AN EXPERIMENTAL TEST OF THE CONCEALMENT HYPOTHESIS USING AMERICAN GOLDFINCH NESTS

REBECCA G. PEAK^{1,2}

ABSTRACT.—I conducted a vegetation removal experiment using American Goldfinch (*Carduelis tristis*) nests to test the hypothesis that predation rates vary with concealment in old field habitats in eastcentral Illinois. Daily predation rates were 0.05 for manipulated nests and 0.04 for control nests. Although manipulated nests were much less concealed than control nests, the probability of predation did not differ significantly between treatments or years. Logistic regression models indicated that nests initiated earlier in the breeding season had a greater probability of predation than nests initiated later in the breeding season. These results indicate that time of breeding season may be more important than concealment in explaining probability of predation of American Goldfinch nests in this old field system. *Received 20 February 2003, accepted 4 June 2003*.

Since predation is the major cause of nest failure for a wide range of bird species (Ricklefs 1969), identifying factors that affect the probability of predation can provide important insight concerning conservation strategies for breeding birds. Numerous studies have attempted to identify characteristics at the nest site that may reduce the probability of predation (reviewed in Martin 1992, Burhans and Thompson 1998). Many have focused on nest concealment, hypothesizing that predation rates vary with concealment and their results differ among species and habitats. Most studies used natural variation in concealment, but two (Bengston 1972, Howlett and Stutchbury 1996) tested the hypothesis by experimentally manipulating the amount of vegetation surrounding the nest. Bengston (1972) found a difference in predation rates between duck nests (genera Aythya and Anas, and tribe Mergini) where vegetation had been removed and control nests located in marsh habitats in Iceland. Howlett and Stutchbury (1996) did not find a difference in predation rates between Hooded Warbler (Wilsonia citrina) nests where vegetation had been removed and control nests located in mature deciduous forests in Pennsylvania.

I used experimental vegetation removal to test the hypothesis that predation rates of American Goldfinch (*Carduelis tristis*) nests vary with concealment, and predicted that manipulated nests would be depredated at a greater rate than control nests. American Goldfinches build open cup nests and are common in old fields and flood plains characteristic of early successional growth, but also use cultivated lands, roadsides, orchards, and gardens (Middleton 1993). My study of American Goldfinch nests increases the number of species and habitats (and the associated predators) examined by experimental vegetation removal, and thus provides further understanding of the effects of concealment on predation risk.

METHODS

Study area.—I conducted this study in eastcentral Illinois on two sites during the 1996 and 1997 breeding seasons. One site is a 77-ha area of the Middle Fork River Forest Preserve (40° 22′ N, 87° 57′ W). This preserve includes approximately 619 ha along the Middle Fork of the Vermilion River. The other site is a 73-ha area of the former Chanute Air Force Base (44° 17′ N, 88° 08′ W). This public use area includes approximately 860 ha along the Salt Fork of the Vermilion River. Study sites had been abandoned 7-9 years prior to the study and previously were used for farming, livestock grazing, and recreational activities. Study sites were located in a predominantly agricultural landscape; row crop agriculture (primarily corn and soybeans) covers 75% of the land area in eastcentral Illinois (Mankin and Warner 1997). Bottomland forests were dominated by silver maple (Acer saccharinum), American sycamore (Platanus occidentalis), and black walnut (Juglans nigra). Open habitats, including old fields, prai-

¹ Rantoul Township High School, 200 South Sheldon St., Rantoul, IL 61866, USA.

² Current address: The Nature Conservancy, P.O. Box 5190, Fort Hood, TX 76544-0190, USA; e-mail: rpeak@tnc.org

rie restorations, croplands, and public areas (campgrounds, picnic pavilions, and parking lots) were dominated by oaks (*Quercus* spp.), hawthorns (*Craetagus* spp.), and plums (*Prunus* spp.), with herbaceous cover of goldenrod (*Solidago* spp.), thistle (*Cirsium* spp.), and big blue stem (*Andropogon gerardi*).

Nest searching and monitoring.—I conducted nest searches once every 4 days from July through September. I systematically traversed each study site and used behavioral cues to locate nests. Nest locations were marked at distances at least 5 m from the nest with plastic flagging. I monitored nests every 3–4 days during the beginning of the nest cycle and daily as hatching and fledging dates approached. For each visit I recorded date of visit and occurrences of parasitism and predation.

I considered a nest successful if it fledged at least 1 host young. I looked for confirmation of fledging by sighting nestlings, listening for nestling begging calls, and by sighting parents carrying food or scolding near the nest. I attributed nest failure to unknown causes when nest contents remained unchanged and adults were not present during at least three subsequent visits. I attributed nest failure to Brown-headed Cowbird (Molothrus ater) parasitism after a cowbird egg was deposited in the nest and adults were not present during at least three subsequent visits. I attributed nest failure to predation if they were empty prior to the expected date of fledging and there were no signs of fledging, cowbird parasitism, or failure due to unknown cause.

Nest site measurements.—I measured height of nest from ground to base of nest and recorded species of nest tree (or shrub). I scored concealment using methods outlined in Holway (1991). I estimated percentage of the nest concealed to the nearest 20% at 45 degree compass intervals (N, NE, E, SE, S, SW, W, NW) 1 m from the nest at three levels: ground, nest height, and 1.5 m above ground. Also, I made one estimate from directly above the nest at a height of 1 m. I calculated mean concealment which ranged from 0% for no concealment to 100% for a completely hidden nest at each of the three levels and overall concealment (mean of the 25 estimates) for analyses.

Experimental vegetation removal.—I paired

nests that were active at the same time, located on the same study site, and in the early incubation stage of the nest cycle. Initial concealment was greater than 50% at all three levels. I randomly assigned one nest in each pair to the manipulated treatment.

I followed a vegetation removal protocol similar to that outlined in Howlett and Stutchbury (1996). Using hand-held pruning shears, I clipped vegetation from within a 1-m radius of the nest. To control for disturbance, I simulated this treatment at the control nest on the same day by sorting through the vegetation as if I was actually going to remove it. The simulation lasted 25 minutes, approximately the same time required to complete an actual manipulation. I estimated concealment for manipulated nests immediately following vegetation removal and again for both manipulated and control nests within one day after they became inactive.

Data analyses.—I excluded from analyses all nests that failed for any reason other than predation. I calculated daily predation rates by the Mayfield method (Mayfield 1961, 1975). I used program MICROMORT (Heisey and Fuller 1985) to calculate daily predation rates and 95% confidence intervals (CI) for each year, site, and treatment and to calculate likelihood values for models with and without year and treatment effects. I assumed that daily survival was constant throughout the nest cycle (Mayfield 1975) and calculated Mayfield estimated interval nest success as the daily survival rate raised to the length of the entire nest cycle (Middleton 1993). I compared mean daily predation rates and 95% CIs of manipulated and control nests. I compared survival models with and without year and treatment effects using log likelihood ratio tests.

I used multivariate logistic regression to examine the effects of nest site factors and time of breeding season on the probability of predation. Although logistic regression does not correct for the exposure period of individual nests, the nests used in this study were located during building or during egg laying, which minimizes the potential for this bias. Candidate variables for the logistic regression models included concealment at ground level, nest height, 1.5 m above ground, and 1 m directly above the nest, and overall concealment; date

of clutch initiation; and nest height. I selected these variables because results of previous studies suggest they may be important in explaining predation of songbird nests (Thompson and Nolan 1973, Martin 1992, Schaub et al. 1992, Filliater et al. 1994, Burhans and Thompson 1998). I used the best subsets selection method (SAS Institute, Inc. 1995) to evaluate all possible models created from the set of candidate variables. I compared these models with the log likelihood statistic, R^2 , Pvalues of the overall model, and the significance of the variables that were included. When appropriate, I used a log likelihood ratio test to evaluate which of the models was most suitable for explaining probability of predation.

RESULTS

I located 103 American Goldfinch nests during the two breeding seasons, but only 22 (11 manipulated and 11 control) nests in 1996 and 46 (23 manipulated and 23 control) nests in 1997 were eligible for analysis. The major cause of nest failure was predation, 45 (66%) of these 68 nests were depredated. Two nests (3%) were abandoned following parasitism by the Brown-headed Cowbird and one nest (1%) was abandoned for unknown reasons.

Mean overall concealment (95% CI) was 73.6% (69.4–77.7%) in 1996 and 74.8% (72.5-77.0%) in 1997. Before vegetation removal, mean concealment of control and treatment nests was similar for all five concealment measurements (mean difference, 95% CI; ground level: 2.5%, -4.3-9.3%; nest level: 0.1%, -4.6-4.7%; 1.5-m level: 4.6%, -2.3-11.5%; above nest: 0.6%, -6.0-7.2%; overall: 1.3%, -2.8-5.3%). After vegetation was removed, mean concealment of manipulated nests was much less than that of control nests for all five concealment measurements (mean difference, 95% CI; ground level: 46.2%, 40.3–52.1%; nest level: 40.6%, 35.9– 45.4%; 1.5-m level: 44.2%, 38.5-50.0%; above nest: 55.3%, 49.8-60.8%; overall: 44.3%, 40.7–48.0%).

The overall daily predation rate (95% CI) was 0.04 (0.02–0.07) or an interval nest success estimate of 37% for a 25-day nest cycle. The daily predation rate (95% CI) for nests located on the Middlefork Forest Preserve and on the former Chanute Air Force Base was

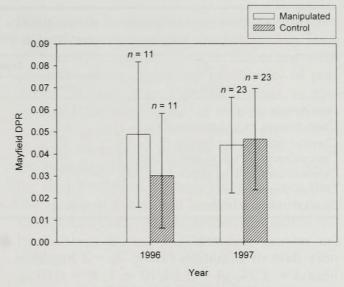


FIG. 1. Daily predation rates (mean ± 95% confidence intervals) for control and manipulated (some concealing vegetation removed) American Goldfinch nests were not significantly different in old field habitats located in eastcentral Illinois, 1996–1997.

0.04 (0.03–0.06) and 0.06 (0.03–0.08), respectively. In 1996, the daily predation rate for manipulated nests was greater than the daily predation rate for control nests; however, the CIs overlap (Fig. 1). Results from 1997 show a reverse of this trend. The daily predation rate for control nests was greater than the daily predation rate for manipulated nests; however, these CIs also overlap (Fig. 1). Likelihood ratio tests comparing models with year and treatment effects to a model with year and treatment pooled demonstrate that the probability of predation did not differ significantly between treatments ($\chi^2 = 0.10$, df = 2, P = 0.75) or years ($\chi^2 = 0.20$, df = 2, Q = 0.85).

I calculated mean and 95% CIs for variables considered in the logistic regression analysis (Table 1). Nests initiated earlier in the breeding season were more likely to be depredated than nests initiated later in the breeding season (Table 2; -2 log likelihood for model = 63.00, χ^2 = 19.56, df = 1, P = 0.0001). Nests more concealed from above were more likely to be depredated than nests less concealed from above (Table 2; -2 log likelihood for model = 59.76, χ^2 = 22.80, df = 2, P = 0.0001). Likelihood ratio tests between these two models demonstrate that adding the variable concealment above nest to the model did not explain more variation in probability of predation than the model containing

TABLE 1. Nest site characteristics of depredated (n = 45) and nondepredated (n = 23) American Goldfinch nests were similar. Data are from eastcentral Illinois, 1996-1997.

		Depredated	Nondepredated		
Variable	Mean	95% CI	Mean	95% CI	
Nest height (cm)	175	156–194	168	141–196	
Concealment at ground level (%)	67	65–70	67	61–73	
Concealment at nest height (%)	57	55-60	57	54-80	
Concealment at 1.5 m above nest (%)	76	74-78	76	71-82	
Concealment at 1 m above nest (%)	75	69-81	81	74-88	
Overall concealment (%)	67	66-69	67	65–70	
Date of clutch initiation	9 Aug.	7 Aug. to 10 Aug.	29 Aug.	22 Aug. to 6 Sept.	

only date of initiation (Table 2; -2 log likelihood = 3.24, χ^2 = 3.24, df = 1, P = 0.072).

DISCUSSION

I found that daily predation rates for American Goldfinch nests did not differ significantly between treatments or years. The width of the 95% CIs for daily predation rates indicates a high degree of variation within the sample, so even if a real difference existed, I may not have detected it because of low statistical power (Steidl et al. 1997). For example, daily predation rates for control nests in 1997 ranged from 0.02–0.07, which represents a biologically important difference in nest success (60–12%, for the 25-day nest cycle), yet the 95% CIs for treatments in 1997 overlap.

Previous studies also have found that less concealed songbird nests are not always depredated at a greater rate than more concealed songbird nests (reviewed in Martin 1992, Burhans and Thompson 1998, Howlett and Stutchbury 1996, Braden 1999). This result may reflect cues used by predators to locate nests. If predators in this study used olfactory cues to locate nests (Henry 1969, Willis 1973, Lill 1974, Grant and Morris 1971, Eichholz and Koenig 1992, Schaub et al. 1992, Whelan et al. 1994), or depredated songbird nests incidentally (Vickery et al. 1992), my results would be expected because sight would not be important in nest detection. Burhans (1996) found no relationship between concealment and predation rates of Field Sparrow (Spizella pusilla) or Indigo Bunting (Passerina cyanea) nests in old field habitats in central Missouri. Results of video camera studies conducted at those sites found that snakes were important predators in old field habitats (Thompson et al. 1999). Robinson et al. (1999) found that fox snakes (Elaphe vulpina) and blue racers (Coluber constrictor) were more frequently associated with open habitats (old fields and grasslands) than forest habitats in eastcentral Illinois. Predation may be influenced more by nestling and parental activity (Skutch 1949, Young 1963, Perrins 1965, Nias 1986) or olfactory cues (Eichholz and Koenig 1992, Schaub et al. 1992) than by concealment if

TABLE 2. Probability of predation was negatively associated with date of clutch initiation and positively associated with concealment from 1 m directly above the nest for American Goldfinch nests (n = 68) in eastcentral Illinois, 1996-1997.

Model	Partial r ²	Parameter estimate	SE	Wald χ^2	P	Odds ratio
Model 1a	0.6	m draw 3h				1000
Intercept		19.03	5.08	14.04	0.0002	- Pa
Date of clutch initiation		-0.08	0.02	13.18	0.0003	0.93
Model 2 ^b	0.29					
Intercept		17.70	5.10	12.04	0.0005	_
Date of clutch initiation		-0.08	0.02	12.38	0.0003	0.93
Visibility 1 m above nest		0.02	0.01	3.06	0.0800	1.02

 $[^]a$ -2 log likelihood for intercept and covariates = 63.00; χ^2 = 19.56, P = 0.0001. Maximum rescaled R^2 = 0.36. b -2 log likelihood for intercept and covariates = 59.76, χ^2 = 22.80, P = 0.0001. Maximum rescaled R^2 = 0.41.

snakes are dominant predators in open habitats.

Other nest site factors as well as local scale factors can be important determinants of nest success (reviewed in Martin 1992, 1993; Paton 1994; Andren 1995), but results of studies examining these relationships vary among species, habitats, and regions. This variation may exist because smaller spatial scale effects are constrained by processes operating at larger spatial scales (Donovan et al. 1997, Hartley and Hunter 1998, Thompson et al. 2002). In the midwestern United States, predation rates are negatively correlated with forest fragmentation at the landscape scale (Robinson et al. 1995). Furthermore, many species of potential nest predators are abundant and widespread in these highly fragmented, predominantly agricultural landscapes (Andren 1992, Pedlar et al. 1997, Heske et al. 1999, Dijak and Thompson 2000, Chalfoun et al. 2002). The surrounding agricultural landscape likely provides additional food sources for nest predators, which may increase their abundance throughout the landscape (Andren 1995, Marzluff et al. 1998, Dijak and Thompson 2000). Perhaps my result that predation rates did not vary with concealment was because the highly fragmented landscape may be saturated with nest predators, thus constraining the ability to detect any concealment effect.

Logistic regression models indicated that predation decreased as the breeding season progressed. Variation in predation rates during the breeding season may reflect changes in the activity patterns of the predator community or in the availability of alternate prey (Thompson and Nolan 1973). Robinson et al. (1999) found that mammalian predators, particularly raccoons (Procyon lotor), were abundant in eastcentral Illinois and that they moved into agricultural areas as the summer progressed and crops ripened. If generalist predators are abundant in these old field patches at the beginning of the breeding season, but increase their use of crop fields later in the breeding season, this could lead to a decline in predation rates in edge habitats as the breeding season progresses.

Concealment does not appear to affect the predation rate of American Goldfinch nests located in old field habitats in eastcentral Illinois. This result may reflect cues used by

predators to locate nests or abundance patterns of predators throughout the landscape. Time of breeding season is more important than concealment in explaining probability of predation of American Goldfinch nests in this system. The importance of this factor in explaining probability of predation may reflect changes in activity patterns of predators over the breeding season. Further studies identifying nest predators, documenting the cues they use to locate nests, and examining how large scale factors affect their abundance and activity patterns during the breeding season are needed.

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