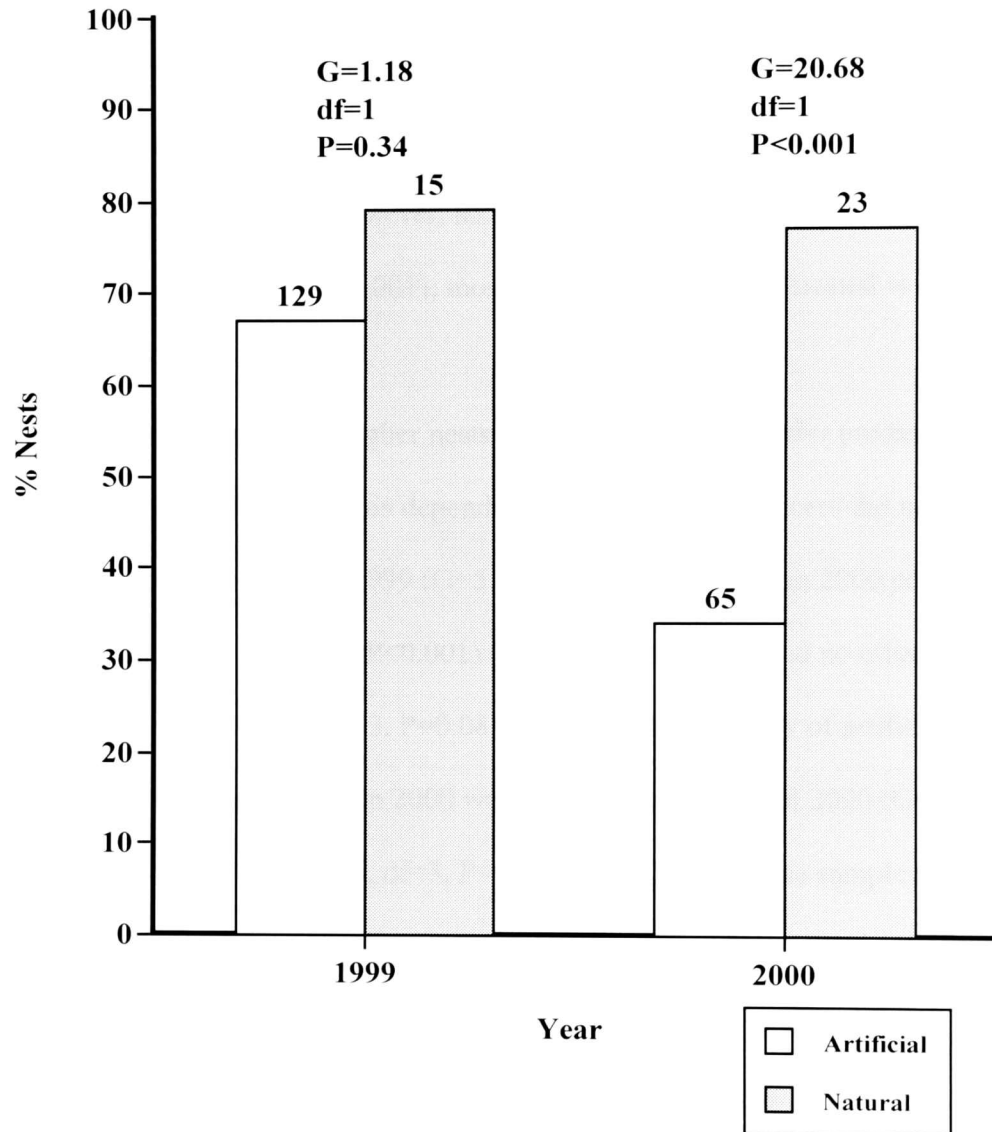


Figure 4. Success of artificial and natural nests during the two years of study (1999 and 2000). Numbers above the bars represent the total number of nests in each year.

Do higher nests have lower predation rates?

Because of heavy browsing by white-tailed deer and the preliminary observations of unusually high nests on St. Catherine's Island, I predicted that shrub and ground nests would have higher predation rates than nests at other heights. Because of the experimental design, artificial nests were equally distributed among height categories ($G=4.66$, $df=3$, $P=0.20$). However, natural nests were not equally distributed among heights ($G=39.66$, $df=3$, $P<0.001$); most (33/49) natural nests located were in the shrub layer (Fig. 5).

For artificial nests, higher nests were more likely to suffer predation ($G=18.18$, $df=3$, $P<0.001$). However, this depended upon year. Nest success did not vary among heights in artificial nests in 1999 ($G=5.23$, $df=3$, $P=0.16$), but in 2000 predation increased with height ($G=28.59$, $df=3$, $P<0.001$) (Fig. 6). Nest height had no effect on the success of natural nests ($G=6.79$, $df=3$, $P=0.08$) (Fig. 6). The tendency of artificial nest success to decrease with nest height in 2000 was apparent in both April 2000 ($G=13.62$, $df=3$, $P=0.004$) and May ($G=23.37$, $df=3$, $P<0.001$) (Fig. 7). Because sample sizes were small for most heights, I did not compare natural nest success among heights between years or between months.

Do nests in more vegetated sites have lower predation?

Based on the 16 vegetation variables measured at each nest, artificial and natural nests differed in vegetation (Wilks' $\lambda =0.89$, $F_{15, 421}=3.58$, $P<0.001$). Natural nests were in areas with more deciduous saplings, greater ground cover, lower basal area, fewer

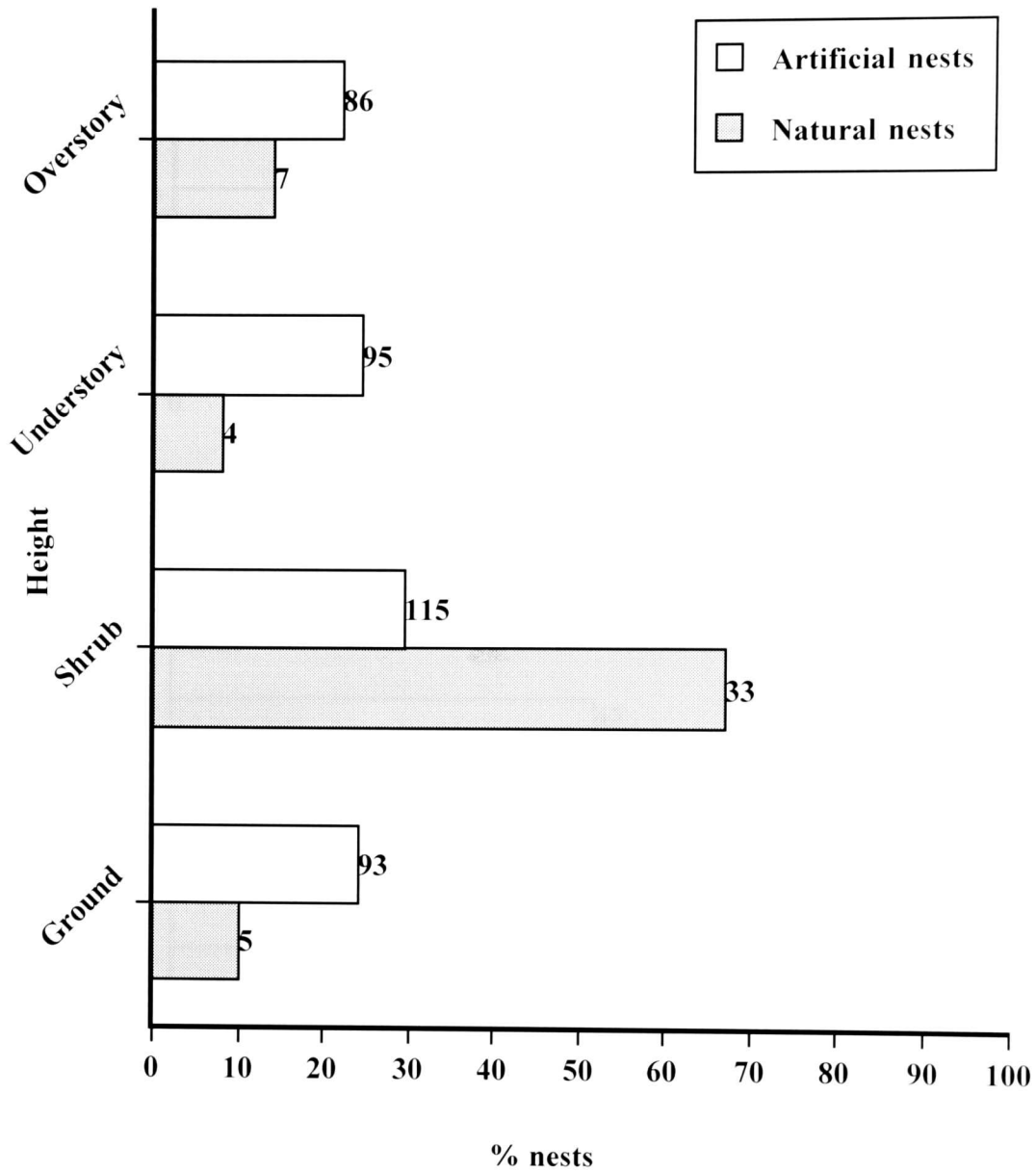


Figure 5. Overall height distribution of artificial and natural nests. Numbers above the bars represent the total number of nests at each height category.

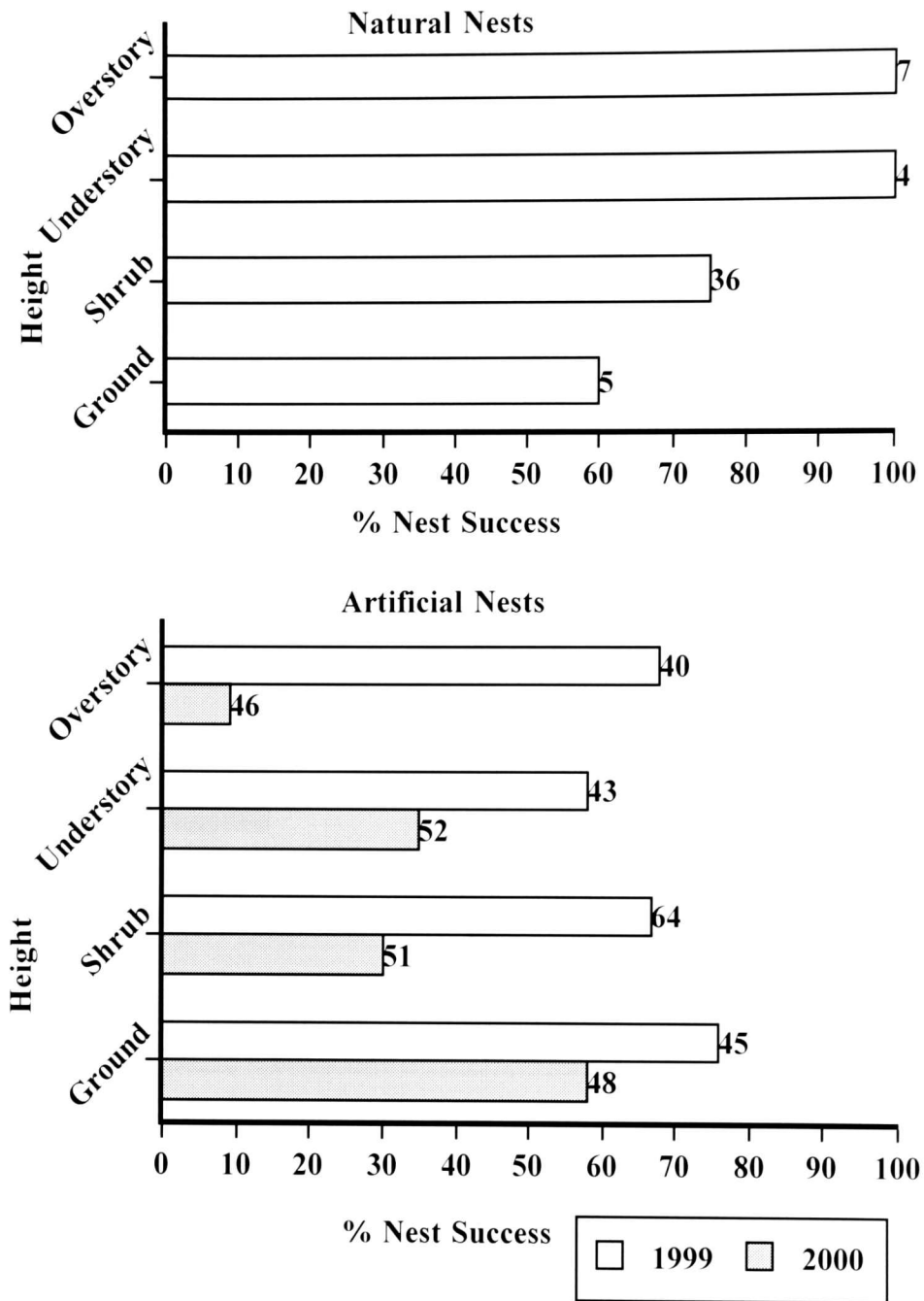


Figure 6. Effects of nest height on success of natural (years combined) and artificial (1999 and 2000 separately) nests. Numbers above bars represent the total number of nests at each height.

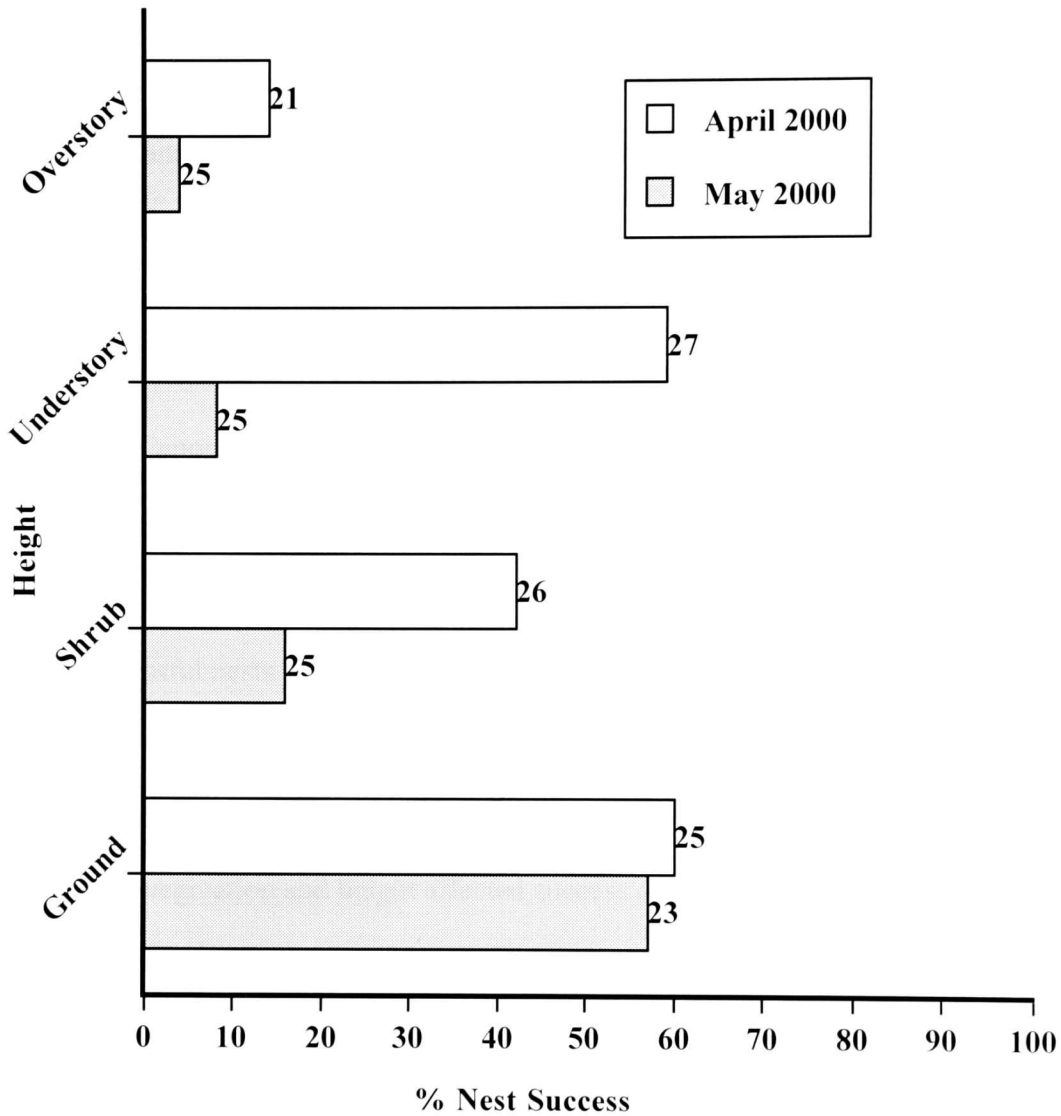


Figure 7. Success of artificial nests among heights during the two months of study in 2000 (April and May). Numbers above the bars represent the total number of nests at each height.

overstory trees, and less vegetation below the nest than artificial nests (Table II).

Because artificial and natural nests were in different habitat, the effects of vegetation on success were analyzed separately for each nest type.

Vegetation affected the success of artificial nests (Table III). Canonical discriminant analysis of the 16 vegetation variables was able to discriminate between successful and unsuccessful artificial nests (Wilks' $\lambda=0.91$, $F_{17,371}=2.31$, $P=0.003$). Successful artificial nests tended to be farther from the edge of the tree or shrub in which they were located and have greater horizontal vegetative coverage 1-3 m from the nest (Table IV). Canonical discriminant analysis failed to discriminate between successful and unsuccessful natural nests (Wilks' $\lambda=0.67$, $F_{17,31}=0.97$, $P=0.51$). However, successful natural nests had more horizontal vegetation cover ($\chi^2=4.53$, $df=15$, $P=0.04$) than unsuccessful nests.

Are the effects of vegetation consistent across nest heights?

Both vegetation and height affected success of artificial nests. Thus, I asked whether the vegetation characteristics associated with successful nests were similar at all nest heights. Canonical scores decreased with nest height ($F_{1,386}=27.81$, $P<0.001$), consistent with the decrease in nest success among higher nests. This decrease in canonical scores with nest height was similar in both successful and unsuccessful nests (ANCOVA, homogeneity of slope, $F_{3,384}=1.26$, $P=0.29$), and canonical discriminant analysis of the 16 vegetation variables was able to discriminate between successful and unsuccessful artificial nests across nest height ($F_{3,384}=16.5$, $P<0.001$) (Fig. 8).

Table II. Mean and standard error of vegetation characteristics for both artificial (n=389) and natural (n=49) nests used in this study.

| | Variable | Artificial | | Natural | | Mann-Whitney | |
|--------------|-----------------|------------|------|---------|------|----------------|-------|
| | | Mean | SE | Mean | SE | X ² | P |
| Microhabitat | Veg. Height | 7.86 | 0.31 | 6.84 | 0.89 | 0.44 | 0.160 |
| | Nest-Can | 4.86 | 0.27 | 3.65 | 0.76 | 3.77 | 0.050 |
| | Nest-Edge | 0.49 | 0.03 | 0.26 | 0.05 | 2.50 | 0.110 |
| | Hor. Cover 0-1m | 15.66 | 0.34 | 15.53 | 0.94 | 0.01 | 0.930 |
| | Hor. Cover 1-3m | 7.77 | 0.39 | 9.45 | 1.09 | 1.80 | 0.180 |
| | Veg. Below | 5.03 | 0.18 | 2.69 | 0.50 | 19.71 | 0.001 |
| Macrohabitat | Veg. Above | 4.25 | 0.12 | 4.67 | 0.35 | 1.72 | 0.190 |
| | Dec. Saplings | 4.06 | 0.34 | 7.46 | 1.39 | 8.63 | 0.003 |
| | Pine Saplings | 0.75 | 0.08 | 2.21 | 0.73 | 0.00 | 0.960 |
| | Basal Area | 12.16 | 0.78 | 9.35 | 1.68 | 23.70 | 0.001 |
| | Ground Cover | 47.62 | 1.23 | 57.55 | 3.47 | 6.97 | 0.008 |
| | Canopy Cover | 60.49 | 1.08 | 57.35 | 3.04 | 0.87 | 0.350 |
| | Tot. Understory | 0.68 | 0.18 | 1.84 | 0.50 | 1.09 | 0.300 |
| | Dec.-Pine Under | 0.87 | 0.04 | 0.94 | 0.11 | 2.96 | 0.090 |
| | Tot. Overstory | 3.75 | 0.24 | 2.77 | 0.48 | 5.23 | 0.020 |
| | Dec.-Pine Over | 2.34 | 0.05 | 2.39 | 0.14 | 0.26 | 0.610 |

Table III. Mean and standard error of vegetation characteristics for unsuccessful (n=195) and successful (n=194) artificial nests.

| | Variable | Not Successful | | Successful | | Mann-Whitney | |
|----------------|------------------|----------------|------|------------|------|----------------|-------|
| | | Mean | SE | Mean | SE | X ² | P |
| Microhabitat | Veg. Ht. | 8.19 | 0.42 | 7.52 | 0.48 | 4.88 | 0.030 |
| | Nest -Can. | 5.02 | 0.38 | 4.70 | 0.39 | 0.98 | 0.320 |
| | Nest-Edge | 0.59 | 0.04 | 0.82 | 0.05 | 9.92 | 0.002 |
| | Hor. Cover 0-1m | 15.10 | 0.44 | 16.20 | 0.51 | 2.76 | 0.100 |
| | Hor. Cover 1-3m | 6.01 | 0.44 | 9.55 | 0.58 | 18.68 | 0.001 |
| | Veg. Below | 4.78 | 0.26 | 5.28 | 0.26 | 1.05 | 0.300 |
| | Veg. Above | 4.32 | 0.18 | 4.17 | 0.18 | 0.19 | 0.670 |
| Macrohabitat | Dec. Saplings | 2.74 | 0.42 | 3.15 | 0.53 | 0.20 | 0.650 |
| | Pine Saplings | 0.42 | 0.11 | 0.43 | 0.11 | 0.24 | 0.620 |
| | Basal Area | 43.77 | 1.11 | 43.67 | 1.11 | 0.02 | 0.900 |
| | Ground Cover | 46.87 | 1.78 | 46.57 | 1.70 | 0.58 | 0.450 |
| | Canopy Cover | 60.25 | 1.42 | 60.72 | 1.60 | 0.27 | 0.610 |
| | Total Understory | 0.52 | 0.24 | 0.83 | 0.26 | 0.97 | 0.330 |
| | Dec.-Pine Under | 0.89 | 0.06 | 0.84 | 0.06 | 0.21 | 0.650 |
| | Total Overstory | 6.10 | 0.20 | 5.83 | 0.22 | 0.01 | 0.940 |
| Dec.-Pine Over | 2.33 | 0.07 | 2.36 | 0.07 | 0.01 | 0.910 | |

Table IV. Correlations between original vegetation variables and canonical axis discriminating successful and unsuccessful artificial nests.

| | Variable | Correlation to Canonical Axis |
|--------------|----------------------------|-------------------------------|
| Microhabitat | Nest Height (m) | -0.23 |
| | Veg. Ht. (m) | -0.15 |
| | Nest - Can. (m) | -0.08 |
| | Nest - Edge (m) | 0.56 |
| | Hor. Cover 0-1m (# hits) | 0.26 |
| | Hor. Cover 1-3m (# hits) | 0.78 |
| | Vert. Cover Below (# hits) | 0.24 |
| | Vert. Cover Above (# hits) | -0.13 |
| Macrohabitat | Decid. Saplings | 0.09 |
| | Pine Saplings | 0.03 |
| | Basal Area | -0.01 |
| | Ground Cover (%) | -0.15 |
| | Canopy Cover (%) | 0.05 |
| | Total Understory | 0.15 |
| | Dec. - Pine Under | -0.01 |
| | Total Overstory | -0.02 |
| | Dec. - Pine Over | -0.16 |

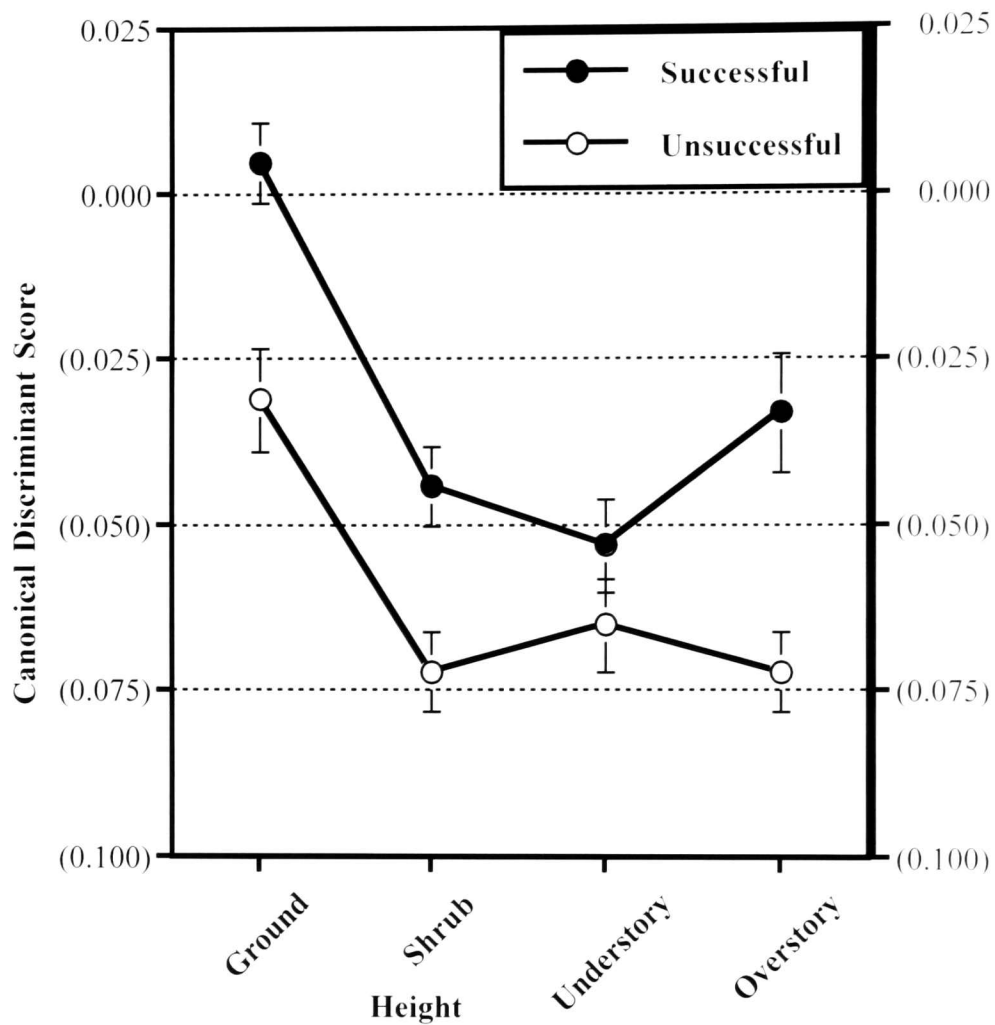


Figure 8. Mean (\pm SE) canonical discriminant scores for successful and unsuccessful artificial nests at each of the four heights. Successful and unsuccessful nests show the same relationship between scores and height (ANCOVA; homogeneity of slope, $F=1.59$, $df=3$, $P=0.19$). Canonical scores can discriminate nest fate across all nest heights (ANCOVA; $F=32.29$, $df=3$, $P<0.001$)

Does egg type affect predation rates of artificial nests?

I used 389 Japanese Quail eggs and 298 Zebra Finch eggs to bait 389 artificial nests. Of the 194 unsuccessful nests, 105 had both eggs removed, 17 had the Japanese Quail egg removed, and 77 had the Zebra Finch egg removed (Fig. 9). In those artificial nests that had only one egg taken, Zebra Finch eggs were more likely to be removed than Japanese Quail eggs ($G=52.99$, $df=1$, $P<0.001$).

Type of nest failure (Japanese Quail egg removed, Zebra Finch egg removed, or both eggs removed) varied with nest height ($G=19.36$, $df=6$, $P=0.004$). Removal of both eggs from artificial nests increased with nest height, but removal of only the Japanese Quail egg or Zebra Finch egg did not vary with nest height ($G=7.31$, $df=3$, $P=0.06$) (Fig. 10). In 2000, when nest contents were comparable between months, differences in timing of incubation (setup) existed with types of eggs removed ($G=20.50$, $df=2$, $P<0.001$). In April, removal of the Zebra Finch egg (28/99) was greater than the removal of both eggs (24/99) and the Japanese Quail egg (2/99). In May, removal of both eggs (63/98) was greater than removal of the Zebra Finch (15/98) and Japanese Quail egg (0/98). Height did not affect the type of egg removed in April ($G=5.41$, $df=6$, $P=0.49$) or May 2000 ($G=2.8$, $df=3$, $P=0.42$).

For artificial nests, survival of the eggs varied ($G=7.40$, $df=2$, $P=0.02$). The median survival time for the removal of the Japanese Quail egg was 7 days, for the Zebra Finch egg 14 days, and for both eggs 12 days. However, differences were found in the survival of egg types in 1999 ($G=261.50$, $df=18$, $P<0.001$) and 2000 ($G=270.78$, $df=21$, $P<0.001$). Japanese Quail eggs were consistently more successful throughout the 15-day incubation period in 1999 and 2000 than Zebra Finch eggs (Fig. 9).

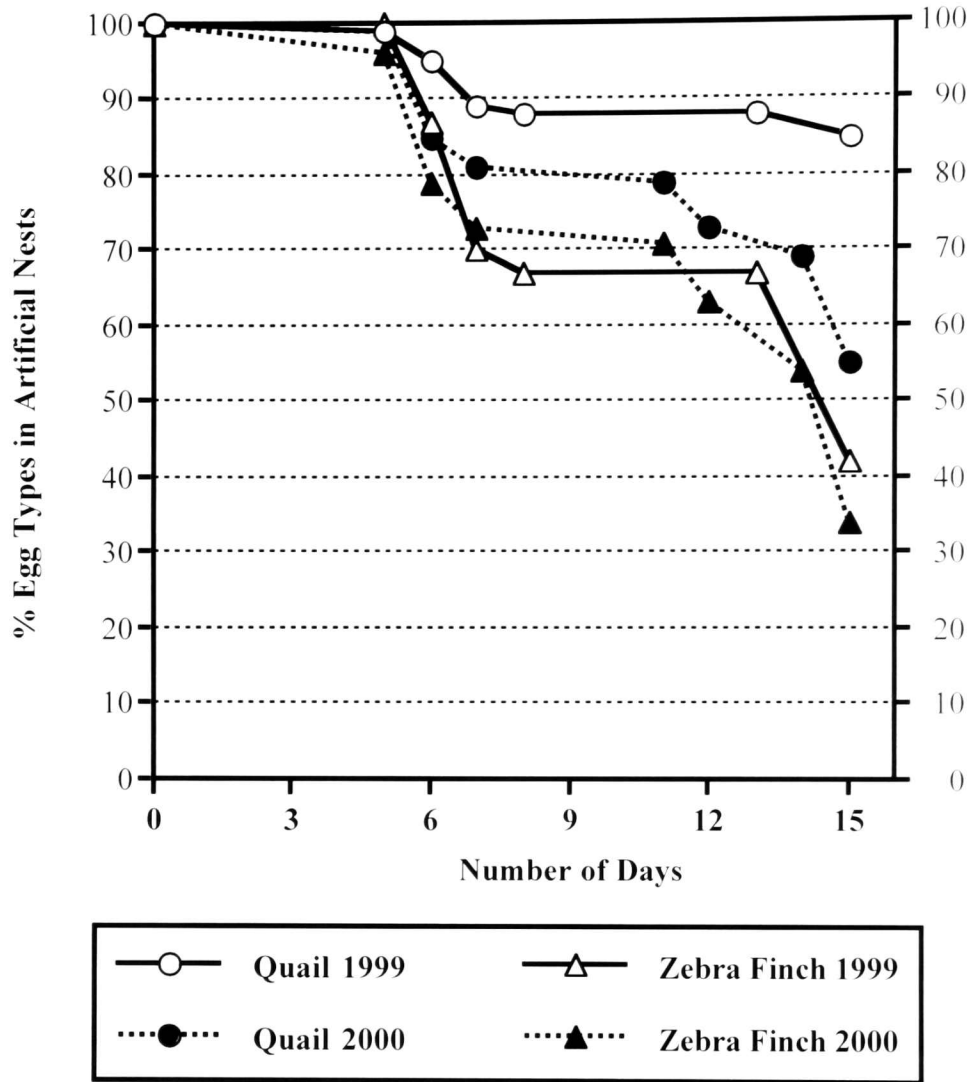


Figure 9. Survival of Japanese Quail and Zebra Finch eggs (1999 and 2000) in artificial nests over a 15-day incubation period.

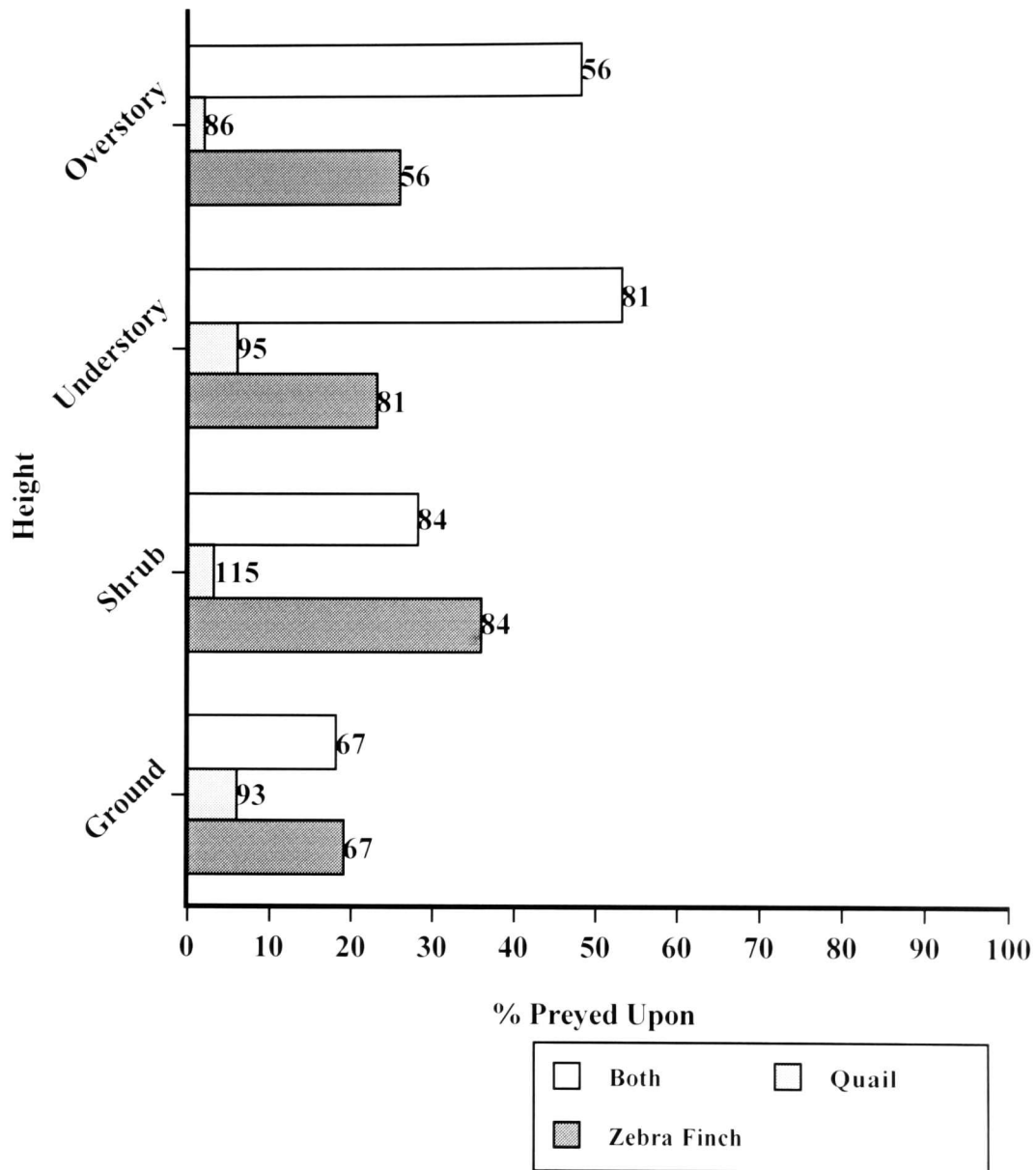


Figure 10. Effect of nest height on predation of Japanese Quail and Zebra Finch eggs in artificial nests. Numbers above the bars represent the total number of eggs at the corresponding height.

Chapter IV

Discussion

Based on the results of this study, natural nests were more successful than artificial nests (Fig. 3). Vegetation around natural and artificial nests differed, with differences in vegetation affecting success only of artificial nests (Table II). Nest height did not affect success of natural nests, but artificial nests were less successful at greater heights (Fig. 6). The effects of vegetation on artificial nest success were consistent among nest heights. The type of egg used to bait artificial nests may explain some differences in success of artificial and natural nests.

Differences in success of artificial and natural nests

Other studies have shown natural nests to be more successful than artificial nests (Major and Kendal 1996, Ortega et al. 1998, Wilson and Brittingham 1998, Buler and Hamilton 2000). However, artificial nests can have similar, if not better, success than natural nests (Major and Kendal 1996). Natural nests may have had greater success on St. Catherine's Island for several reasons. First, not all of the natural nests were located at the nest-building or egg-laying stages, which could have biased results in favor of increased nest success because those nests preyed upon early in the incubation stage would not have been discovered. However, if we consider only those natural nests found prior to incubation (n=23), 14 of these (61%) were successful. Thus, natural nests were

more successful than artificial nests even when considered over directly comparable time frames. Second, the presence of adult birds on natural nests may reduce nest predation by hiding eggs during incubation or mobbing predators. In Red-winged Blackbirds, however, the presence of parents at the nest had no such effect on nest success (Cresswell 1997). Third, because birds did not create the artificial nests used in this study, the appearance of the artificial nests or the habitat in which they were placed (Table II) may have differed from natural nests in such a way as to attract more visual predators. Although attempts were made to minimize odors, human scent on the artificial nests could have attracted more olfactory predators. Because of these differences, artificial nests were unable to provide information on absolute predation rates of natural bird nests on St. Catherine's Island.

Nonetheless, artificial nests may still be useful to explore factors that affect nest success, such as the effects of height and vegetation on nest success (Ortega et al. 1998). In this study, however, height and vegetation affected the success of artificial and natural nests in different ways. Artificial nests had lower success as height increased and horizontal vegetation decreased, while nest height and surrounding vegetation did not affect success of natural nests. This may be because humans cannot replicate the process that passerines use to select nest sites (Cresswell 1997, Hoover and Brittingham 1998). However, because both artificial and natural nests were being depredated by natural nest predators, it is of interest to explore trends for each nest type further.

Differences in nest success among nest height

Most studies have shown nest predation to increase with nest height (review by Major and Kendal 1996). However, a few studies have demonstrated either that height did not affect nest success for natural and artificial nests (Ortega et al. 1998) or that lower nests were preyed upon more than higher ones (Wilcove 1985, Major and Kendal 1996). Predation on artificial nests may have increased with height on St. Catherine's Island because higher nests were exposed to more effective nest predators than lower nests. I suspect that unattended nests above 2 m may have been particularly exposed to visual predators such as Blue Jays and corvids (Buler and Hamilton 2000, Maier and DeGraaf 2000). It is relevant to note that when high nests failed, both eggs were usually taken (Fig. 10). High nests were apparently preyed upon by animals large enough to take both Zebra Finch and Japanese Quail eggs.

If nest predators are more effective or more abundant at greater heights, success of natural nests should have also decreased with height. This was not the case. The behavior of adults may have minimized exposure of natural nests to visual predators. It is also possible that small sample sizes (low statistical power) limited the ability to distinguish between differences in nest predation among heights of natural nests.

Differences in nest success with vegetation

High vegetation cover around a nest either can increase nest success (Major and Kendal 1996, Cresswell 1997, Hoover and Brittingham 1998) or have no effect (Major and Kendal 1996). In this study, increased horizontal vegetation cover had a positive effect on success of artificial nests and tended to be greater in successful natural nests.

The simplest explanation is that horizontal cover limited visibility of the nest to predators that hunt visually. Minimizing detection is an important component of avian nest-site selection (Cresswell 1997, Hoover and Brittingham 1998). Interestingly, the vegetation features associated with successful artificial nests were similar across all nest heights (Fig. 8). The fact that there were no strong effects of vegetation on natural nest success may have been due to birds consistently building nests in vegetation with greater cover.

Because vegetation around natural nests differed from that around randomly placed artificial nests, passerines on St. Catherine's Island appear to select nest sites non-randomly. Past studies have also found that birds choose nest sites non-randomly, mainly to minimize detection by potential predators, thus increasing the chance of success (Cresswell 1997, Hoover and Brittingham 1998). However, in this study, successful natural nests tended to have more horizontal cover adjacent to the nest, suggesting slight variation in vegetation around natural nests. The level of experience of the nest-builder may explain this variation; birds nesting for the first time would be more susceptible to predation than experienced birds (Major and Kendal 1996). Thus, vegetation differences between artificial and natural nests were most likely due to placement of the artificial nests. Because vegetation around artificial nests did not mimic that of natural nests, differences in success between artificial and natural nests can further be explained by variations in vegetation. However, the importance of nest concealment varies among species (Burhans and Thompson 1998) and types of predators (Rangen et al. 1999).

Differences in nest success with egg type

Egg type also appeared to contribute to variation in success of artificial nests. The most common result was for both eggs to be removed from depredated nests. This implies that larger predators (raccoons, hogs, Blue Jays, corvids), which are capable of handling Japanese Quail eggs (Roper 1992, Bayne et al. 1997, Ettel et al. 1998), were responsible for most nest predation. Other studies have shown that in areas with numerous corvids as potential predators, artificial nests baited with quail eggs had lower success than natural nests (Buler and Hamilton 2000). However, both eggs were taken less often at lower nests (Fig. 10), implying that smaller predators (mice, small snakes) were more abundant or more active at lower heights. When one egg was taken from artificial nests, it was usually the Zebra Finch egg, again suggesting smaller predators played a role in nest predation.

Artificial nests baited with smaller eggs (e.g. House Sparrow [*Passer domesticus*], Zebra Finch) have been shown to be less successful than artificial nests baited with Japanese Quail eggs (Maier and DeGraaf 2000). The size of eggs in natural nests fell between the size of Zebra Finch and Japanese Quail eggs used to bait the artificial nests in this study. Zebra Finch eggs were the smallest and had the thinnest shell among all the eggs preyed upon, regardless of nest type. It is possible that Zebra Finch eggs emitted a stronger odor through the thinner shell, thus attracting more predators and decreasing success on artificial nests, particularly in 2000 when artificial nests in both months were baited with Zebra Finch eggs. Eggs of natural nests used in this study probably did not emit as strong an odor, or the parents masked the odor of the eggs and reduced the risk of detection by predators. Japanese Quail eggs, on the other hand, were the largest and had

the thickest shell among all the eggs preyed upon, regardless of nest type. The larger size may have attracted more visual predators in this study, but the thicker shell would have deterred smaller predators (Roper 1992, Bayne et al. 1997, Ettel et al. 1998). Thus, artificial nests baited with only Japanese Quail eggs could underestimate predation by biasing the types of predators able to prey upon the larger Quail eggs.

The number of depredated artificial nests with Japanese Quail eggs removed increased between April and May for both years, while the number of nests with only Zebra Finch eggs removed decreased from April to May. Other studies have shown changes in nest success through time (Major and Kendal 1996), and attributed that change to variation in types of predators (Mermoz and Reboreda 1998). Because the artificial nests were placed within the same transects for both months within both years, my results suggest that larger predators capable of handling Japanese Quail eggs were more common or more active during May. The warmer temperatures of late spring may have been especially important for large snakes. Furthermore, predators may have habituated with the study sites, thus partially explaining the increased predation on artificial nests in May of both years, as well as both months in 2000.

Conclusions

Based on preliminary observations of unusually high nests and heavy browsing by white-tailed deer on St. Catherine's Island, I hypothesized that nest success would increase with height and increased vegetation. Nest success actually decreased with height, but vegetation density was important to nest success. Despite heavy browsing, sufficient vegetation appears to remain for nesting by songbirds. However, browsing

could limit the number of available nest sites in the shrub layer, resulting in fewer shrub-nesting passerines nesting in the area (compare DeCalesta 1994). Because the majority of Neotropical migrants nest in the shrub layer and are vulnerable to the effects of nest predation (Askins et al. 1990, Peterjohn et al. 1995), future research should be done to assess the effects of populations of white-tailed deer on vegetation in southeastern maritime forests. Careful consideration should be taken when managing habitat in eastern maritime forests, especially in areas where white-tailed deer management does not exist, such as on St. Catherine's Island.

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