EFFECTS OF TIME AND NEST-SITE CHARACTERISTICS ON CONCEALMENT OF SONGBIRD NESTS[1]

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Abstract. We studied the effect of time and nest-site characteristics on nest concealment measurements and analyzed differences in concealment between parasitized, nonparasitized, depredated, and fledged nests. Mean concealment at nests of three old-field bird species was best explained by bird species, nest plant, and height of the nest. Nests lost concealment over time, particularly those placed high in shrubs or roses (*Rosa* spp.). Mean and minimum concealment did not explain occurrence of predation or brood parasitism for any of the three bird species, and concealment at parasitized versus unparasitized nests and depredated versus fledged nests did not change differently over time. A literature review showed that most studies of real passerine nests using visual nest concealment have taken measurements after nest termination, and few studies indicated that concealment was important in explaining nest predation or brood parasitism. Late concealment measurements may be an additional source of error in nesting studies, especially if predation or parasitism is more likely to occur at nests sharing similar vegetation characteristics.

Key words: brood parasitism, Cardinalis cardinalis, nest concealment, nest predation, nest-site selection, Passerina cyanea, Spizella pusilla.

INTRODUCTION

Concealment at the nest has been an important component of many studies of nest-site selection and nesting success. Some studies have measured concealment and its relationship to nest predation (Martin and Roper 1988, Howlett and Stutchbury 1996, Kligo et al. 1996a, 1996b), its relation to nest-site selection (Holway 1991, Götmark et al. 1995), or its relationship to brood parasitism (Barber and Martin 1997, Burhans 1997). The condition of nest vegetation at the time of termination is of primary interest at depredated nests, and most studies take vegetation measurements after termination to minimize disturbance to the nest site as well. Questions related to nest-site selection, however, should reflect the status of nest vegetation when the nest site was selected by the bird. Similarly, research relating brood parasitism to nest vegetation should reflect nesting conditions early in the cycle, because brood parasites typically find nests during host songbird's nest-building or laying period (Hann 1941, Friedmann 1963). Thus, nest concealment measures taken after nest termination may not always reflect nest-site conditions relevant to the research question being asked. Even if the question of interest pertains to nest concealment at the time of nest termination, the

demands of fieldwork during the breeding season often force researchers to postpone vegetation measurements, further delaying data collection and potentially biasing results.

In this study we analyze concealment at the nests of three old-field songbird species. Our primary goals were (1) to document and explain changes in nest concealment as measured from the time the nest was found to long after nesting termination, (2) to examine relationships between nest concealment, predation, and brood parasitism, and (3) to determine whether measurements taken at later dates either disagreed with measurements taken at the "proper" time, or yielded spurious results. In addition, we review and summarize results from studies analyzing nest concealment at songbird nests and evaluate its importance, with attention to when measurements were taken. We chose to measure nest concealment because these measures are easy to do and can be quickly taken at active nests with minimal disturbance to the birds and nest site. However, our goal was to look at temporal variation in measurements due to vegetational change, while considering that patterns in changing nest concealment also may pertain to other nest-site vegetation measurements.

METHODS

We located bird nests from April through August 1997 in old fields on the 920-ha Thomas S. Bas-

kett Wildlife Research and Education Center (38°45′N, 92°12′W) near Ashland, Missouri (Boone County). Old fields were located in a matrix of forest and have been the subject of yearly old-field songbird studies since 1992 (Burhans 1996, 1997, Dearborn 1997). In addition, we also searched for nests in a cool-season grass agriculture field (30.8 ha). We used the nests of Field Sparrows (*Spizella pusilla*), Indigo Buntings (*Passerina cyanea*), and Northern Cardinals (*Cardinalis cardinalis*) because they are among the most abundant nesting species. We searched sites daily for nests and marked them with plastic flagging at least 3 m distance from the nest. Nests were monitored every 2–3 days until fledging approached, after which we monitored them daily to document fledging. Fledging was documented either by video camera (Thompson et al., in press) or during early morning visits on the expected day of fledging. We looked for evidence of fledging by nestling begging calls, the sight of nestlings, parents carrying food, or parents chipping rapidly nearby. Nests empty prior to this were considered depredated unless we saw evidence of premature fledging; nests where we did not observe these activities were classified as unknown.

CONCEALMENT MEASUREMENTS

We took concealment measurements at nest-height level from four cardinal directions (N, E, S, W) 1 m from the nest. We estimated percentage of the nest concealed (to the nearest 10%) based upon viewing the nest; i.e., a nest for which 20% of the nest was visible from one of the directions received an 80% score for that measurement. We also measured minimum concealment, the smallest percent of the nest concealed at any angle at or above nest level from 1 m distance. The minimum concealment measure was made to quantify the most exposed view of the nest that might increase its detectability to either predators or brood parasites. In addition, we made concealment estimates at 1 m above nest height (45°) in four cardinal directions and one estimate from 1 m directly overhead. However, concealment at higher nests could not be accurately measured 1 m above nest height. Preliminary analysis indicated possible bias of results due to differing protocols for high and low nests, so we eliminated 45° and overhead measurements from the final analysis. We analyzed the mean of the four horizontal measurements and minimum concealment separately. Concealment could be taken at active nests in ≤ 3 min with minimal disturbance, and all measurements were taken by the first author to ensure consistency. We also measured height to the top of the nest cup (to the nearest 5 cm) and recorded the species of the nest plant.

We measured nest concealment before the nest was terminated (pre-termination) and 1-week, 3-weeks, and 6-weeks post-termination (hereafter, post-termination referred to as "post"). For nests found during the building stage, pre-termination measurements were taken after laying commenced so that our presence would not cause nest abandonment. If breeding birds were in the nest vicinity during the laying period, we took measurements soon after the start of incubation for the same reason. If nests were found at a later stage, measurements were taken the day the nest was found. Although timing of pre-termination measurements varied in relationship to nest initiation dates, we assume that the pre-termination measurements we took were the closest approximation to the "true" nest concealment at the time the nest site was chosen. For Field Sparrow, Indigo Bunting, and Northern Cardinal nests, 34%, 28%, and 50%, respectively, of pre-termination measurements were taken at the laying stage; 50%, 48%, and 43% of measurements were taken during incubation, and 16%, 24%, and 7% were taken during nestling stage (see Table 2 for sample sizes).

The timing of the 1-week post measurement in relation to the pre-termination measurement varied depending upon how long the nest was active (median 15 days after the first measurement, range 6–35 days). The variability in timing of pre-termination measurements among nests to both "true" pre-termination concealment and 1-week post concealment should not affect statistical analysis of change of concealment because we employed a repeated-measures approach for which between-subject sources of variation are excluded from experimental error (Neter et al. 1990, Stevens 1992). Three-week post measurements were taken at a median of 14 days (range 10–19 days) after 1-week post; 6-week post measurements were taken at a median of 21 days (range 17–25 days) after 3-week post measurements. We eliminated nests that were sampled outside of the ranges of dates specified above. Post-termination measurements were not taken at nests that were tipped or torn by pred-

ators; however, measurements were taken at nests mildly tipped ($< 30°$) during the course of nesting. We also did not take later measurements at nests that were mowed, grazed by cattle, or otherwise disturbed. To characterize vegetation in the vicinity of the nest other than the nest plant, we took cover measurements at nest sites with a frame measuring 1 m on a side (Daubenmire 1959). We took these measurements in four adjoining 1 m^2 quadrats centered on the nest at the time of the 6-week post measurement. For each quadrat, we estimated percent cover (to nearest 10%) of shrubs, forbs, grasses, and bare ground. These data were averaged for a mean percent for each cover type for the nest site.

CHANGE IN CONCEALMENT

We analyzed change in mean nest concealment over the four visits with a repeated-measures ANOVA (Proc GLM; SAS 1990). We performed preliminary repeated-measures analyses to screen additional variables having important effects on change in mean nest concealment. All preliminary analyses were run using a repeated factor for the four concealment measurements (visit). Measures for the three bird species were combined and all preliminary models included a factor for nesting species. The preliminary models we tested included a model for (1) nest height, which has been inversely correlated with concealment in other studies (Best and Stauffer 1980, Murphy 1983). As we had no predetermined values for which to compare concealment by nest height, we separated nest height posthoc into two factors based upon median height of all species combined (median = 0.55 m). We tested a model for (2) nest plant type, i.e., forb, grass, shrubs exclusive of roses, or rose. We added the latter category because we noted that many nests in multiflora rose (*Rosa multiflora*) and pasture rose (*R. setigera*) became very exposed over time. We also ran a preliminary model (3) with two factor-levels for nesting date ("season"), to determine whether change of nest concealment varied over the season (median date for first measurement was 7 June 1997). Finally, we ran one preliminary model each (model 4–7) for the four cover variables from frame readings (percent shrub, forb, grass, and bare cover). Each of these cover-variable factors had two levels based upon the medians of percent cover for that variable. We constructed a full model from the bivariate models above and

sequentially eliminated variables having nonsignificant ($P > 0.05$) between-group effects. The final model then contained all variables and interactions with significant between-group effects and the repeated concealment (visit) factor.

PARASITISM AND PREDATION

When analyzing parasitism, we analyzed only those nests initiated before Brown-headed Cowbird (*Molothrus ater*) parasitism ended at our sites (8 July 1997). We compared concealment samples only from initial concealment readings ("pre-termination"), because these should best reflect nest conditions at the time cowbirds locate nests. Similarly, when analyzing nest predation we only used samples from 1 week after termination (1-week post). We considered nests from the entire season for which we were confident of fledging or nest predation. We analyzed both parasitism and predation using a univariate ANOVA comparing arcsine square-root transformed concealment means. We conducted separate analyses each for minimum and mean concealment and added factors for nesting species to account for variability in nest concealment between Field Sparrows, Indigo Buntings, and Northern Cardinals. We also tested for species × predation and species × parasitism interactions and retained them if they were significant.

TIME OF MEASUREMENT AND IMPORTANCE OF CONCEALMENT

We evaluated the importance of time of measurement on mean concealment differences between parasitized versus unparasitized or depredated versus successful nests by a repeated measures analysis similar to that above. Our goal was to adopt the approach of a standard nesting study as if mean concealment was measured only at one visit, but to do so for each of the four visits. We used the repeated measures analysis to interpret significant visit × parasitism or visit × predation interactions as indicating a change in concealment differences over the four visits. Sample sizes of nests declined over the season as nests became mowed or disturbed, so we analyzed only the set of nests for which all four visits were sampled. This resulted in fewer nests available for analysis than the parasitism and predation analyses above. We included a species factor to account for variability in concealment between nesting species. We tested for species × predation and species × parasitism

interactions and retained them if between-group effects were significant.

Concealment means were arcsine square-root transformed (Sokal and Rohlf 1981) for all analyses, but we present untransformed concealment means in tables and figures to facilitate interpretation. All sphericity tests (SAS 1990, Stevens 1992) in repeated-measures tests were rejected, so we interpreted within-subject effects with adjusted F-tests using the Greenhouse-Geisser adjustment (SAS 1990, von Ende 1993). This test results in conservatively adjusted degrees of freedom for within-subject F-tests (SAS 1990, Stevens 1992, von Ende 1993). We do not report adjusted degrees of freedom for these F-tests, but report sample sizes where appropriate. Results for statistical tests reporting means are indicated as mean ± SE.

We conducted a literature survey of songbird nesting studies employing methodologies similar to ours; i.e., studies that used quantitative measurements of nest concealment based upon views of the nest by eye, including those that viewed the nest against a density board. We listed the studies in accordance with the focus of the study: nest predation, brood parasitism, or nest predation. We noted whether the studies found significant effects of nest concealment and the time at which concealment measurements were taken in relation to the nesting cycle. We contacted authors of studies where we could not determine when measurements were taken.

RESULTS

CHANGE IN CONCEALMENT

The model that best explained change in nest concealment over the four measurements was a model including nesting species, nest height, nest plant, and nesting species × nest height and nest plant × nest height interactions in addition to the repeated visit factor (Table 1). Field Sparrow nests were the most concealed (Table 2, Fig. 1), as were nests in grass substrates and lower nests in general (Table 2, Figs. 1, 2). Changes in concealment were greater between measurements for high nests compared to low nests (Fig. 1). Nests using grass substrates changed little over successive measurements, whereas concealment was poorer in other substrates and declined more steeply over time, particularly at high nests (Fig. 2).

TABLE 1. Results from repeated measures analysis of variance model on change in nest concealment of three old-field songbirds in Missouri.

Source	Between-subject effects		
	F-value	df	P
Species	16.2	2, 83	<0.001
Nest plant	6.5	3, 83	<0.001
Nest height	11.3	1, 83	0.001
Species × nest height	15.2	1, 83	<0.001
Nest plant × nest height	4.0	2, 83	<0.05
	Within-subject effects[a]		
Visit	8.8		<0.001
Visit × species	1.1		0.35
Visit × nest plant	2.1		<0.05
Visit × nest height	4.4		<0.01
Visit × species × nest height	3.0		<0.05
Visit × nest plant × nest height	2.3		<0.05

[a] P-values from F-tests where degrees of freedom were adjusted with Greenhouse-Geisser's Epsilon.

PARASITISM AND PREDATION

The analysis of variance testing for differences in mean nest concealment among parasitized and unparasitized nests and nesting species was significant (ANOVA, overall $F_{3,111} = 23.6$, $P < 0.001$). Differences in concealment, however, were due to nesting species ($F_{2,111} = 28.3$, $P < 0.001$) rather than parasitism ($F_{1,111} = 0.5$, $P = 0.5$). There also were differences in pre-termination minimum concealment due to nesting species but not parasitism (ANOVA, overall $F_{3,111} = 3.0$, $P < 0.05$; parasitism $F_{1,111} = 0.2$, $P = 0.6$; species $F_{2,111} = 3.4$, $P < 0.05$).

The analysis of variance model testing for differences in mean concealment among species and depredated and fledged nests was significant but differences were due to nesting species rather than predation (ANOVA, overall $F_{3,88} = 27.8$, $P < 0.001$, species $F_{2,88} = 40.0$, $P < 0.001$, predation $F_{1,88} = 1.5$, $P = 0.2$). Minimum concealment similarly differed because of nesting species rather than predation (ANOVA, overall $F_{3,88} = 5.2$, $P < 0.01$; predation $F_{1,88} = 0.4$, $P = 0.6$; nesting species $F_{2,88} = 7.8$, $P < 0.001$).

TIME OF MEASUREMENT AND IMPORTANCE OF CONCEALMENT

Concealment measurements did not change differently between parasitized and unparasitized nests over the four visits when analyzed by repeated measures analysis (Fig. 3; visit × para-

TABLE 2. Parasitism and predation frequencies and nest-site characteristics (mean ± SE) for three species of old-field songbirds in Missouri.

Variable	Field Sparrow	Indigo Bunting	Northern Cardinal
Proportion parasitized[a]	0.14 (71)	0.52 (29)	0.40 (15)
Proportion fledged[b]	0.41 (54)	0.38 (26)	0.25 (12)
Concealment			
Pre-termination (%)[c]	91.6 ± 1.2 (50)	75.3 ± 2.5 (29)	81.1 ± 2.5 (14)
1-week post (%)	91.8 ± 1.4	74.9 ± 2.4	74.8 ± 3.3
3-week post (%)	89.8 ± 2.0	68.2 ± 3.1	74.3 ± 3.6
6-week post (%)	87.4 ± 2.6	63.8 ± 3.8	68.3 ± 4.9
Nest height (m)	0.4 ± 0.0	0.8 ± 0.0	1.1 ± 0.1
Nest plant (% of nests)			
Grass	22.0	0.0	0.0
Forb	10.0	20.7	0.0
Shrub	46.0	69.0	35.7
Rose	22.0	10.3	64.3
Percent cover			
Grass	31.6 ± 5.5	15.1 ± 5.2	18.8 ± 7.2
Forb	52.2 ± 4.5	43.5 ± 6.0	25.9 ± 6.7
Shrub	17.5 ± 3.0	38.5 ± 5.0	66.3 ± 3.8
Bare	6.7 ± 1.1	9.8 ± 2.1	12.9 ± 4.9

[a] Sample sizes in parentheses are number of nests during cowbird activity, pre-termination visit only.
[b] Sample sizes in parentheses are numbers of fledged and depredated nests, 1-week post visit only.
[c] Sample sizes for this row and those following are nests with all four visits used in repeated-measures analysis of change in nest concealment.

sitism interaction: $F_{Adj.} = 0.2$, $P = 0.9$). There was a significant visit effect ($F_{Adj.} = 4.3$, $P < 0.01$), but concealment did not change differently by nesting species over time (visit × species interaction: $F_{Adj.} = 2.0$, $P > 0.05$). Parasit-

ism did not explain overall variation in concealment ($F_{1,71} = 0.4$, $P = 0.5$), but species did ($F_{2,71} = 29.0$, $P < 0.001$).

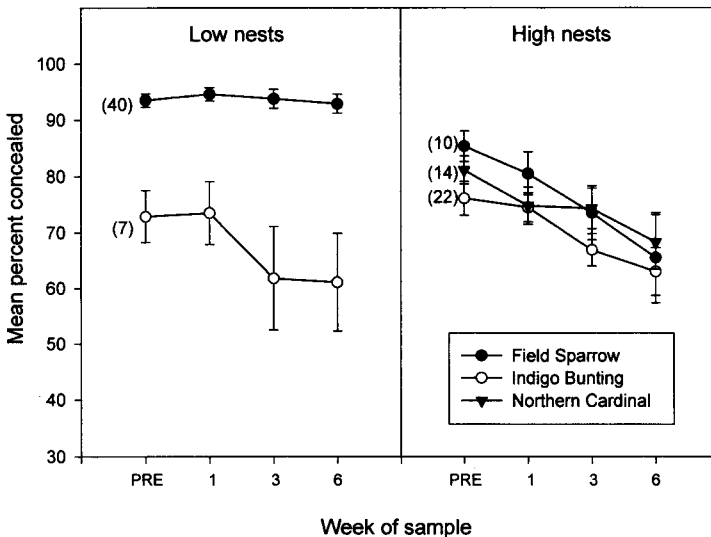Concealment did not change differently between depredated and fledged nests over visits

FIGURE 1. Mean (± SE) change in nest concealment at nests of three species by nest height (median height 0.55 m; sample sizes in parentheses). "Pre" refers to pre-termination visit; "1," "3," and "6" designate samples taken 1, 3, and 6 weeks after nest termination, respectively.
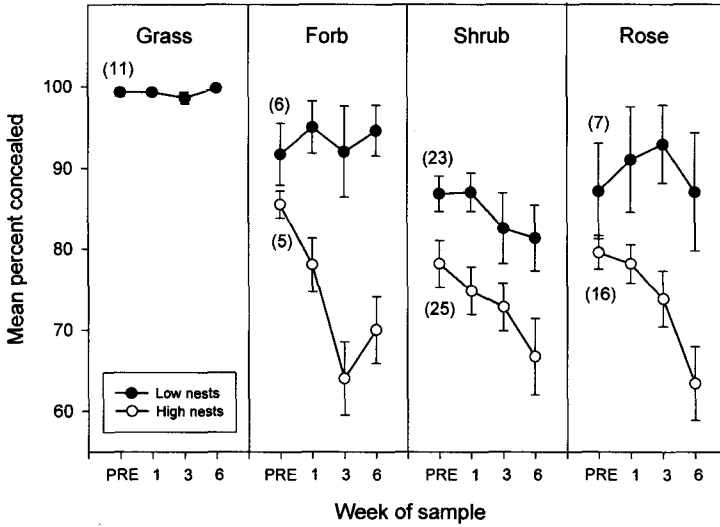
FIGURE 2.   Mean ($\pm$ SE) change in nest concealment of combined species by nest height and nest plant type (sample sizes in parentheses). Week of sample as in Figure 1 legend.

(Fig. 4; visit $\times$ predation interaction: $F_{Adj.} = 1.4$, $P = 0.3$). As in the previous repeated-measures analyses, there was a significant visit effect ($F_{Adj.} = 5.2$, $P < 0.01$). Concealment did not change differently over time depending upon species (visit $\times$ species interaction: $F_{Adj.} = 2.1$, $P > 0.05$). Species explained overall variation in

concealment ($F_{2,73} = 32.1$, $P < 0.001$), but predation did not ($F_{1,73} = 0.2$, $P = 0.7$).

We identified 26 studies of concealment at active passerine nests using methodologies similar to ours. Twelve of these indicated significant effects of nest concealment in explaining predation, brood parasitism, or nest-site
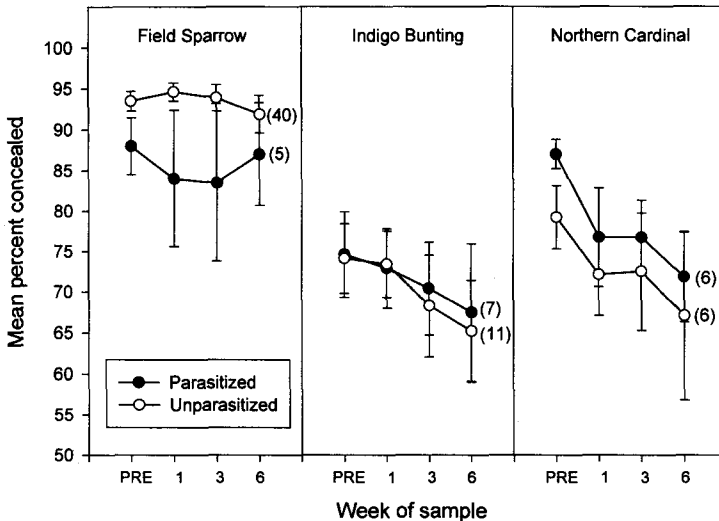

FIGURE 3.   Differences in mean percent concealment between parasitized and unparasitized nests by species ($\pm$ SE, sample sizes in parentheses) for repeated samples taken over four visits. Week of sample as in Figure 1 legend.
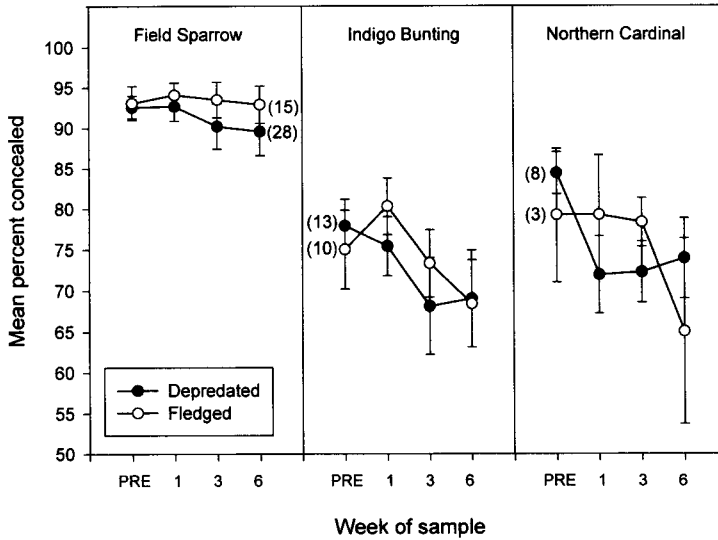
FIGURE 4.   Differences in mean percent concealment between depredated and fledged nests by species (± SE, sample sizes in parentheses) for repeated samples taken over four visits. Week of sample as in Figure 1 legend.

selection (Table 3). Of nine studies analyzing concealment in relation to nest-site selection or brood parasitism, one took concealment measurements at active bird nests, and concealment was important only in 7 of 23 studies of nest predation.

DISCUSSION

Concealment at our nests varied from the time of active nesting to several weeks thereafter. Nest concealment measurements varied depending upon bird species, nest height, and nest plant, and tended to change the most at higher nests in shrubs or

TABLE 3.   Number of studies finding an effect or no effect of nest concealment by research question and time of measurement.

Study question	Effect/no effect	When measured	Reference
Nest-site selection	1/0	soon after termination	1
	2/0	after nest termination	2, 3
	1/0	after completion of study	4
Total	4/0		
Brood parasitism	1/0	early nest cycle	5
	1/3	after nest termination	6, 7, 8, 9
Total	2/3		
Nest predation	1/1	early nest cycle	5, 10[a]
	1/1	immediately after nesting	11, 12
	0/1	soon after termiation	1
	0/1	within 3 weeks of termination	13
	2/9	after nest termination	2, 3, 9, 10[a], 14, 15, 16, 17, 18, 19, 20
	1/2	(specified date or range of dates)	21, 22, 23
	2/1	after breeding season	24, 25, 26
	0/1	after completion of study	4
Total	7/16		

Sources: (1) Holway 1991, (2) Kligo et al. 1996a, (3) Kligo et al. 1996b, (4) Götmark et al. 1995, (5) Nias 1986, (6) Barber and Martin 1997, (7) Briskie et al. 1990, (8) Burhans 1997, (9) Conner et al. 1986, (10) Sockman 1997, (11) Best and Stauffer 1980, (12) Johnson 1997, (13) Howlett and Stutchbury 1996, (14) Filliater et al. 1994, (15) Haggerty 1988, (16) Haggerty 1995, (17) Martin and Roper 1988, (18) Mitchell et al. 1996, (19) Murphy 1983, (20) Murphy et al. 1997, (21) Hanski et al. 1996, (22) Kelly 1993, (23) Tarvin and Smith 1995, (24) Cresswell 1997, (25) Erhart and Conner 1986, (26) Tuomenpuro 1991.
[a] Used both pre- and post-termination measurements.

roses (Figs. 1, 2). Concealment was not related to occurrence of predation or cowbird parasitism when the effect of nesting species was included, and parasitized and unparasitized or depredated and fledged nests did not change concealment differently over time (Table 1, Figs. 3, 4).

Several studies have indicated that concealment decreases with increasing nest height (Best and Stauffer 1980, Murphy 1983), and nest height generally increases over the breeding season (Best 1978, Best and Stauffer 1980). In the present study, Field Sparrow nests were the lowest and best concealed of the three species (Table 2, Fig. 1). The breeding season during which these measurements were taken was dry, which could have resulted in leaf-drop and reduced foliage (DEB, pers. observ.). The same nests that experienced a loss of concealment could potentially have had increased concealment under more favorable growing conditions.

In a previous study at these same sites using larger sample sizes, concealment explained parasitism for Indigo Buntings and marginally for Field Sparrows (Burhans 1997). However, samples in the latter study were taken after nesting termination. Cowbirds appear to focus on host behavior in finding nests (Norman and Robertson 1975, Thompson and Gottfried 1981) but may be unable to find some nests that are well-concealed.

Martin's review (1992) concluded that improved concealment led to decreased rates of nest predation, but his survey reviewed studies that we did not survey, including those using qualitative measurements, foliage density measures, artificial nests, and nonpasserine species (see also Howlett and Stutchbury 1996). Importance of nest concealment to predation may be related to predator type, and several studies have noted effects with artificial nests that were lacking with real nests (Storaas 1988, Cresswell 1997; but see Gottfried and Thompson 1978). In a survey of waterfowl studies, Clark and Nudds (1991) found that concealment was important when predation by birds was prevalent but less important for mammals and other predators (see also Colwell 1992). Another study examining the relationship of nest predation to nest microhabitat measurements at these sites found no relationship between nest concealment and nest predation (Burhans 1996). Recent video camera studies at our sites (Thompson et al., in press) indicate that snakes are principal predators at

Field Sparrow and Indigo Bunting nests. Concealment from below the nest may be important where snakes are predators, but the variability in heights of these species' nests made it difficult for us to standardize measurements made from below. Best (1978) and Wray and Whitmore (1979) believed that nest cover did not influence snake predation at Field Sparrow and Vesper Sparrow (*Pooecetes gramineus*) nests. If snakes are important predators, nestling and parental activity (Skutch 1949, Nias 1986) or olfactory cues (Eichholz and Koenig 1992, Schaub et al. 1992) may have more influence on predation than concealment.

Because many studies have shown no influence of nest concealment on nesting success, the apparent selection of well-concealed sites is puzzling. However, among the passerine nest-site selection studies of which we are aware, only Götmark et al. (1995) extensively surveyed concealment at potential nest sites. They concluded that Song Thrushes (*Turdus philomelos*) chose intermediate concealment, possibly to permit incubating adults to view approaching predators. Concealment at the fine scale also may be a by-product of selection for denser vegetation at the scale of the nest patch (Martin and Roper 1988, Martin 1992). Numerous studies have shown that nesting sites may have higher stem or foliage densities than random sites (Holway 1991, Sedgewick and Knopf 1992). Dense sites may impede some mammals (Bowman and Harris 1980, Holway 1991), screen the actions of parents (Holway 1991, Kelly 1993), or contain more potential nest sites for a foraging predator to search (Martin and Roper 1988). Filliater et al. (1994) suggested that Northern Cardinals and perhaps other passerines are subject to a rich guild of predators and follow a few simple rules regarding site selection, including concealment of the nest, which also did not influence nesting success in their study. Holway (1991) similarly believed that many random aspects of predation might mask the importance of nest concealment. Further research identifying predators at real nests (Thompson et al., in press) or use of experimental methods (Bowman and Harris 1980) are needed to identify important predators and the mechanisms by which both predation and nest-site selection operate.

We cannot predict the direction or amount of temporal change in nest vegetation for other habitats or how it might affect measurement of

nest concealment for other studies, but this study shows that concealment as measured can change with time. Patterns of change in nest concealment may differ between habitats, and concealment also could vary in different directions in the same habitat depending upon seasonal effects of weather on vegetative growth. Late samples did not affect the relationship of measured concealment to occurrence of brood parasitism or nest predation in our study. However, biases in our study could have occurred with late measurements if predation or brood parasitism were more likely at nests of certain heights (Knapton 1978, Best and Stauffer 1980, Martin 1993) or substrates (Nias 1986, Alonso et al. 1991). We suggest that researchers avoid delaying concealment samples and other measurements of foliage vegetation, and that they take these measurements at a time appropriate to the research question of interest. We also suggest that other measures of foliage vegetation, including foliage density (Wray and Whitmore 1979, Sedgewick and Knopf 1992), Robel measurements (Robel et al. 1969), and density board or vegetation profile techniques (MacArthur and MacArthur 1961, Nudds 1977) may vary depending on time of measurement.

ACKNOWLEDGMENTS

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