

FACTORS AFFECTING PREDATION AT SONGBIRD NESTS IN OLD FIELDS

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Abstract: We determined the effects of microhabitat, year, weather, time of season, stage of the nesting cycle, and brood parasitism on nest predation from a 7-year dataset on field sparrows (*Spizella pusilla*) and indigo buntings (*Passerina cyanea*) in central Missouri, USA. Year, site, and the interaction of species and 2-week interval of the season were important factors explaining nest predation. The only microhabitat variable that consistently explained predation was nest height: nests over 3 m high almost always fledged. Validation of the model parameters on an independent set of nests resulted in proper categorization (e.g., lost or not lost to predation) of 61.5% of nests. In models testing weather and temporal effects, year was related to daily survival for indigo buntings, and 2-week interval of the season explained daily survival for both species. Nest predation was higher overall in the nestling stage than in the incubation stage for indigo buntings, and indigo buntings parasitized by brown-headed cowbirds (*Molothrus ater*) experienced higher predation than nonparasitized buntings. Temporal patterns within the breeding season were consistent between years, and between-year variance appeared to be important, whereas microhabitat was generally unimportant. Research on the mechanisms underlying temporal variability in nest mortality due to predation may identify management options to reduce nest predation.

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Nest predation is a major force in the evolution of life histories of songbirds (Ricklefs 1969, Martin 1988). Perhaps because nest site microhabitat and the accompanying fitnesses of nesting birds reflect choices made by the bird (Martin 1998), numerous studies have researched relationships between nest site factors and songbird nest predation (Martin 1992, Filliater et al. 1994, Howlett and Stutchbury 1996, Burhans and Thompson 1998). In addition, nest site characteristics can be easily measured and are sometimes amenable to management (Martin 1992).

However, other aspects of nesting, while not necessarily within the control of the nesting bird, can be closely linked to the frequency of nest predation. For instance, predation may vary by time of the breeding season (Thompson and Nolan 1973, Schaub et al. 1992), by changes in predator activity or abundance (Nolan 1963), or due to shifts in predator foraging (Vickery et al. 1992). Predation also may vary according to time of the nesting cycle; i.e., nests may experience higher predation after chicks are hatched than when eggs are present (Young 1963, Robertson 1972,

Schaub et al. 1992, Morton et al. 1993). Adult behaviors at the nest may cue predators to the location of the nest; these behaviors may in turn be accentuated by the begging of chicks (Haskell 1994, but see Halupka 1998), clutch or brood size (Skutch 1949, Cresswell 1997), or brood parasites in the nest (Dearborn 1999). With the exception of some recent studies of begging behavior and nest predation (Haskell 1994, Halupka 1998, Dearborn 1999), comparatively little attention has been directed to aspects of predation other than nest site characteristics. Variation in predation due to external factors such as predator phenology may be less amenable to hypothesis testing or experimental manipulation, but temporal or nesting stage predation patterns have been described frequently (e.g., Roseberry and Klimstra 1970, Thompson and Nolan 1973, Beaver 1975, Sockman 1997) and merit further attention.

We examined the relationships between nest predation and microhabitat, weather, time of season, stage of nesting, and brood parasitism. Our objectives were (1) to determine the effects of nest site characteristics on nest predation; (2) to determine the effects of time and weather on nest predation; and (3) to determine differences in nest predation among nesting stages and

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between nests where brood parasites were and were not present.

METHODS

We located nests from April 1992 through August 1998 in successional old fields on or adjacent to the 920-ha Thomas S. Baskett Wildlife Research and Education Center near Ashland, Boone County, Missouri, USA (38°45'N, 92°12'W). Successional old fields that are burned on a biennial basis (described in Burhans 1997) were located in a matrix of forest and have been the subject of yearly songbird studies since 1992 (Burhans 1997; Burhans and Thompson 1998, 1999; Dearborn 1998, 1999). Old fields were located in both upland and bottomland habitats. In addition, we monitored nests in adjoining pasture (described in Burhans 1997).

We used the nests of field sparrows and indigo buntings because they were the most abundant nesting species. Field sparrow nests were not monitored during 1996 or after July during 1995. We searched sites daily for nests and marked them with plastic flagging ≥ 3 m from the nest. We were careful not to make "dead-end" trails that might lead predators directly to nests. 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 for some nests from 1997 to 1998 (Thompson et al. 1999) or during early morning visits on the expected day of fledging. Other evidence of fledging included fledgling begging calls, the sight of fledglings, parents carrying food, or parents chipping rapidly nearby. Nests empty prior to this were considered depredated unless we found evidence of premature fledging; nests where we did not observe these activities were classified as unknown. Cameras did not increase frequency of predation (Thompson et al. 1999).

Microhabitat Effects

We sampled microhabitat variables within 1 month after termination of nesting. We obtained microhabitat measurements for all nests during 1992–1994 but did not obtain measurements from 1995 to 1998 with the exception of nest height. Nest height was measured to the bottom of the nest cup, except during 1997, when it was measured to the top of the nest cup for a different study (Burhans and Thompson 1998). To combine heights using the 2 methods, we subtracted the mean vertical dimension of a sample of field

sparrow nests (7.1 ± 0.3 cm [mean \pm SE], $n = 23$) and indigo bunting nests (7.6 ± 0.2 cm, $n = 42$) from the measured nest height for 1997 nests.

We estimated top and side nest concealment as percent of the nest concealed when viewed from the side at nest height from each of the 4 cardinal directions at a distance of 1 m (Burhans and Thompson 1998). Top concealment was measured from above at a distance of 1 m. For analysis, side concealment was taken as a mean of the 4 side measures, and top concealment was considered a separate variable. Concealment and vertical foliage density measurements were not taken for nests where trampling by animals had occurred, or where flooding during 1993 disturbed vegetation. Concealment measurements could not be taken for nests pulled from vegetation by predators.

We sometimes saw snakes, especially blue racers (*Coluber constrictor*), perched in shrubs near nests. To determine whether predation was related to shrub density near the nest, we counted the number of shrubs (>1 m tall) in 3 stem-diameter categories within a 5-m radius of the nest: (1) <2 cm diameter at breast height (dbh), (2) 2–5 cm dbh, and (3) 6–10 cm dbh.

Common shrubs at our sites having distinctive growth forms included blackberry (*Rubus allegheniensis*), coralberry (*Symphoricarpos orbiculatus*), and red cedar (*Juniperus virginiana*). We counted the numbers of these shrubs in a 5-m circle centered on the nest plant.

We estimated distance to the nearest forest edge by pacing to the point where canopy overhangs the field. Indigo bunting nests that occurred under forest canopy close to forest-field edges (forest nests) were classified separately from nests in old fields (nonforest nests). Nests directly under the forest dripline (distance to edge = 0 m) were classified as nonforest nests.

For the microhabitat analysis, we retained only nests that we were confident had fledged or become depredated; this sample did not include abandoned nests, nests destroyed by weather, or nests having uncertain fates. We used multiple logistic regression to analyze the probability of predation for 11 continuous microhabitat variables, 3 categorical variables, and 2 categorical temporal variables. Logistic regression analysis does not consider the time a nest has been exposed to potential predation (Mayfield 1961); however, most nests were found relatively early in the nesting cycle, so effects of exposure period should have been minimal. Most field sparrow and indigo bunting nests used for the logistic

regression analyses were found before the nestling period (85% and 83%, respectively); 44% of 374 field sparrow and 40% of 307 indigo bunting nests were found before commencement of incubation. Microhabitat variables included mean side nest concealment; top nest concealment; nest height; vertical foliage density at 1 m from the nest; distance to habitat edge; stem-density variables; and densities of blackberry, coralberry, and red cedar. We included categorical variables for species (field sparrow or indigo bunting), site (upland or bottomland), and a classification for forest and nonforest indigo bunting nests.

To determine within-season temporal effects, we assigned each nest a value of 1–8 representing the 2-week interval of the breeding season (week) that the nest fledged or was depredated. To account for between-year variation in nesting success, we first classified nests by year and used the Mayfield method (Mayfield 1961) to calculate daily nest mortality for each species during each year. We then created a dichotomous year variable whose value was 0 or 1 if daily mortality was higher or lower, respectively, than the mean for that species.

We used univariable tests to reduce the number of candidate variables for the logistic models. We retained continuous variables that differed between depredated and nondepredated nests ($P < 0.25$; Hosmer and Lemeshow 2000). We considered interactions that were potentially biologically relevant. We tested for interactions between (1) species and candidate variables, (2) forest versus nonforest indigo buntings, and (3) other candidate variables. We then examined the score statistic for all possible models (best subsets selection; SAS Institute 1995) and chose a reduced set by selecting models from the approximate point where additional parameters resulted in small increases in the score statistic. We then used Akaike's Information Criterion, modified for small sample size (AIC_c ; Burnham and Anderson 1998) to rank these models from best to worst, and present models with an AIC_c of ≤ 2 . Our analysis was exploratory in the sense that we first generated a set of potential models from all possible models using the best subsets option (SAS Institute 1995), but only included the variables that we considered biologically meaningful. The model with the lowest AIC_c ($i = 0$) was the best approximating model for the data, and nested models with differences in AIC_c (i) of < 2 relative to the lowest value in the set may represent potential best models (Burnham and Anderson

1998:63). We report Hosmer and Lemeshow goodness-of-fit tests (Hosmer and Lemeshow 2000) and maximum-rescaled r -square approximations (SAS Institute 1995) for all models.

Microhabitat Model Validation.—With the exception of nest height measurements, we collected extensive microhabitat data only during 1992–1994. Because we had additional nesting data from subsequent years, we could test the model with nesting data collected in 1997 and 1998 (although nest height was not measured during 1995–1996). Using a final model selected as described above, we tested the predictive accuracy of the model by calculating predicted values for nest predation from the new data. If the predicted probability of predation was ≥ 0.50 , the nest was classified as depredated; predicted values < 0.50 were classified as fledged. We determined the concordance (percent of nests correctly classified; SAS Institute 1995) between predicted and actual fates for both depredated and fledged nests for nests from the 1992–1994 and 1997–1998 datasets. We then computed the Brier Score (SAS Institute 1995) for the new observations from the 1997–1998 dataset. The range of the Brier Score is 0 to 1; a smaller score indicates better predictive ability of the model (SAS Institute 1995).

Weather and Temporal Effects

To determine the relationship of predation to weather, we obtained weather readings from the Columbia Regional Airport, Boone County, Missouri (38°49'N, 92°13'W) located 3 km from the study area. For each 2-week interval of each season, we obtained (1) cumulative average degree days, which was the sum of average temperature readings for each of the 14 days of the interval; (2) cumulative maximum degree days, the sum of maximum temperature readings for each of the 14 days; (3) cumulative rainfall, the summed rainfall for the 14-day interval; and (4) rainy days, the numbers of days with ≥ 0.025 -cm rainfall for the 14-day interval.

We calculated daily nest mortality (Mayfield 1961) and standard errors (Johnson 1979) for all active nests within each 2-week period for intervals having ≥ 10 nests/species. We used analysis of variance (ANOVA) to test for differences in daily mortality by species among 2-week intervals and years according to average degree days, maximum degree days, cumulative rainfall, and number of rainy days. We used a weighted ANOVA model in which the mortality estimate for each 2-

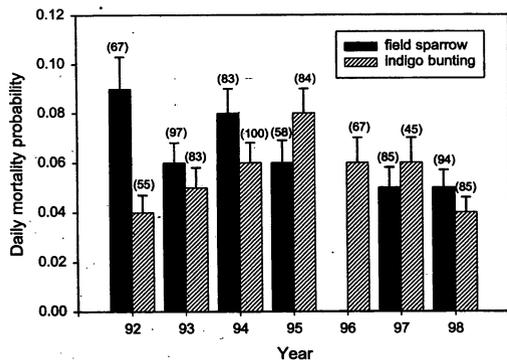


Fig. 1. Annual daily mortality estimates (\pm SE) for field sparrow and indigo bunting nests from the Thomas S. Baskett Center, Ashland, Missouri, USA, by year, 1992–1998. Sample sizes of nests shown above bars.

week interval was weighted by the standard error of the estimate (Neter et al. 1990). We tested for interactions between the factors and retained effects with $P \leq 0.05$ in a final ANOVA model.

Nesting Stage Effects

We compared daily mortality estimates between laying, incubation, and nestling stages using unbalanced fixed-effects ANOVA. To control for effects of season, we divided the nesting season into 3 segments—(1) early, 30 April–10 June; (2) middle, 11 June–22 July; and (3) late, 23 July–September—and calculated daily mortality estimates within each. Within each stage \times segment group we included only those samples having ≥ 10 nests. We performed the analysis separately for each species because there were insufficient samples of both species' nests across all stages for all segments. We compared individual nesting stages within seasonal segments by least-significant-difference tests at $P \leq 0.05$ (Day and Quinn 1989).

Brood Parasitism Effects

To compare predation between parasitized and nonparasitized nests we excluded nests initiated after the window of brown-headed cowbird (hereafter cowbird) laying within each year (second week of July; Burhans 1997). For each species, we compared daily survival between parasitized and nonparasitized nests within laying, incubation; and nestling stages. Field sparrows frequently abandoned nests in response to parasitism, so we included abandoned parasitized nests up to the day of abandonment, but did not count abandonment as a source of nest mortality.

For parasitized nests from the nestling stage, we included only nests having cowbird nestlings because we wanted to test specifically for an effect of cowbird chicks. We used program CONTRAST (Hines and Sauer 1989) to compare daily mortality estimates. In all statistical tests, we considered $P \leq 0.05$ as the level of statistical significance.

RESULTS

We located and monitored 484 field sparrow and 519 indigo bunting nests from 1992 to 1998. Daily mortality due to predation varied between years (Fig. 1) for both field sparrows ($\chi^2_5 = 12.72$, $P = 0.026$; $n = 4,607$ observation days) and indigo buntings ($\chi^2_6 = 16.44$, $P = 0.012$; $n = 5,137$ observation days). Daily nest mortality over all years was 0.064 ± 0.004 for field sparrows and 0.055 ± 0.003 for indigo buntings and did not differ between species ($\chi^2_1 = 3.49$, $P = 0.062$).

Microhabitat Effects

We identified 8 candidate models with i scores < 2 from 54 possible models identified with the best subsets criterion (Table 1; SAS Institute 1995). All 8 models included the variables year, site, nest height, and the interactions for species \times week and species \times site (Fig. 2). We chose the model with the lowest i to validate 1997–1998 data because it also contained all of the variables from the 1992–1994 data. This model correctly classified 71.8% of the predicted probabilities and observed responses ($n = 401$ nests) from the 1992–1994 dataset and correctly classified 61.5% of the responses using nests from the 1997–1998 dataset (Brier score = 0.24; $n = 265$ nests).

All models explaining nest predation indicated that higher nests were less likely than lower nests to experience depredation (Table 1, Fig. 3). The indicator variable distinguishing bottomland sites from upland old field and pasture sites was important and indicated higher predation in bottomland sites (Table 1, Fig. 4). Two models indicated that distance to edge or the interaction of edge distance with species was important in explaining predation (Fig. 4), and 1 model indicated higher predation with more coralberry in the nest patch (Table 1).

Weather and Temporal Effects

Only the temporal variable week was important in the model testing for weather and temporal effects on nest mortality for field sparrows (Fig. 2; $F_{6, 27} = 3.10$, $r^2 = 0.41$, $P = 0.019$). Both year and week were important in the indigo bunting model (Overall: $F_{12, 29} = 4.61$, $r^2 = 0.66$, $P < 0.001$; week: $F_{6, 29} = 5.09$, $P = 0.001$; year: $F_{6, 29} = 2.63$, $P = 0.037$).

Table 1. Final models explaining nest predation in field sparrows and indigo buntings from the Thomas S. Baskett Center, Ashland, Missouri, USA, 1992–1994.

Model number	Logistic regression model	AIC _c	Δ _i	-2log _e (L)	R ² _{adj}	P ^a	Fit ^b
1	3.929* + (-0.874 yr)* + (-2.454 site)* + (-1.734 nest height)* + (-0.200 species × week)* + (0.799 species × nest height) + (0.997 species × site)*	448.69	0	434.40	0.205	0.0001	0.623
2	3.932* + (-0.896 yr)* + (-2.952 site)* + (-0.577 nest height)* + (-0.179 species × week)* + (1.246 species × site)*	449.12	0.43	436.90	0.198	0.0001	0.024
3	3.854* + (-0.872 yr)* + (0.173 week) + (-2.996 site)* + (-2.375 nest height)* + (-0.291 species × week)* + (1.170 species × nest height) + (1.300 species × site)*	449.62	0.93	433.253	0.209	0.0001	0.807
4	3.828* + (-0.872 yr) + (-2.359 site)* + (-1.685 nest height)* + (0.003 coralberry) + (-0.194 species × week)* + (0.766 species × nest height) + (0.925 species × site)	450.21	1.52	433.843	0.207	0.0001	0.493
5	3.949 + (-0.873 yr)* + (-2.455 site)* + (-1.757 nest height)* + (-0.002 species × edge distance) + (-0.194 species week)* + (0.807 species × nest height) + (0.983 species × site)*	450.34	1.65	433.971	0.207	0.0001	0.328
6	3.966* + (-0.875 yr)* + (-2.442 site)* + (-1.736 nest height)* + (-0.197 species × week)* + (0.978 species × site)* + (-0.003 edge distance) + (0.794 species × nest height)	450.48	1.79	434.11	0.207	0.0001	0.334
7	2.397* + (-0.889 yr)* + (-2.420 site)* + (-2.296 nest height)* + (0.987 species) + (0.324 week) + (-0.399 species × week)* + (0.972 species × site) + (1.118 species × nest height)	450.56	1.87	432.10	0.212	0.0001	0.382
8	3.265* + (-0.900 yr)* + (0.478 species) + (-2.326 site)* + (-0.574 nest height) + (-0.196 species × week)* + (0.896 species × site)	450.57	1.88	436.282	0.200	0.0001	0.052

^a Probability value for likelihood ratio χ^2 test of model covariates.

^b Probability value for Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000).

* Indicates significance of parameter ($P < 0.05$) based on Wald χ^2 statistic.

Weather variables had no effect on interval nest mortality for either species; Spearman correlation coefficients between the weather variables and daily mortality all had absolute values ≤ 0.13 .

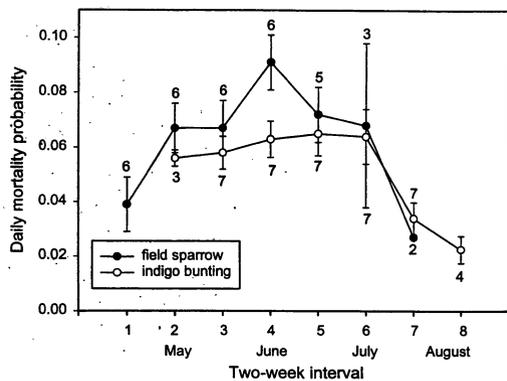


Fig. 2. Daily mortality estimates by 2-week intervals throughout nesting season for all nests at the Thomas S. Baskett Center, Ashland, Missouri, USA, 1992–1998. Error bars indicate standard error of yearly means across year (field sparrows: sample size of years above filled circles; indigo buntings: sample size of years below open circles).

Nesting Stage Effects

There were no differences in nest mortality by nesting stage for field sparrows (Fig. 5; overall: $F_{10, 19} = 2.02$, $r^2 = 0.52$, $P = 0.090$; stage: $F_{2, 19} = 5.55$, $P = 0.013$). Indigo bunting daily mortality differed according to nesting stage (Fig. 5; overall:

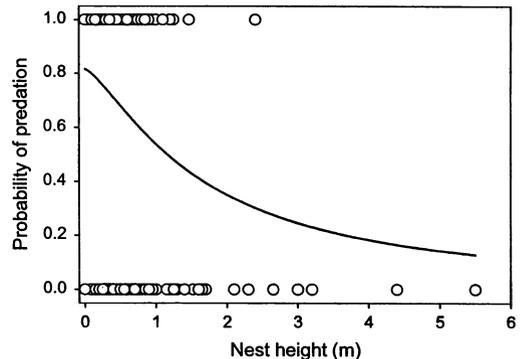


Fig. 3. Relationship of nest height to probability of nest predation for nests of field sparrows and indigo buntings, Thomas S. Baskett Center, Ashland, Missouri, USA, 1992–1994. Circles represent actual nest outcomes (1 = depredated, 0 = fledged).

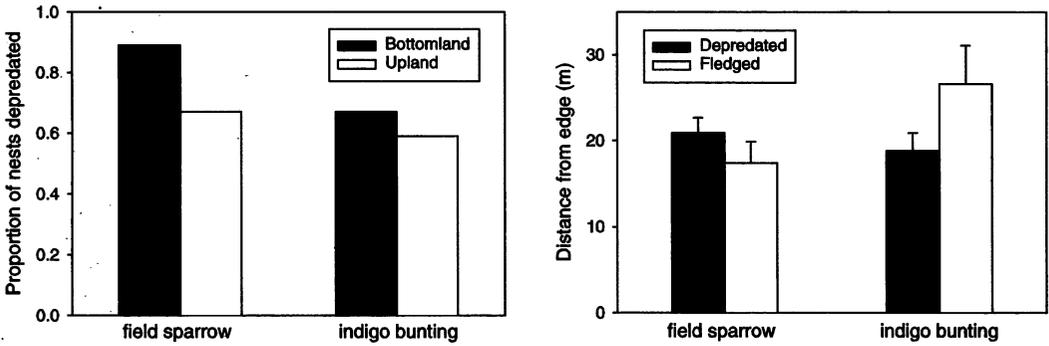


Fig. 4. Proportion of nests depredated at Thomas S. Baskett Center, Ashland, Missouri, USA, according to site type (bottomland, upland) and distance to habitat edge, by species (1992–1994).

$F_{13, 30} = 3.24, r^2 = 0.58, P = 0.004$; stage: $F_{2, 30} = 4.81, P = 0.015$ and segment of the season ($F_{2, 30} = 8.59, P = 0.001$). Year and the interaction of segment and year were not important (year: $F_{6, 30} = 2.03, P = 0.092, F_{3, 30} = 2.72, P = 0.062$, respectively). Early segment daily mortality for buntings during the nestling stage was higher than both the laying stage ($P = 0.003$) and the incubation stage ($P = 0.038$). There were insufficient sample sizes to calculate daily mortality for laying stage bunting nests during the late segment of the breeding season.

Brood Parasitism Effects

Predation did not differ between parasitized and nonparasitized field sparrow nests over all nesting stages combined (Fig. 6; $\chi^2_1 = 0.78, P = 0.376; n = 340.5$ and $3,610.5$ days, parasitized, nonparasitized nests, respectively). Daily mortality due to predation was lower at parasitized nests during the laying stage (parasitized: $0.000, n = 54.5$ days; nonparasitized $0.040 \pm 0.010, n = 424.5$ days; $\chi^2_1 = 17.73, P < 0.001$). Predation did not differ between parasitized and nonparasitized field sparrow nests for the incubation (parasitized: $0.037 \pm 0.013, n = 218$ days; nonparasitized $0.058 \pm 0.005, n = 2,136$ days; $\chi^2_1 = 2.46, P = 0.117$) and nestling stages (parasitized: $0.176 \pm 0.046, n = 68$ days; nonparasitized $0.095 \pm 0.009, n = 1,011$ days; $\chi^2_1 = 3.00, P = 0.084$). Daily mortality was higher at parasitized than nonparasitized indigo bunting nests overall (Fig. 6; $\chi^2_1 = 4.38, P = 0.036, n = 1,535$ and $1,530$ days, parasitized, nonparasitized nests, respectively). However, daily mortality did not differ between parasitized and nonparasitized bunting nests within any of the nesting stages (laying, parasitized: $0.046 \pm 0.016, n = 175$ days;

nonparasitized $0.053 \pm 0.019, n = 132$ days; $\chi^2_1 = 0.08, P = 0.774$; incubation, parasitized: $0.064 \pm 0.008, n = 973$ days; nonparasitized $0.045 \pm 0.007, n = 884$ days; $\chi^2_1 = 3.12, P = 0.078$; nestling, parasitized: $0.102 \pm 0.018, n = 284$ days; nonparasitized $0.069 \pm 0.011, n = 578.5$ days; $\chi^2_1 = 2.50, P = 0.114$).

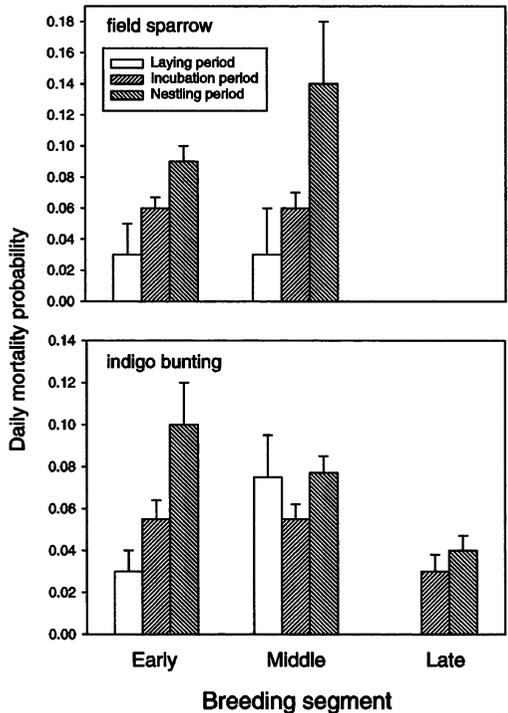


Fig. 5. Daily mortality estimates and standard errors by nesting stage for field sparrow and indigo bunting nests from Thomas S. Baskett Center, Ashland, Missouri, USA, 1992–1998, by segment of breeding season (early: 30 Apr–10 Jun; middle: 11 Jun–22 Jul; late: 23 Jul–Sep).

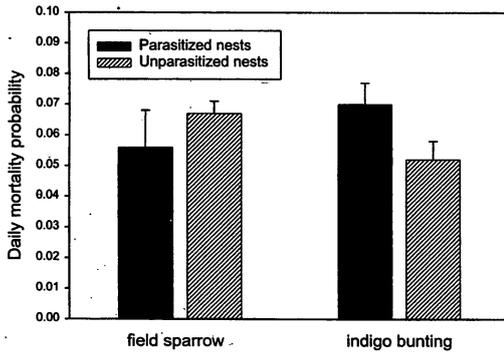


Fig. 6. Daily mortality estimates and standard errors for parasitized and unparasitized field sparrow and indigo bunting nests from Thomas S. Baskett Center, Ashland, Missouri, USA, 1992–1998.

DISCUSSION

Within-season temporal trends in nest predation were important in both the microhabitat model and analysis of weather effects. Although nest success varied between years and species, within a given year, predation was low in spring, peaked in June and July, and dropped to a very low level by August. Few of the microhabitat variables we measured were important in explaining nest predation; however, the logistic regression model that included temporal, site, nest height, and species \times week and species \times site correctly classified 61.5% of the nests when tested on a sample from later years.

Our approach did not permit comparison of effects of time, microhabitat, weather, and nest stage in 1 model. For example, we could not use logistic regression to test the influence of nesting stage on the probability of predation, because all nests assigned successful outcomes contained nestlings on the last visit. Accordingly, high probabilities of success would be associated with all nests having nestlings, whereas our data and those of others (Young 1963, Robertson 1972, Schaub et al. 1992) show that nests during the nestling stage may experience higher predation compared to nests having only eggs. Similarly, it is difficult to relate weather to nest predation because it is not usually possible to determine weather conditions at the exact time of nest termination; intervals between nest visits typically extend over several days. Alternative approaches for modeling nest survival are now available that permit comparison of habitat and time-dependent covariates in the same model (Allison 1995, White and Burnham 1999).

Microhabitat Effects

We found little influence of nest site characteristics on predation except for nest height, which was important in all models. Our pattern may have been influenced by successful fledging at extremely tall nests >3 m, all of which successfully fledged, and that are unusually high especially for field sparrows (see also Nolan 1963). We found that presence of coralberry was important in 1 model. Martin and Roper (1988) found that predation at hermit thrush (*Catharus guttatus auduboni*) nests decreased with the number of preferred nest plants in the nest patch, as predicted by the potential prey site hypothesis (Martin and Roper 1988, Martin 1993). However, hermit thrushes at those sites nested almost exclusively in white fir (*Abies concolor*), whereas our study species use many species of plants (D. E. Burhans, unpublished data). In the case of hermit thrush, predators should benefit from searching a particular nest plant, whereas nest plants used at our study sites may be too varied to confer an advantage to predators using a search image.

Other studies have noted relationships between predation and the frequency of certain nesting substrates or shrubs near the nest (Martin and Roper 1988, With 1994). Blackberry, coralberry, and red cedar were common shrubs having distinctive growth forms at our sites. They frequently were used as nest plants by both species with the exception that indigo buntings rarely used red cedars.

Although some of the many studies on nest microhabitat have found relationships between nest site factors and predation, many of these studies have found little or no importance of microhabitat components (e.g., Filliater et al. 1994, Howlett and Stutchbury 1996, Burhans and Thompson 1998). Lack of a discernible pattern does not mean that a relationship does not exist, because the mechanisms linking predation and nest site features may not be apparent (Schmidt and Whelan 1999) or may require analysis specific to certain predators.

Weather and Temporal Effects

Both year and week effects were important in models; these effects may reflect some aspect of predation whose mechanism we were not able to discern or measure, such as temporal differences in predator activity, abundance, or prey selection. Other nesting studies in midwestern old-field habitats found midsummer peaks in predation similar to ours (Best 1978, Zimmerman 1984) and similar declines in predation by late summer (Nolan 1963,

Best 1978, Zimmerman 1984). However, other old-field studies have reported low predation in midsummer (Thompson and Nolan 1973), which was when our predation levels were highest.

We did not detect any relationships between nest predation and weather variables. Research with black rat snakes (*Elaphe obsoleta*), the major predator at our sites (Thompson et al. 1999), indicates that they are more active at higher ambient air temperatures (Withgott and Amlaner 1995). Further research is needed to reveal relationships between predator activity, weather, and temporal predation patterns. Our approach of relating nest success to mean or cumulative weather conditions during 2-week intervals may have been insensitive to short-duration weather events affecting predation.

Nesting Stage Effects

Many studies have reported higher predation during the nestling stage (Young 1963, Robertson 1972, Schaub et al. 1992), although others have noted higher predation during laying or incubation (Roseberry and Klimstra 1970, Sockman 1997). High predation at nests with nestlings may be due to temporal coincidence of predator activity with timing of the nest cycle (Thompson and Nolan 1973), but could also be due to preferred predation on nestlings, perhaps due to olfactory cues (Eichholz and Koenig 1992, Schaub et al. 1992) or increased movement at the nest (MacDonald 1973, Herzog and Burghard 1974, Mullin and Cooper 1998). Video cameras and observations at our nests indicate that nestlings are taken by snakes more frequently than eggs (Thompson et al. 1999).

Brood Parasitism Effects

Higher daily mortality at parasitized indigo bunting nests is also consistent with the hypothesis that cues from nestlings influence predation, although we did not find a similar relationship for field sparrows. Using a subset of the indigo bunting nests in the present study, Dearborn (1999) found that predation was higher at parasitized nests for both the incubation and entire nesting cycles. His artificial nest experiment suggested that louder vocalization by cowbird nestlings was partly the cause, although daily mortality also was higher at parasitized bunting nests during the incubation stage. We did not find evidence that predators are cued by louder cowbird chicks, as daily mortality did not differ between parasitized bunting nests with cowbird chicks and nonparasitized nests with host chicks only. The

positive relationship between predation and parasitism at indigo bunting nests provides weak support for the possibility that predation and parasitism both are more likely at the same nests, perhaps because of birds' selection of inferior nest sites. Another study on yellow-breasted chats (*Icteria virens*) at the same sites also indicated that parasitism was positively related to frequency of nest predation (Burhans and Thompson 1999).

MANAGEMENT IMPLICATIONS

We cannot offer specific habitat management guidelines for mitigating nest predation on the basis of this study. This study does indicate, however, that important temporal variation exists in nest predation, and understanding the factors contributing to this variation should have conservation implications. We recommend that further attention be devoted to identifying and studying nest predators and to determining the relevance of temporal patterns in nest predation. When predators are known, habitat, microhabitat, and temporal patterns in nest predation can be understood from predator life histories, search strategies (Bowman and Harris 1980, Mullin et al. 1998), and predator habitat use (Dijak and Thompson 2000); understanding these relationships may result in improved management recommendations or mitigation measures. By placing temporal variation in nesting success into a demographic context, we can determine the extent that bird populations are affected by temporal windows wherein nest predation is relaxed or increased. During low predation years, a given songbird population may be demographically viable, whereas it may not produce enough offspring to replace itself in high predation years (Anders et al. 1997); this temporal scheme may be analogous to the spatial structuring of songbird populations in sources and sinks (Donovan et al. 1995, Trine 1998). In comparison to microhabitat studies, there is a paucity of work on predator identification, predator temporal activity, and the cues from the nest that elicit predation. Research to better understand nest predation based on knowledge of predators may provide insights currently lacking from nest site studies alone.

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