

## THE RELATIONSHIP BETWEEN PREDATION AND NEST CONCEALMENT IN MIXED-GRASS PRAIRIE PASSERINES: AN ANALYSIS USING PROGRAM MARK

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*Abstract.* Nest predation is the principle cause of nest failure in most upland avian communities. In this paper, we explore the relationship between nest predation and nest-site concealment for six passerine species that co-occur in mixed-grass prairie of north-central Montana (1997–2002). Since ground-nesting passerines are susceptible to a wide range of predators, we hypothesized that selection processes would favor nest sites with more vegetative concealment to minimize the probability of nest detection. Although nests in our study were generally well concealed, concealment estimates were variable within and among species. We estimated daily nest-survival rates using the program MARK and covariates that were modeled included mean percent concealment, site, and year; models were evaluated within an information-theoretic framework. Nest concealment was negatively related to daily nest survival in Savannah Sparrows (*Passerculus sandwichensis*), Baird's (*Ammodramus bairdii*) Sparrows, and Chestnut-collared Longspurs (*Calcarius ornatus*) across all years, and Grasshopper Sparrows (*Ammodramus savannarum*) during some years. In the dome-nesting species, Sprague's Pipits (*Anthus spragueii*) and Western Meadowlarks (*Sturnella neglecta*), our results suggest that daily nest-survival rates increased with greater nest concealment. Although our precision was relatively poor, our results indicate that predation rates may actually increase with greater concealment for the four cup-nesting species, in some years, providing contradictory evidence that concealment deters predation for some grassland bird species of the northern plains.

*Key Words:* daily survival rate, grassland passerines, mixed-grass prairie, Montana, nest predation, nest concealment, nest success, program MARK.

## LA RELACIÓN ENTRE DEPREDACIÓN Y OCULTACIÓN DE NIDO EN COLORINES DE PASTOS MIXTOS DE PRADERA: UN ANÁLISIS UTILIZANDO PROGRAMA MARK

*Resumen.* La depredación de nidos es la principal causa del fracaso de nidos en la mayoría de las comunidades de aves de tierras altas. En este artículo exploramos la relación entre depredación de nido y ocultación de nido de sitio para seis especies de colorines que co-ocurren en praderas mixtas de pasto, del norte central de Montana (1997–2002). Debido a que los colorines que anidan en el suelo son susceptibles a un amplio rango de depredadores, nuestra hipótesis es que procesos de selección favorecerían a sitios de nidos con mayor ocultación de vegetación, para minimizar la probabilidad de detección de nido. A pesar de que los nidos en nuestro estudio se encontraban en su mayoría bien conectados, las estimaciones de ocultación fueron variables dentro y entre las especies. Estimamos las tasas diarias de sobrevivencia de nido utilizando el programa MARK, así como las covariantes que fueron modeladas, incluyendo el porcentaje de la media de ocultación, sitio, y año; los modelos fueron evaluados dentro de un marco teórico de información. La ocultación de nido estuvo negativamente relacionada a la sobrevivencia diaria de nido en Gorrión Sabanero (*Passerculus sandwichensis*), Gorriónes de Baird (*Ammodramus bairdii*), Escribano Collar Castaño (*Calcarius ornatus*) durante todos los años; y en Gorrión Chapulín (*Ammodramus savannarum*) durante algunos años. En las especies anidadoras de domo, Bisbita Llanera (*Anthus spragueii*) y en Pradero Occidental (*Sturnella neglecta*) nuestros resultados sugieren que las tasas diarias de sobrevivencia de nido incrementaron con mayor ocultación de nido. A pesar de que nuestra precisión fue relativamente pobre, nuestros resultados indican que las tasas de depredación de hecho quizás incrementen con mayor ocultación para las cuatro especies anidadoras de tasa en algunos años, mostrando evidencia contradictoria de que la ocultación disuade la depredación en algunas especies de aves de tierras de prados de las planicies del norte.

Nest predation is typically the most significant factor affecting productivity in ground-nesting passerines, regardless of taxon, habitat, or geographic area (Ricklefs 1969, Murphy 1983; Martin 1993, 1998), and is considered the primary cause of nest failure in grassland passerines of North America (Johnson and Temple 1990, Vickery

et al. 1992, Winter 1999; Davis 2003, 2005). Although a number of other factors contribute to nest failure, nest predation should exert a major evolutionary force on nest-site selection and be a dominant factor directing nest-site-selection patterns (Martin 1998). As in other landscapes, nonrandom nest-site placement has been

documented in grasslands (Clark and Shutler 1999, Dieni and Jones 2003; Davis 2003, 2005). Most species have evolved several anti-predator strategies, including direct effects, e.g., parental behavior and nest defense, and indirect effects, including nest-site selection, timing of nesting, double brooding, length of incubation, and nestling periods (Weidinger 2002). A well-concealed nest appears to be an obvious response to nest predation since high cover reduces the communication of auditory, visual, and olfactory cues from the nest to potential predators (Martin 1993). By selecting safe sites, birds can reduce nest failure either by decreasing the nest encounter rate for incidental nest predation or by decreasing nest detectability for actively searching predators (Weidinger 2002). The relative importance of nest-site characteristics to other nest-defense strategies is crucial to understanding the evolution of life-history traits and population limitations (Cresswell 1997).

The nest-concealment hypothesis predicts decreased predation risk for nests with greater surrounding vegetation (Martin 1993). Indeed, some cup-nesting passerines select nest sites that have higher vegetation densities than surrounding areas (Petit and Petit 1996, Dieni and Jones 2003) and, in some cases, predation rates have been found to be lower at nests with greater concealment (Martin and Roper 1988, Clark and Shutler 1999, Schmidt and Whelan 1999, Davis 2005). However, other studies have found no relationship between nesting success and nest concealment (Filliater et al. 1994, Clark and Shutler 1999, Davis 2005). The lack of a relationship between concealment and nest success has led to other hypotheses to explain how birds avoid nest predation including, nest-defense (parental compensation) hypothesis, potential-prey-site hypothesis, trade-off hypothesis, and others.

Active nest defense may compensate for poorly concealed nests through parental behavior which may include direct attacks, mobbing, nest guarding, vocalizations, e.g., alarm calls, injury feigning and distraction displays (Cresswell 1997, Martin and Menge 2000, Remes 2005). Passive nest-defense strategies include crypsis, e.g., camouflaging the nest contents while sitting on the nest (Weidinger 2002). The potential-prey-site hypothesis is based on the premise that search efficiency of a predator declines as the number of potential nest sites increases (Liebezeit and George 2002), and it predicts that nests surrounded by many potential nest sites should have a lower probability of depredation than those surrounded by few nest sites (Liebezeit and George 2002). The trade-off hypothesis states that nest-site choice is often a

trade-off between the need for concealment and the need for individuals to maintain some view of the surrounding, to reduce the risk of predation on the adults (Götmark et al. 1995).

We tested the hypothesis that nest-site-selection strategies in the grasslands of the northern prairie may maximize vegetative concealment to minimize the probability of detection by predators. If nest concealment affects nest-predation rates, then poorly concealed nests should have a higher probability of being depredated, provided that significant variation occurs in concealment values. In the undisturbed arid grasslands of north-central Montana, structurally homogeneous graminoids are the dominant vegetation, while woody vegetation is limited. The predator community here is diverse using a variety of techniques to locate nests, including visual, olfactory, and random-search strategies. Nest placement is restricted to the ground, which makes the nests accessible to all potential predators.

To determine if nest predation varies in relation to nest concealment, we modeled daily nest survival as a function of vegetative nest concealment using the nest-survival model in program MARK (Dinsmore et al. 2002, White 2005). Six common grassland species that co-occur in north-central Montana were studied: Sprague's Pipit (*Anthus spragueii*), Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows, Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*).

## METHODS

### STUDY AREA

During 1997–2002, we conducted this study at Bowdoin National Wildlife Refuge in Phillips County, north-central Montana (48°25'N, 107°39'W; ~700 m in elevation). The study area consisted of four permanent plots (26–59 ha), situated 1.6–3.8 km apart and comprising 183 ha of flat to gently rolling native northern mixed-grass prairie. The climate is continental and semiarid, characterized by strong winds and high evaporation rates. Long-term annual and seasonal (May–July) precipitation totals are 33.7 and 18.2 cm, respectively. Annual and seasonal precipitation totals averaged 31.0 and 16.6 cm, respectively during the study period. Western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), dense clubmoss (*Selaginella densa*), and fringed sagewort (*Artemisia frigida*) were the dominant herbaceous species. Shrubs (*Sarcobatus vermiculatus*, *Artemisia cana*, *Ceratoides lanata*)

were sparse and trees largely absent, except Russian olive (*Elaeagnus angustifolia*) and cottonwood (*Populus deltoides occidentalis*), which occurred sporadically along the edges of two study sites. The study area had not been grazed by cattle for  $\geq 29$  yr. A 3-ha portion of one study site burned in 1994; otherwise no burning events have occurred since refuge documentation began in 1936.

Potential or suspected terrestrial nest predators included badger (*Taxidea taxus*), long-tailed weasel (*Mustela frenata*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*) (Peitz and Granfors 1998), mice and voles (*Zapus*, *Reithrodontomys*, *Peromyscus*, and *Microtus*), ground squirrels (*Spermophilus tridecemlineatus* and *S. richardsonii*), bull snake (*Pituophis melanoleucus*), garter snake (*Thamnophis* spp.), and western rattlesnake (*Crotalus viridis*). Avian predators such as Northern Harrier (*Circus cyaneus*), gulls (*Larus* spp.), Short-eared Owl (*Asio flammeus*), Loggerhead Shrikes (*Lanius ludovicianus*), Black-billed Magpie (*Pica hudsonia*) and Western Meadowlark have been observed on or within the immediate vicinity of the study sites. Sprague's Pipit and Baird's Sparrow nests ( $N = 13$ ) monitored with micro-cameras (Peitz and Granfors 2000) documented garter snake, Northern Harrier, Short-eared Owl, Western Meadowlark, and deer mouse depredation of nestlings within the study area (P. J. Gouse and S. L. Jones, unpubl. data).

#### NEST SEARCHING AND MONITORING

Sites were searched for nests 3–5 times per week from mid-May through mid-August in an attempt to locate all active nests each year (Dieni and Jones 2003). Search techniques included behavioral observation (Martin and Geupel 1993), foot surveys, and rope dragging (Davis 2003). Once located, nests were marked for relocation by placing a discreet strip of plastic flagging on the ground approximately 2.5 m on either side of the nest. Nests were monitored every 2–4 d thereafter. Nesting outcomes were: (1) successful fledging (at least one young of the host species), (2) complete depredation, (3) abandonment (eggs or nestlings left permanently unattended), or (4) outcome unknown. Observations of fledglings within 3 d of expected fledging, minimal nest disturbance, the presence of feces and feather scales in the nest, fledglings near the nest, or adults uttering alarm calls nearby or feeding new fledglings within 50 m of the nest were treated as evidence of success. Depredation was assumed when the nest, eggs or nestlings too young to fledge disappeared or were destroyed.

Within 2–4 d following nest termination, we estimated percent cover from directly above the nest and in the four cardinal directions. Five ocular estimates of percent concealment of the constructed nest (not nest contents) were obtained for each nest, as viewed from a distance of 1 m in the four cardinal directions at ground level, and from directly above (Dieni and Jones 2003). The arithmetic mean of those five measurements was used as the concealment value for each nest.

#### ANALYSIS

We estimated daily survival rates (DSR) for nests using the survival model in program MARK (White 2005). Program MARK uses a generalized linear approach to modeling daily nest-survival rates, using maximum likelihood estimation to estimate regression coefficients (Rotella et al. 2004). Our objective was to determine if mean vegetative concealment of the nest was inversely related to nest predation rates, and if so, estimate the strength of that relationship. All nests that failed from reasons other than predation (e.g., inclement weather, parasitism, or unknown) were excluded from the analysis to focus on concealment using only those nests with known fates, either depredated or successful. Estimates of DSR in this context served also as an inverse measure of nest depredation rates.

Analyses were conducted independently for the six dominant passerine species found on the study area. Six linear-regression models predicting daily nest survival were constructed and evaluated for each bird species, using a combination of explanatory variables—constant DSR (intercept-only model), nest concealment, and nest concealment—while simultaneously controlling for the effects of site and year, with and without their respective interactions. Nest concealment was the parameter of interest; however, site and year were also used in the models because of the plausibility that nest fates were not independent within sites or years (Winter et al. 2005a), a fundamental assumption of the nest-survival model in program MARK (Dinsmore et al. 2002). Regression models were constructed using the logistic transformation (logit) as the link function, using natural logs.

Encounter histories are constructed in program MARK, which required the following data for each nest (Rotella 2005): (1) the day the nest was found, (2) the last day the nest was checked when still active, (3) the last day that the nest was checked, and (4), the fate of the nest. For successful nests, an attempt was made to estimate the actual day that the nest

fledged young, rather than simply using the last day checked. The latter, if different, would unjustifiably add survival days to a nest when failure was no longer possible (Rotella 2005). Days were standardized so that the earliest date across all years when a nest (or nests) was first found was coded as day 1, with subsequent dates numbered sequentially relative to the first day (Rotella 2005). Analyses were conducted independently for each bird species, thus each species potentially had a different standardized earliest date. Since we had 6 yr of data for each species, the earliest date across all years was standardized as day 1, thus subsequent dates were numbered relative to this date, regardless of year.

Model covariates included mean concealment, year, and site. Mean concealment was treated as a proportion in the analysis and reported as such in the results. Site and year variables were treated as categorical (four and six levels, respectively), with each level introduced into the regression model as an artificial explanatory variable with the usual 0 or 1 coding scheme. Cross-product terms were also added accordingly for concealment and site-year interactions.

Each set of candidate models was evaluated within an information-theoretic framework (Burnham and Anderson 2002). For each model within a set, program MARK calculated Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ), and ranked each model in ascending order of  $AIC_c$  values (Burnham and Anderson 2002). Models with lower  $AIC_c$  values indicate greater empirical support, which can be roughly interpreted as a compromise between explaining more variance and limiting the number of parameters (Cooch and White 2005).

Our goal was not to determine the best model per se, but rather to make a general estimate of the direction and magnitude of the effects of concealment on DSR. We considered this relationship both in a bivariate context, and while controlling for the simultaneous effects of year and site. Models with and without interaction terms were judged to have received similar support from the data if their  $AIC_c$  values were within two units of each other: in which case, we viewed the evidence of an interaction as weak and consequently dropped the interaction from further consideration. We then used the model-averaging approach (Burnham and Anderson 2002) for the remaining models to estimate an average regression coefficient for concealment for each bird species, with an unconditional estimate of the variance. Coefficient estimates were weighted according

to that model's likelihood in the set (Akaike's weights;  $w_i$ ). Model-averaged coefficients may provide better estimates of precision because the variance component dealing with model-selection uncertainty is included in the variance estimator (Burnham and Anderson 2002). Intercept-only models (where the regression coefficient for concealment is set to 0) were included in the set of models to be averaged, which serves to reduce model-selection bias of the estimate (Burnham and Anderson 2002). The magnitude of the estimated regression coefficient can be interpreted in terms of its effect on the odds of daily nest survival. This is achieved by taking the antilog of both sides of the logistic equation. The right-hand side of the equation has the exponential form,  $e^{bx}$ , which gives the estimated factor change in DSR for every unit increase in nest concealment (Agresti and Finlay 1986).

## RESULTS

From 1997–2002, 1,014 nests of 19 species (excluding waterfowl) were discovered and monitored; here we report on the six dominant passerines species that composed >90% ( $N = 919$ ) of the total nests located (Table 1). Predation accounted for 82% of all known nest failures; among abandoned nests ( $N = 89$ ), 33% were directly attributed to severe weather events (e.g., heavy rain and hailstorms). Only a small number of nests had nesting fates that were unknown ( $N = 11$ ; Table 1).

Mean nest concealment varied within and among bird species. Across all nests, Chestnut-collared Longspurs had the least concealed nests, with the most variability ( $\bar{x} = 58\%$ ,  $CV = 38\%$ ), while mean nest-concealment estimates for the five remaining species were higher but less variable ( $\bar{x} = 83\text{--}89\%$ ,  $CV = 13\text{--}22\%$ ).

Except for Grasshopper Sparrows, nest-survival models that included interaction terms between nest concealment and site or year variables received little empirical support, suggesting that the relationship between nest concealment and daily nest survival varied little across sites or years. Constant-survival models (y-intercept only) and models including bivariate relationships between DSR and nest concealment all had substantial support for all bird species (Table 2). Models controlling for site and year all had reasonable empirical support ( $\Delta AIC_c < 8$ ) for all species (Table 2).

Model-averaged regression coefficients are presented in Table 3. Both Sprague's Pipits and Western Meadowlarks showed a positive relationship between nest concealment and DSR, although the precision of those estimates was

TABLE 1. RELATIVE FREQUENCIES (NUMBER OF NESTS WITH BROWN-HEADED COWBIRD [*MOLOTHRUS ATER*] PARASITISM) OF NESTING OUTCOMES FOR THE DOMINANT BIRD SPECIES AT BOWDOIN NATIONAL WILDLIFE REFUGE (1997–2002).

Species	Abandoned	Depredated	Successful	Unknown	N
Sprague’s Pipit ( <i>Anthus spragueii</i> )	8.7 (1)	52.2 (2)	39.1 (0)	0.0	69
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	17.6 (3)	40.0 (16)	41.8 (4)	0.6	170
Grasshopper Sparrow ( <i>Ammodramus savannarum</i> )	12.5 (0)	29.7 (4)	56.3 (1)	1.6	64
Baird’s Sparrow ( <i>Ammodramus bairdii</i> )	10.2 (0)	47.5 (3)	42.4 (0)	0.0	59
Chestnut-collared Longspur ( <i>Calcarius ornatus</i> )	5.3 (2)	45.2 (7)	47.5 (2)	1.9	469
Western Meadowlark ( <i>Sturnella neglecta</i> )	15.9 (3)	45.5 (15)	38.6 (11)	0.0	88
Total	89 (9)	403 (47)	416 (18)	11	919

TABLE 2. SELECTION RESULTS MODELING DAILY SURVIVAL RATES USING PROGRAM MARK FOR SIX GRASSLAND PASSERINE SPECIES. SIX LINEAR CANDIDATE MODELS WERE CONSIDERED FOR EACH BIRD SPECIES, WHICH INCLUDED THE FOLLOWING VARIABLES: CONSTANT DAILY SURVIVAL (Y-INTERCEPT =  $B_0$ ), MEAN NEST CONCEALMENT ALONE AND CONTROLLING FOR SITE AND YEAR, AND THEIR RESPECTIVE INTERACTIONS. MODELS ARE LISTED IN ORDER OF DESCENDING  $\Delta AIC_c$  BY BIRD SPECIES. NUMBER OF PARAMETERS ( $K$ ) VARIED AMONG SPECIES FOR IDENTICAL MODELS, SINCE SPECIES OCCURRENCE VARIED BY YEAR AND SITE.

Species	Model	$\Delta AIC_c$	$w_i$	$K$
Sprague’s Pipit ( <i>Anthus spragueii</i> )	$b_0 + b_{conceal} + b_{year}$	0.0	0.45	7
	$b_0$	0.7	0.32	1
	$b_0 + b_{conceal}$	2.6	0.12	2
	$b_0 + b_{conceal} + b_{year} + b_{int}$	3.5	0.08	11
	$b_0 + b_{conceal} + b_{site}$	6.8	0.02	5
	$b_0 + b_{conceal} + b_{site} + b_{int}$	8.1	0.01	8
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	$b_0$	0.0	0.39	1
	$b_0 + b_{conceal} + b_{site}$	0.7	0.27	5
	$b_0 + b_{conceal}$	1.3	0.21	2
	$b_0 + b_{conceal} + b_{site} + b_{int}$	3.6	0.06	8
	$b_0 + b_{conceal} + b_{year}$	4.5	0.04	7
	$b_0 + b_{conceal} + b_{year} + b_{int}$	5.4	0.03	12
Grasshopper Sparrow ( <i>Ammodramus savannarum</i> )	$b_0 + b_{conceal} + b_{year} + b_{int}$	0.0	0.98	8
	$b_0$	10.1	0.01	1
	$b_0 + b_{conceal} + b_{site} + b_{int}$	11.0	0.00	6
	$b_0 + b_{conceal} + b_{site}$	11.9	0.00	4
	$b_0 + b_{conceal}$	12.1	0.00	2
	$b_0 + b_{conceal} + b_{year}$	15.5	0.00	6
Baird’s Sparrow ( <i>Ammodramus bairdii</i> )	$b_0 + b_{conceal} + b_{year}$	0.0	0.35	6
	$b_0$	0.5	0.28	1
	$b_0 + b_{conceal}$	0.7	0.24	2
	$b_0 + b_{conceal} + b_{site} + b_{int}$	3.1	0.07	8
	$b_0 + b_{conceal} + b_{site}$	4.2	0.04	5
	$b_0 + b_{conceal} + b_{year} + b_{int}$	6.2	0.02	10
Chestnut-collared Longspur ( <i>Calcarius ornatus</i> )	$b_0 + b_{conceal}$	0.0	0.51	2
	$b_0$	1.3	0.27	1
	$b_0 + b_{conceal} + b_{site}$	2.0	0.19	5
	$b_0 + b_{conceal} + b_{site} + b_{int}$	6.6	0.02	8
	$b_0 + b_{conceal} + b_{year}$	7.4	0.01	7
	$b_0 + b_{conceal} + b_{year} + b_{int}$	13.3	0.00	12
Western Meadowlark ( <i>Sturnella neglecta</i> )	$b_0$	0.0	0.52	1
	$b_0 + b_{conceal}$	1.1	0.30	2
	$b_0 + b_{conceal} + b_{site}$	2.9	0.12	5
	$b_0 + b_{conceal} + b_{year}$	5.6	0.03	6
	$b_0 + b_{conceal} + b_{site} + b_{int}$	6.5	0.02	8
	$b_0 + b_{conceal} + b_{year} + b_{int}$	9.0	0.01	10

TABLE 3. REGRESSION COEFFICIENTS FOR MEAN NEST CONCEALMENT ESTIMATED USING A WEIGHTED AVERAGE ACROSS ALL MODELS, BY BIRD SPECIES. BECAUSE OF STRONG EVIDENCE OF AN INTERACTION BETWEEN YEAR AND CONCEALMENT FOR GRASSHOPPER SPARROW, COEFFICIENTS WERE AVERAGED BETWEEN INTERCEPT-ONLY AND BIVARIATE MODELS FOR EACH YEAR SEPARATELY. GENERALLY LOW PRECISION OF ALL ESTIMATES IS REFLECTED BY THE RELATIVELY WIDE 95% CONFIDENCE INTERVALS. THE MAGNITUDE OF THE ESTIMATED REGRESSION COEFFICIENT CAN BE INTERPRETED IN TERMS OF ITS EFFECT ON THE ODDS OF DAILY NEST-SURVIVAL, WHICH GIVES THE ESTIMATED FACTOR CHANGE IN DAILY SURVIVAL RATE FOR EVERY 0.1 UNIT (10%) INCREASE IN NEST CONCEALMENT.

Species	$b_{\text{conceal}}$	Upper 95% CI	Lower 95% CI	$e^{b(\Delta 10\%)}$
Sprague's Pipit ( <i>Anthus spragueii</i> )	0.6	2.2	-1.1	1.1
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	-0.4	0.5	-1.3	1.0
Grasshopper Sparrow ( <i>Ammodramus saviannarum</i> )				
-1997	-0.5	1.5	-2.5	1.0
-1998	20.2	37.6	2.8	7.5
-2000	5.8	13.9	-2.3	1.8
-2002	-1.9	3.3	-7.0	0.8
Baird's Sparrow ( <i>Ammodramus bairdii</i> )	-0.9	1.3	-3.2	0.9
Chestnut-collared Longspur ( <i>Calcarius ornatus</i> )	-0.4	0.1	-1.0	1.0
Western Meadowlark ( <i>Sturnella neglecta</i> )	0.8	2.4	-0.8	1.1

low (CV = 141% and 107%, respectively). Strong evidence was found of an interaction between nest concealment and year for Grasshopper Sparrows (Table 3). The relationship between nest concealment and DSR was positive for 1997 and 2002, while negative for 1998 and 2000. The three other species studied showed a negative relationship between nest concealment and DSR.

## DISCUSSION

Nest predation was the primary cause of nest failure, which is largely consistent with other reports for grassland passerines (Johnson and Temple 1990, Vickery et al. 1992; Davis 2003, 2005; Winter et al. 2005a). While nest-concealment values varied among species, it was generally high except for Chestnut-collared Longspurs. In this study, if nest concealment did lessen nest predation as predicted the effect was extremely weak or difficult to detect. In the four cup-nesting species, nest concealment had a weak inverse relationship with DSR for Savannah and Baird's sparrows and Chestnut-collared Longspurs, or varied substantially across years in Grasshopper Sparrows, with poor within-year precision. In contrast, both dome-nesting species, Western Meadowlarks and Sprague's Pipits, showed a weak positive relationship between concealment and DSR, but again with relatively low precision.

A number of studies on passerines have also shown a lack of association between nesting success and nest concealment (Filliater et al. 1994, Clark and Shutler 1999, Davis 2005). If nesting songbirds recognize micro-sites that are more susceptible to predation, we would expect strong selection for specific nest-site micro-habitats. However, the predator community in

the mixed-grass prairie is diverse with diverse strategies to locate nests, depending on visual or olfactory cues and random-search methods. This predator diversity may preclude the existence of safe nest sites for ground-nesting songbirds (Filliater et al. 1994, Wilson and Cooper 1998). In addition, the avian community in the northern mixed-grass prairie may be adapted to a suite of predators that differs from what is now present.

Small mammals, considered the primary threat to ground nests in the northern Great Plains (Pietz and Granfors 2000, Davis 2003) opportunistically find grassland bird nests while foraging for invertebrates (Howlett and Stutchbury 1996, Dion et al. 2000). This may eliminate the predictability of successful nest sites (Filliater et al. 1994) since rodents take eggs or nestlings opportunistically from unattended nests (Weidinger 2002). In addition, small mammals may avoid foraging in areas with less vegetative cover to reduce the risk of avian predation on themselves, which may explain why concealed nests were somewhat more likely to be depredated (Howlett and Stutchbury 1996). Moreover, nest defense may actually be more effective on poorly concealed nests, as there may be a trade-off between increased nest cover and the ability of parents on the nest to detect an approaching predator (Götmark et al. 1995).

Avian predators generally rely on visual cues for detecting active nests (Filliater et al. 1994, Dion et al. 2000), and therefore high nest cover should be more effective against avian predators. We documented avian predators (N = 5) depredating nests during the nestling stage, and it is plausible that they located nests in response to increased parental activity or begging calls by nestlings, typical of the late nestling stage (Liebezeit and George 2002).

If nest-site concealment is not effective in reducing nest failure due to diverse predator strategies, adult behavior may be important in nest predator deterrence (Murphy et al. 1977). The effects of parental behavior on nest survival differ among species, generally being either positive or neutral (Weidinger 2002), although increased adult activity at nests could be negative (Halupka 1998, Martin and Menge 2000, Remes 2005). Strong adult nest defense (Murphy et al. 1977), re-nesting, and double-brooding (Murphy 1983, Schmidt and Whelan 1999), faster nestling growth, and early fledging (Ricklefs 1969, Murphy et al. 1977) may all contribute more to nest success than micro-site selection. We suggest that the three species studied that showed a weak negative relationship between concealment and DSR had behavior consistent with the parental compensation, nest-defense, and trade-off hypotheses.

Chestnut-collared Longspurs have high rates of re-nesting and double-brooding, shortened time for nestling development, and commonly exhibit distraction displays when flushed from the nest (Hill and Gould 1997; S. L. Jones and P. J. Gouse, unpubl. data). Chestnut-collared Longspurs and Sprague's Pipits are also noted for their distraction-flight displays when off the nest (Hill and Gould 1997, Robbins 1998). Savannah Sparrows do show nest-site selection patterns that favor nest sites with greater vegetation structure (Dieni and Jones 2003); however, in this analysis no positive relationship was found from concealment to DSR. Conversely, both Davis (2005) in the mixed-grass prairie of southern Saskatchewan and Winter et al. (2005a) in the northern tall-grass prairie of Missouri documented a positive relationship between nest concealment and nest success in Savannah Sparrows, although the latter study did not discount abandoned nests from the analysis. Savannah Sparrows do demonstrate active nest-defense behavior, particularly using alarm calls and distraction displays.

Birds can also increase investment in one nesting attempt by adapting more secretive behavior when visiting the nests (Cresswell 1997). Sprague's Pipits and the *Ammodramus* sparrows are not generally double-brooded (Sutter 1997, Green et al. 2002, Davis 2003) and did not flush until the searcher was extremely close to the nest. Adults of these species are typically quiet and unobtrusive around the nest, using foliage to conceal movements. They return by flying to the vicinity of the nest, but typically travel the last few meters discreetly on foot. This may mimic a running rodent and

serve to divert predators from the nest (Morton et al. 1993). Cryptic alternate plumages are typical for the species studied here; their plumages are particularly cryptic when the incubating or brooding individual is on the nest. Therefore, these species may rely more on crypsis than nest concealment to avoid visually oriented predation and may be under strong directional selection from nest predators to choose nest sites that allow them to blend into the background.

Nest-site selection is likely a trade-off among several competing constraints, and may not primarily reflect an anti-predation strategy. However, the fact that no functional relationships were uncovered between predation rates and nesting concealment is striking, particularly given the wide variation in concealment values observed within and across the bird species studied here. Our failure to uncover a relationship between nest concealment and nest-predation rates may be a function of the local predator community, in conjunction with adult behavioral strategies. Indeed, parental behavior at the nest may lead to complex relationships between nest concealment and survival and the accumulating evidence is in support of multiple and interactive effects on nest predation (Weidinger 2002). However, micro-site characteristics, in conjunction with adult behavioral adaptations, may still serve to conceal nests through crypsis.

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