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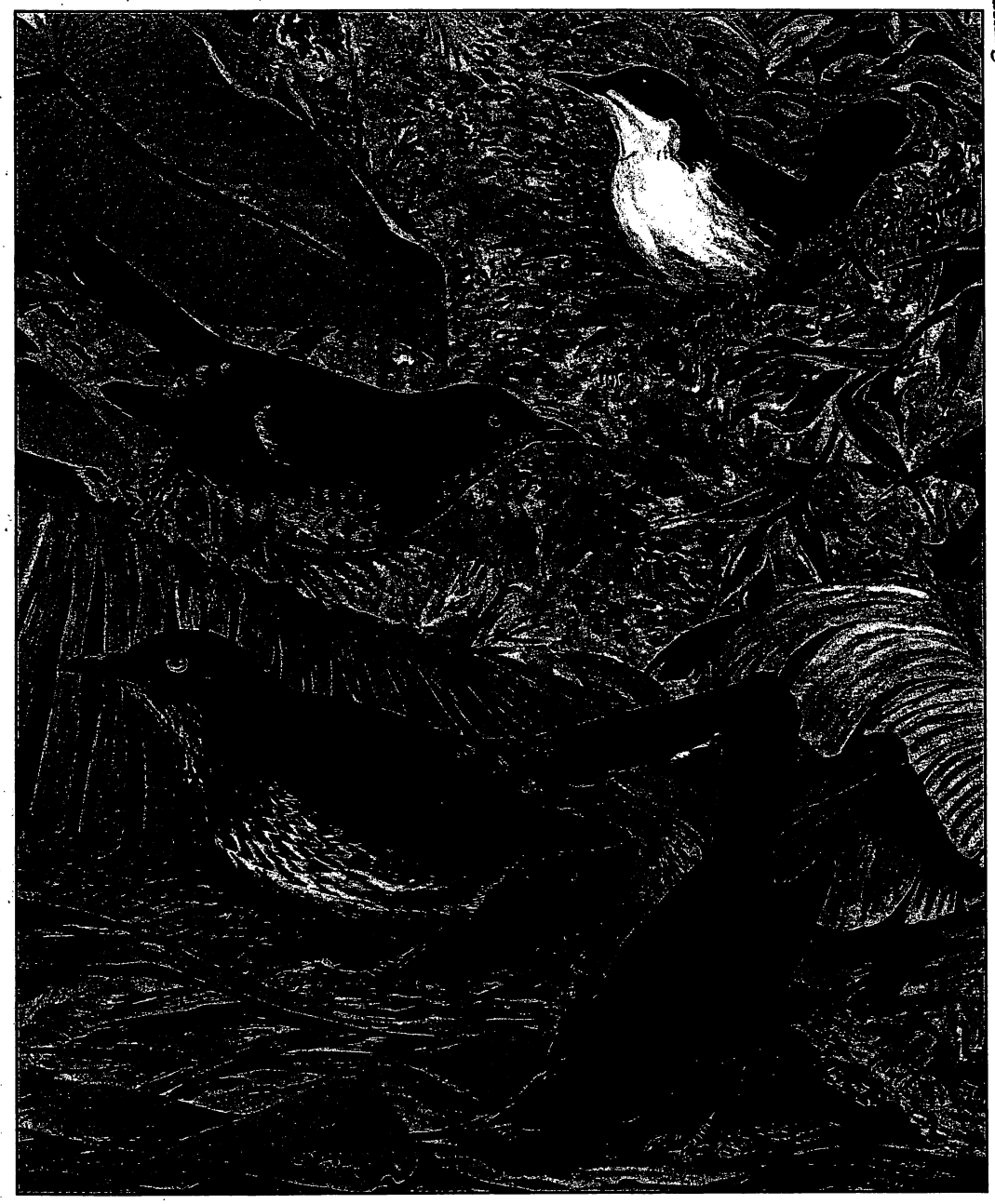

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Relationship of Songbird Nest Concealment to Nest Fate and Flushing Behavior of Adults

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Avoiding predation is an important consideration for any potential prey animal. Failure to escape from a predator results in loss of fitness, so there is strong selection for choices and behaviors that result in successful escape (Lima and Dill 1990). In their cost–benefit approach to flight from predators, Ydenberg and Dill (1986) stressed that flight should be optimized rather than maximized, because there is a cost (usually cessation of feeding) incurred by fleeing from predation. Field studies have largely supported their predictions (see Bonenfant and Kramer 1996).

Whereas for foragers, flight from predators incurs an implicit cost in lost foraging time, birds confronted by a predator at the nest face an explicit choice between loss of current reproduction versus total reproductive loss. A bird flushing from the nest too early may escape, but reveal the nest location to the predator, resulting in loss of the current brood. However, flushing late from the nest could result in loss of both nest contents and the parent bird. Because nests are often hidden in vegetation (Martin 1992a), vegetative concealment could play a role in flight from the predator, much in the same way in which cryptic body coloration may determine flight-initiation distance for animals such as lizards (Heatwole 1968). A perplexing outcome of research done to date on nest concealment is that improved nest concealment is not always correlated with lower nest predation in studies of real songbird nests (Howlett and Stutchbury 1996, Burhans and Thompson 1998, Braden 1999). Studies have similarly shown that frequency of brood parasitism, which typically lowers host fitness, is often not influenced by nest concealment (Burhans and Thompson 1998, Clotfelter 1998).

If a view from the nest is important to adult birds, there should be a relationship between nest concealment and willingness of the adult bird to flush at the approach of a predator. We measured the relationship of flushing behavior to nest concealment for four songbird species having cryptically colored adult females. Our prediction was that nests with better concealment would result in females flushing at a closer distance from an intruder. We also examined the relationship between concealment and frequency of nest predation and avian brood parasitism. Two previous studies at our sites (Burhans 1996, Burhans and Thompson 1998) indicated that nest concealment was not related to nest predation, whereas one of two studies indicated that higher concealment was correlated with reduced frequency of brood parasitism (Burhans 1997).

Methods.—We located nests in old fields and adjoining forests from April through July 1998 at the Thomas S. Baskett Wildlife Research and Education Center near Ashland, Missouri. Those sites have been described previously in Burhans (1997) and have been the subject of songbird nesting and behavior studies since 1992 (Burhans 1997, Burhans and Thompson 1998, Dearborn 1998). We also searched for nests in a nearby agriculture field (30.8 ha). We used nests of Field Sparrows (*Spizella pusilla*), Indigo Buntings (*Passerina cyanea*), Northern Cardinals (*Cardinalis cardinalis*) and Yellow-breasted Chat (*Icteria virens*) because they are among the most abundant nesting species and females are cryptically colored when viewed on the nest. Although we have not measured nest defense responses specifically to humans of those species, they are not tame, and appear to respond to humans as they do to live or model predators. Response to humans near the nest generally includes rapid chipping or scolding and avoidance of the nest, which is similar to responses given to predators (Burhans 2000).

We searched sites daily for nests and marked them with plastic flagging at least 3 m distance from the nest. Nests were monitored every two to three days until fledging approached, after which we monitored them daily to document fledging. Although many studies use presence of an empty nest on expected fledge date as confirmation of nest success, video cameras at our nests (Thompson et al. 1999) indicate that snakes often depredate nests on or immediately prior to the expected fledge date. Fledging thus was documented either by video camera or by behavioral evidence during early morning visits on the expected day of fledging. We looked for confirmation of fledging by nestling begging calls, sight of nestlings, parents carrying food, or parents chipping rapidly nearby. Nests empty prior to that were considered depredated; nests active up to the expected fledging date where we did not observe those activities were classified as unknown. We noted presence of eggs or nestlings of Brown-headed Cowbird (*Molothrus ater*) and categorized nests as parasitized or

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unparasitized. We are reasonably confident that nest-monitoring and other activities (see below) did not increase probability of predation. Other studies done at our sites indicate that nests visited daily for video filming had significantly lower daily mortality for some species (Thompson et al. 1999).

Flush experiments.—We conducted flush experiments to determine relationships among concealment, the bird's view from the nest, and adult vulnerability to predators. Those experiments involved one investigator walking directly to the nest until the adult bird flushed and left the nest. For flush experiments, we walked in a straight line to the nest from a randomly chosen direction where the view of the nest plant was not obstructed by intervening plants. Starting at least 8 m away, we walked (measured at 1 m/pace) silently toward the nest at a rate of 1 pace/s while keeping eyes directly on the nest or incubating bird. If the nest could not be seen, we looked at the known location of the nest based upon previous visits. We walked to the nest up to a distance of about 0.5 m. If the bird had not yet flushed at that distance, we stopped and without pausing extended a hand directly toward the nest. When the bird flushed, we measured "flushing distance" (Barash 1975) with a meter tape or stick (to the nearest 0.1 m) as the horizontal distance from the nest rim to the observer's forward foot for distances >0.5 m or to the fingertip for distances <0.5 m. Only females are known to incubate in all four species we tested and all species use only open-cup nests.

"First flushes" were conducted where birds were not previously encountered at the nest by observers. To determine effects of habituation and to sample additional nests, we also conducted "second flushes." Second flushes were performed at nests where first flushes were already taken or where birds were inadvertently disturbed at the nest during discovery. For nests where first flushes were performed, we conducted second flushes from the same direction as first flushes. For nests where birds were accidentally flushed previously, we randomly determined the direction of the second flush. We conducted all second flushes at least one day after first flushes or inadvertent flushes, but as much as 3 days later if birds were not present during ongoing attempts. We were careful to keep field assistants away from the vicinity of nests where either first or second flushes had not been performed to avoid disturbance that might affect flushing behaviour of birds during experiments.

We attempted to initiate flushing experiments during the first few days of incubation (incubation days 1 to 3) when possible, but included several samples from late in the laying period as well as later in incubation. Mean incubation day for those nests where incubation day could be accurately determined was 1.9 ± SD of 2.1 for first flush experiments (n = 50 nests) and 3.3 ± 2.7 for second flush experiments (n = 95 nests). For both first and second flushes, we examined correlations between flushing distance and incubation day both by species and all species combined and found no significant ($P < 0.05$) correlations.

"Flush concealment" was the estimated percentage of the nest concealed (to the nearest 10%) based upon viewing the nest from our angle of approach; for example, a nest for which 20% of the nest was visible received an 80% score. To standardize measurements, we took all flush concealment samples at eye-level standing upright at a distance of 1 m measured from the nest. Measuring flush concealment using the flushing distance could bias the sample, because birds that flushed far from the observer (sometimes >4 m) could have low concealment scores if the nest was difficult to see from a distance. All flush experiments and flush concealment measurements were performed by the first author to ensure consistency.

In addition to measuring flush concealment, we measured concealment from four cardinal directions (N, E, S, W) at 1 m from the nest to determine mean concealment. We estimated mean percentage of the nest concealed (to the nearest 10%) similarly to the "flush concealment" measurements above except that measurements were at nest-height level (Burhans 1997, Burhans and Thompson 1998). We also measured height to the bottom of the nest cup (to the nearest 5 cm) and recorded the species of the nest plant.

Data analyses.—To determine if there was an effect of habituation on flushing, we conducted a repeated-measures ANOVA using only nests where we obtained first and second flushes at the same nest. In addition to the repeated flush effect ("visit"), that model included a variable for nesting species to account for differences in flushing behavior among species.

We used the sample of first flushes (above) and regressed first flushing distance on both mean nest concealment and flush nest concealment (PROC GLM; SAS 1990). We included a variable for nest height and bird species. Although repeated-measures analysis indicated no difference between first and second flushes at the same nests (see results), we analyzed first and second flushes separately because the repeated-measures analysis used a subsample of available nests. Flushing distances were square-root transformed (Neter et al. 1990) and concealment measurements were arcsine square-root transformed (Sokal and Rohlf 1981) to improve normality, but we present nontransformed results to facilitate interpretation.

We compared concealment between parasitized and unparasitized nests and depredated versus fledged nests with ANOVA models. As in a previous study (Burhans and Thompson 1998), we combined all bird species in those analyses and included a species factor to account for variability in concealment that could be falsely attributed to predation or par-

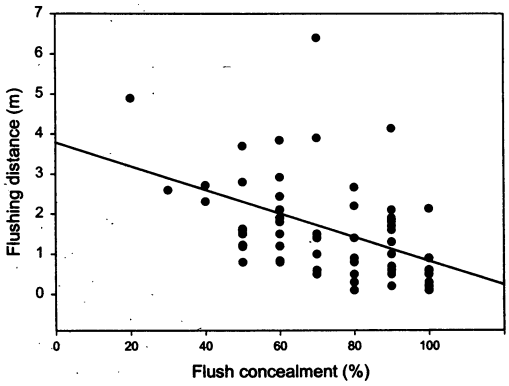

FIG. 1. Relationship between flush concealment and flushing distance for first flushes, all species combined. There were no among-species differences in flushing distance (n = 22 Field Sparrow, 24 Indigo Bunting, 10 Northern Cardinal, and 6 Yellow-breasted Chat nests).

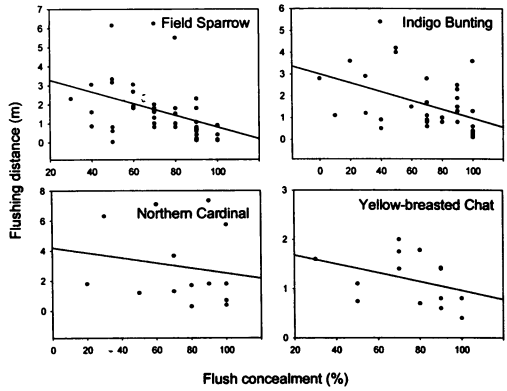

FIG. 2. Relationship between flush concealment and flushing distance for second flushes, by species (n = 41 Field Sparrow, 36 Indigo Bunting, 14 Northern Cardinal, and 14 Yellow-breasted Chat nests).

asitism. When analyzing parasitism, we included only nests initiated before the termination of laying by cowbirds at our field sites (7 July 1998). We used the same sample of nests as the previous analyses.

To determine whether premature flushing behavior could predispose nests to predation, we obtained residuals by regressing flushing distance on flush concealment (by species) using the transformed variables above. We then analyzed probability of predation with a logistic regression, including both indicator variables for species and the residuals as independent variables.

Results.—Repeated-measures analysis indicated that first and second flushing distances did not differ at nests where both first and second flushes were obtained (visit effect, ANOVA: F = 1.9, df = 1 and 53, P = 0.17). Flushing distances differed among bird species (F = 3.2, df = 3 and 53, P = 0.03), but did not differ among species according to visit (visit × species interaction, F = 1.0, df = 3 and 53, P = 0.42).

Flush concealment was inversely related to the distance that birds flushed from the nest in first flush experiments (overall F = 6.0, df = 6 and 55, P < 0.0001, r^2 = 0.40; flush concealment F = 30.9, df = 1 and 55, P < 0.0001; Fig. 1). However, mean nest concealment had no relationship to flushing distance (F = 0.1, df = 1 and 55, P = 0.80). First flushes did not differ among species (F = 1.1, df = 3 and 55, P = 0.36) and no significant effect existed for nest height (F = 1.1, df = 1 and 55, P = 0.31). In second flush experiments, flush concealment was similarly inversely related to the distance that birds flushed from the nest (overall F = 5.2, df = 6 and 98, P < 0.0001, r^2 = 0.24; flush concealment F = 18.5, df = 1 and 98, P < 0.0001; Fig. 2). As with the previous model, mean nest concealment was not related to flushing distance (F = 0.3, df = 1 and 98, P = 0.58) and there was no effect of nest height (F = 0.4, df = 1 and 98, P = 0.55). However, second-flush distances differed among bird species (F = 2.9, df = 3 and 98, P = 0.04; Fig. 2).

The ANOVA model testing for differences in mean concealment between depredated and fledged nests was significant, but differences were due to nesting species rather than predation (Table 1; overall F = 6.2, df = 7 and 102, P < 0.0001, species F = 12.1, df = 3 and 102, P < 0.0001, predation F = 0.03, df = 1 and 102, P = 0.86, species × predation interaction F = 1.8, df = 3 and 102, P = 0.20). Mean concealment similarly differed because of nesting species rather than parasitism for nests in the cowbird parasitism analysis (overall F = 4.8, df = 7 and 100, P < 0.0001; parasitism F = 0.8, df = 1 and 100, P = 0.40; nesting species F = 4.4, df = 3 and 100, P = 0.006, species ×

TABLE 1. Mean nest concealment ± SE (n) for depredated, fledged, parasitized, and unparasitized nests by species.

Species	Depredated	Fledged	Parasitized	Unparasitized
Field Sparrow	91.3 ± 1.6 (25)	88.6 ± 3.7 (16)	92.4 ± 2.5 (3)	89.5 ± 1.9 (38)
Indigo Bunting	74.3 ± 3.2 (21)	71.5 ± 5.2 (17)	68.4 ± 6.7 (11)	76.2 ± 2.7 (25)
Northern Cardinal	83.9 ± 3.7 (12)	70.0 ± 6.8 (4)	74.2 ± 9.6 (3)	81.8 ± 3.8 (13)
Yellow-breasted Chat	74.0 ± 3.3 (11)	86.3 ± 6.3 (4)	78.3 ± 5.6 (5)	76.8 ± 4.1 (10)

parasitism interaction $F = 0.2$, df = 3 and 100, $P = 0.90$).

The logistic regression analysis of residuals indicated that birds flushing earlier were not more likely to experience depredation (parameter estimate for the residual of flushing distance and flush concealment = 0.81 ± SE of 0.48, $\chi^2 = 2.90$, $P = 0.09$; overall model $\chi^2 = 7.1$, $P = 0.13$, $r^2_{adj} = 0.09$). None of the species indicator variables were significant ($P \geq 0.08$, all variables).

Discussion.—Flushing distance was inversely related to the amount of nest concealment measured from the direction in which we approached nests (Figs. 1 and 2), which suggests that those species use nest visibility at the nest in deciding when to evade a potential predator. Nest concealment did not appear to influence nest susceptibility to predators or cowbirds, as mean concealment did not differ between successful and depredated or parasitized and unparasitized nests. Birds that flushed early in relation to their flush concealment were not more likely to experience depredation.

We cannot distinguish whether birds having high flush-concealment scores flushed closer from us because they could not detect our approach or because they were using nest cover to remain cryptic. Despite our silent approach during experiments, we walked over ground vegetation that inadvertently produced noise on our way to the nest; thus, our presence, if not our approach, was surely evident from some distance even to birds whose nests were 100% concealed from our angle of approach. Eye contact and direct approach by a potential predator implies a greater probability that the predator has detected the prey, but also implies a greater chance that the predator will detect it if it moves (Cooper 1997). Our attempt to walk toward and look directly at nests during our approach should have signaled to birds that we had already discovered their nest, although birds at nests with high concealment may have had more difficulty perceiving that intention.

Ydenberg and Dill (1986) emphasized that potential prey may be aware of the predator long before flight actually occurs. In some cases, prey that flees too soon increases its vulnerability, because doing so attracts the attention of the predator. They predicted that well-camouflaged species would, thus, have shorter flight distances (Ydenberg and Dill 1986). Flushing from the nest complicates that scenario; if the enemy is a nest predator, the bird could lose its nest by flushing regardless of the flushing distance. Thus, birds should avoid flushing until they are certain that the nest has been discovered. Our data fit that pattern, as birds on nests with better concealment from our approach tended to remain until the last possible moment before flushing and giving away the nest location.

Although flushing distance was inversely correlated with the "flush concealment" that we measured when approaching the nest, it does not necessarily follow that birds chose their nest site and its concomitant concealment to allow them to flush from a certain distance; mean concealment was not related to flushing distance. Mean concealment also was not related to frequency of brood parasitism or nest predation, a finding consistent with many other songbird nesting studies (Howlett and Stutchbury 1996, Burhans and Thompson 1998, but see Burhans 1997), including other studies on the same species (Best 1978, Conner et al. 1986, Filliater et al. 1994). Relationships between nest predation and nest site features may exist, but may not be evident because the mechanisms influencing predation vary depending upon predator (Schmidt and Whelan 1999), and most nests are subject to a variety of predators (Filliater et al. 1994). Recent work with video cameras indicates that snakes are the main predators at our old field sites (Thompson et al. 1999). Concealment may not be an advantage where snakes are predators, because they may use olfaction or other cues in detecting nests (Eichholz and Koenig 1992, Schaub et al. 1992). Better concealment may similarly not help where cowbirds are concerned, because they appear to use adult host behavior in locating nests (Clotfelter 1998, Strausberger 1998). Nest concealment may be of greater importance where mammalian or avian predators (Clark and Nudds 1991) are responsible for nest predation.

Presumably, the flushing responses we observed apply to visual predators; they may even be unique to "human predators." Birds face a variety of predators, some of which are nonvisual or search randomly, and flushing strategies may vary with predator. For instance, Common Yellowthroat (*Geothlypis triochas*) females often leave the nest cryptically before human observers can visually detect them; they then may flush at a distance from the nest (D. Burhans pers. observ.; Gross 1953). Female Yellow-breasted Chats sometimes dropped below the nest while flushing, but were always directly observable to us in the act of flushing.

Although the relationship of nest concealment to predation has received considerable attention, comparatively little attention has been devoted to the role of incubating birds in revealing the nest site. The finding that real nest sites have better concealment than unused sites selected at random suggests that birds choose nest sites at least in part because of concealment (Holway 1991, Kilgo et al. 1996a, b; but see Götmark et al. 1995). If birds give away the nest location by flushing and can afford to flush later at well-concealed nests, then concealed nests should show lower predation frequencies. However, parent birds can also reduce predation by aggressive, cryptic, or distraction behaviors (Gochfeld 1984, Martin 1992b). Behaviors such as parental defense may compensate for poor concealment and explain in part why nest predation is not always explained by nest-

site features; studies at real nests (Ricklefs 1977, McLean et al. 1986, Murphy et al. 1997) and comparing predation at artificial versus real nests (Cresswell 1997, King et al. 1999) support that interpretation. The relationship between nest-site characteristics and nest predation remains a valuable area for study, but research thus far has often yielded conflicting or inconclusive results. Predation-related behaviors such as flushing, nest defense, and crypsis and their interactions with nest-site characteristics could provide explanations for patterns in predation that are presently lacking from nest-site vegetation studies alone.

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Literature Cited

Barash, D. P. 1975. Evolutionary aspects of parental behavior: Distraction behavior of the Alpine Accentor. Wilson Bulletin 87:367–373.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

Bonenfant, M., and D. L. Kramer. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. Behavioral Ecology 7:299–303.

Braden, G. T. 1999. Does nest placement affect the fate or productivity of California Gnatcatcher nests? Auk 116:984–993.

Burhans, D. E. 1996. Anti-brood parasite defenses and nest-site selection by forest-edge songbirds in central Missouri. Ph.D. dissertation, University of Missouri, Columbia.

Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. Condor 99:866–872.

Burhans, D. E. 2000. Avoiding the nest: Responses of Field Sparrows to the threat of nest predation. Auk 117:803–806.

Burhans, D. E., and F. R. Thompson III. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. Condor 100:663–672.

Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: The crucial experiments have not been performed. Wildlife Society Bulletin 19:534–543.

Clotfelter, E. D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird nests? Animal Behaviour 55:1181–1189.

Conner, R. N., M. E. Anderson, and J. G. Dickson. 1986. Relationships among territory size, habitat, song, and nesting success of Northern Cardinals. Auk 103:23–31.

Cooper, W. E. 1997. Threat factors affecting antipredatory behavior in the broad-headed skink (*Eumeces laticeps*): Repeated approach, change in predator path, and predator's field of view. Copeia 1997:613–619.

Cresswell, W. 1997. Nest predation: The relative effects of nest characteristics, clutch size and parental behavior. Animal Behaviour 53:93–103.

Dearborn, D. C. 1998. Begging behavior and food acquisition by Brown-headed Cowbird nestlings. Behavioral Ecology and Sociobiology 43: 259–270.

Eichholz, M. W., and W. D. Koenig. 1992. Gopher snake attraction to birds' nests. Southwestern Naturalist 37:293–298.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: Does choice of nest site matter? Condor 96:761–768.

Gochfeld, M. 1984. Antipredator behavior: Aggressive and distraction displays of shorebirds. Pages 289–377 *in* Shorebirds: Breeding Biology and Populations (J. Burger and B. L. Olla, Eds.). Plenum Press, New York.

Götmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: A tradeoff between concealment and view of the surroundings? Journal of Avian Biology 26:305–312.

Gross, A. O. 1953. Northern and Maryland Yellowthroats. Pages 542–565 *in* Life Histories of North American Wood Warblers, vol. 2 (A. C. Bent, Ed.). Reprint, Dover Publications, New York 1963.

Heatwole, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. Copeia 1968: 109–113.

Holway, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. Condor 93:575–581.

Howlett, J. S., and B. J. Stutchbury. 1996. Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. Auk 113: 1–9.

Kilgo, J. C., R. A. Sargent, B. R. Chapman, and K. V. Miller. 1996a. Nest-site selection by Hooded Warblers in bottomland hardwoods of South Carolina. Wilson Bulletin 108:53–60.

Kilgo, J. C., R. A. Sargent, K. V. Miller, and B. R. Chapman. 1996b. Nest sites of Kentucky Warblers in bottomland hardwoods of South Carolina. Journal of Field Ornithology 67:300–306.

KING, D. I., R. M. DEGRAAF, C. R. GRIFFIN, AND T. J. MAIER. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? Journal of Field Ornithology 70: 257–262.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

MARTIN, T. E. 1992a. Breeding productivity: What are the appropriate habitat features for management? Pages 455–473 *in* Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

MARTIN, T. E. 1992b. Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology 9:163–197.

MCLEAN, I. G., J. N. M. SMITH, AND K. G. STEWART. 1986. Mobbing behaviour, nest exposure, and breeding success in the American Robin. Behaviour 96:171–186.

MURPHY, M. T., C. L. CUMMINGS, AND M. S. PALMER. 1997. Comparative analysis of habitat selection, nest site and nest success by Cedar Waxwings (*Bombycilla cedorum*) and Eastern Kingbirds (*Tyrannus tyrannus*). American Midland Naturalist 138:344–356.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied Linear Statistical Models. Richard D. Irwin, Homewood, Illinois.

RICKLEFS, R. E. 1977. Reactions of some Panamanian birds to human intrusion at the nest. Condor 79: 376–379.

SAS INSTITUTE INC. 1990. SAS/STAT Users' Guide version 6, 4th ed. SAS Institute, Inc., Cary, North Carolina.

SCHAUB, R., R. L. MUMME, AND G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. Auk 109:585–593.

SCHMIDT, K. A., AND C. J. WHELAN. 1999. Nest placement and mortality: Is nest predation a random event in space and time? Condor 101:916–920.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco.

STRAUSBERGER, B. M. 1998. Evident nest-searching behavior of female Brown-headed Cowbirds while attended by males. Wilson Bulletin 110: 133–136.

THOMPSON, F. R. III, W. DIJAK, AND D. E. BURHANS. 1999. Video Identification of predators at songbird nests in old fields. Auk 116:259–264.

YDENBERG, R. C., AND L. M. DILL. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229–249.

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