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TIME-SPECIFIC VARIATION IN PASSERINE NEST SURVIVAL: NEW INSIGHTS INTO OLD QUESTIONS

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ABSTRACT.—Understanding nest survival is critical to bird conservation and to studies of avian life history. Nest survival likely varies with nest age and date, but until recently researchers had only limited tools to efficiently address those sources of variability. Beginning with Mayfield (1961), many researchers have averaged survival rates within time-specific categories (e.g. egg and nestling stages; early and late nesting dates). However, Mayfield's estimator assumes constant survival within categories, and violations of that assumption can lead to biased estimates. We used the logistic-exposure method to examine nest survival as a function of nest age and date in Clay-colored Sparrows (*Spizella pallida*) and Vesper Sparrows (*Pooecetes gramineus*) breeding in north-central North Dakota. Daily survival rates increased during egg laying, decreased during incubation to a low shortly after hatch, and then increased during brood rearing in both species. Variation in survival with nest age suggests that traditional categorical averaging using Mayfield's or similar methods would have been inappropriate for this study; similar variation may bias results of other studies. Nest survival also varied with date. For both species, survival was high during the peak of nest initiations in late May and early June and declined throughout the remainder of the nesting season. On the basis of our results, we encourage researchers to consider models of nest survival that involve continuous time-specific explanatory variables (e.g. nest age or date). We also encourage researchers to document nest age as precisely as possible (e.g. by candling eggs) to facilitate age-specific analyses. Models of nest survival that incorporate time-specific information may provide insights that are unavailable from averaged data. Determining time-specific patterns in nest survival may improve our understanding of predator–prey interactions, evolution of avian life histories, and aspects of population dynamics that are critical to bird conservation. *Received 11 May 2004, accepted 29 November 2004.*

Key words: Clay-colored Sparrow, logistic exposure, nest survival, *Pooecetes gramineus*, *Spizella pallida*, Vesper Sparrow.

Variation Temporelle de la Survie des Nichées chez les Passereaux: De Nouvelles Informations pour des Vieilles Questions

RÉSUMÉ.—La survie des nichées constitue un élément important en termes de conservation et de traits d'histoire de vie chez les oiseaux. La survie des nichées varie probablement en fonction de l'âge et de la date de la nichée, mais jusqu'à récemment les chercheurs ne bénéficiaient que d'outils limités afin d'évaluer

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efficacement ces sources de variabilité. À commencer par Mayfield (1961), de nombreux chercheurs ont effectué la moyenne des taux de survie en fonction de périodes temporelles (e.g. étapes de ponte et de nidification, dates précoces et tardives de nidification). Néanmoins, l'estimateur de Mayfield présume que la survie reste constante à l'intérieur de ces périodes et la violation de cette prémisse peut conduire à des estimations biaisées. Nous avons utilisé la méthode "logistic-exposure" ("exposition logistique") pour examiner la survie des nichées en fonction de la date et de l'âge de la nichée chez *Spizella pallida* et *Poocetes gramineus* qui nichent dans la partie centrale nord du Nord Dakota. Le taux de survie journalier augmentait au cours de la couvaison, diminuait durant l'incubation et ce, jusqu'au taux le plus bas, et augmentait à nouveau lors de l'élevage des couvées pour les deux espèces. Les variations de survie en fonction de l'âge de la nichée suggère que la méthode de Mayfield ou des méthodes similaires auraient été inappropriées dans le cadre de cette étude. La survie des nichées variait également avec la date. Pour les deux espèces, la survie était élevée lors du pic d'initiation des nids à la fin mai et début juin et déclinait, par la suite, tout au long de la saison de nidification. Sur la base de nos résultats, nous encourageons les chercheurs à considérer des modèles de survie des nichées qui intègrent des variables évoluant de manière continue dans le temps (e.g. âge et date de la nichée). Nous encourageons également les chercheurs à documenter l'âge des nichées aussi précisément que possible (e.g. en mirant les œufs) afin de faciliter les analyses basées sur l'âge. Les modèles de survie des nichées qui intègrent un aspect temporel pourraient fournir des informations qui ne sont pas disponibles à partir de données moyennes. En déterminant les patrons temporels de la survie des nichées, il serait possible d'améliorer notre compréhension des interactions prédateurs-proies, l'évolution des traits d'histoires de vie chez les oiseaux, et certains aspects de la dynamique des populations qui sont d'importance en termes de conservation.

BIRD CONSERVATION REQUIRES AN UNDERSTANDING of factors that influence habitat selection, survival, and productivity of avian populations. Predation is the primary source of nest mortality in most passerine species (Ricklefs 1969, Martin 1992) and has undoubtedly influenced the evolution of avian morphology, physiology, and behavior (e.g. Skutch 1949, Martin et al. 2000, Martin 2002). Beginning with Mayfield (1961), ornithologists have worked to develop improved methods to estimate nest success (reviewed in Williams et al. 2002 and Shaffer 2004). The objective of many nesting studies is to relate survival to various explanatory variables, with the goal of understanding how those variables affect nest predation or brood parasitism.

For many species, risk of nest predation may change in relation to one or more time-specific variables, such as nest age or nest initiation date. Nest survival is usually estimated using Mayfield's (1961) or similar methods (e.g. Johnson 1979), with data often averaged within categories of time-specific variables. Categories may have a biological basis (e.g. egg vs. nestling

stage) or be somewhat arbitrarily defined (e.g. early, middle, and late incubation). Researchers often examine differences in survival rates among laying, incubation, and brood rearing or, alternatively, between egg and nestling stages. However, Mayfield's estimator assumes constant survival within each nest stage, and violation of that assumption can bias estimates (Klett and Johnson 1982) and may lead to invalid conclusions. Among studies using categorical averages for time-specific variables, no general pattern of nest success has emerged. Some studies have reported higher nest survival during incubation, others during brood rearing, and some detected no differences among stages (see below). Some passerine studies showed that nest survival varied during the breeding season, though few studies have rigorously modeled the effects of date on nest survival (e.g. Winter 1999). Recent advances in analytical techniques (Dinsmore et al. 2002, Shaffer 2004) have provided innovative tools for examining nest survival at finer temporal scales than were previously possible.

In 1997, 1998, and 2002, we monitored survival of Clay-colored Sparrow (*Spizella pallida*) and Vesper Sparrow (*Poocetes gramineus*) nests located in grasslands in north-central North Dakota. On the basis of other studies (e.g. Pietz and Granfors 2000, Burhans et al. 2002) and our own experiences, we suspected that nest survival might vary with nest age or nest initiation date. We were concerned that averaging data by nest stage (e.g. laying, incubation, and brood rearing) or date (e.g. early-season, late-season) might mask true biological differences in time-specific survival. We therefore modeled nest survival as a function of time using the logistic-exposure method developed by Shaffer (2004), in which date and age were treated as continuous explanatory variables. Our objectives were to describe age- and date-specific patterns of nest survival for Clay-colored and Vesper sparrows and investigate how those patterns compared with those shown by traditional estimators of nest survival (e.g. Mayfield 1961) that averaged data by nest stage or date. We also wished to compare patterns of nest initiation and nest survival by date for the two species, as part of our exploration of the role that nest predation might play in shaping those patterns.

METHODS

Nest monitoring.—Our study was located in the northern mixed-grass prairie physiographic region, but the area can be considered a southern extension of the aspen parkland ecoregion (Grant and Berkey 1999). Vegetation was dominated by a needle grass-wheatgrass (*Stipa* sp.—*Agropyron* sp.) association intermingled with two exotic grasses, Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*). Native prairie was interspersed with short (<1 m) brush dominated by western snowberry (*Symphoricarpos occidentalis*), tall (2–3 m) shrub dominated by chokecherry (*Prunus virginiana*), and woodland dominated by quaking aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*).

Nest searching and monitoring were conducted from about 15 May to 15 July of each year. Between 0630 and 1500 hours CST, we systematically located nests by flushing adult birds using a 25-m weighted rope with tin cans attached every 0.5 m, pulled between two people. We also located nests fortuitously and by using behaviors of adult birds as cues to locations of nests (e.g.

carrying food). We marked nests using survey flags placed 3 m to the north and south of the nest, with the top of the flag placed just above the average height of the vegetation. To estimate nest age, we candled 1–2 eggs in each nest (Lokemoen and Koford 1996) or aged nestlings from voucher photographs of known-age young. We monitored each nest every 2–5 days until it either fledged young or failed. Nests survived the interval between visits if at least one egg or nestling was alive on the latter visit or if at least one young had fledged on or before the final visit. Within 1–3 days of predicted fledging, we visited the nest daily to minimize uncertainty in assigning the final nest fate. Nest visits rarely lasted >5 s and most nests were viewed from 1 to 3 m away. We used the behaviors of the parents (e.g. alarm calling, carrying food), presence of young near the nest, nestling age at the previous visit, evidence of nest disturbance, evidence of nestling mortality, and presence of feces or feather scales at the nest to classify nests as successful or failed. We censored nests that were probably abandoned as a result of researcher disturbance (e.g. nests abandoned with only one egg that had not been incubated).

Candidate models.—We expected that daily survival rates for nests of Clay-colored and Vesper sparrows were probably not constant but varied in relation to either nest age or date (or both). We used information-theoretic methods (Burnham and Anderson 2002) to evaluate 24 candidate models that explained variation in daily nest survival. In addition to a model that assumed constant daily survival, we considered models that included (1) either a linear, quadratic, or cubic effect of age; (2) either a linear or quadratic effect of date; (3) a categorical year effect; and (4) all combinations of age, date, and year effects. We use the term “quadratic effect” when referring to polynomial models that included both linear (x) and quadratic (x^2) terms. Similarly, “cubic effect” refers to a model that involved linear, quadratic, and cubic (x^3) terms. We believed that the relationship between daily survival rate and age could be different during egg laying, incubation, and brood rearing, thus making a cubic effect of age plausible. We considered a quadratic effect of date because some studies have reported nest survival to be higher at mid-season than at the start or end of the breeding season (e.g. Zimmerman 1984, Burhans et al. 2002). Our

global model included year, a cubic effect of age, and a quadratic effect of date.

Modeling and estimating nest survival.—We used the logistic-exposure method (Shaffer 2004) to fit each of 24 candidate models. Logistic-exposure models are similar to logistic-regression models in that daily survival rate for any nest on a given day is modeled as a logistic function of the values of explanatory variables for the nest on that day. We used the GENMOD procedure of SAS Institute (1997) to estimate the regression coefficients in our logistic-exposure models (Shaffer 2004). We then estimated daily survival rates from the resulting logistic function (see Shaffer 2004 for details). Each interval between visits to a nest was treated as one observation in the analysis. Explanatory variables were based on nest age and date at the interval midpoint. Period survival rates were calculated as the product of daily survival rates during egg laying, incubation, and brood rearing. We used periods of 4 days for egg laying and 11 days for incubation for both species, and 7 and 9 days for brood rearing for Clay-colored and Vesper sparrows, respectively.

We used the Hosmer and Lemeshow goodness-of-fit test to assess the fit of the global model (Hosmer and Lemeshow 2000). We identified a best model for each species by choosing the candidate model with the smallest value of Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002). We used the effective sample size (n ; Rotella et al. 2004) to compute AIC_c (i.e. n = total number of days that nests were known to survive + total number of intervals in which a failure occurred). We employed model averaging to guard against potential effects of model-selection uncertainty (Burnham and Anderson 2002); but because model-averaged estimates of parameters and their standard errors were similar to estimates from the best model, we report estimates of both daily and period survival from the best model. We compared AIC_c values and period survival estimates from the best model with values and estimates derived from a logistic-exposure model that assumed constant survival within egg laying, incubation, and brood rearing. The latter survival estimates are akin to Mayfield (1961) estimates.

Estimating numbers of initiated nests.—We were interested in the relationship between timing of nest initiations and nest survival rates.

For this analysis to be meaningful, we needed to depict the temporal distribution of nest initiations for each species. Patterns of nest initiations constructed from samples of nests can be misleading unless they are adjusted for nests that do not survive long enough to be detected. Therefore, we used the Horvitz-Thompson method described by Dinsmore et al. (2002) to account for such nests. For example, consider a nest that was initiated on day 127 and discovered on day 130. The nest would be three days old when found. Denote the probability that a nest initiated on day 127 survives days 127, 128, and 129 as $\Psi = S_{127} S_{128} S_{129}$. We can think of the single nest found on day 130 as representing $(1/\Psi)$ initiated nests. We used the best model to estimate S_{127} , S_{128} , and S_{129} , and thus, Ψ . We then computed the expected number of nest initiations represented by the example nest as $1/\hat{\Psi}$. We applied the above logic to every nest in the sample, and used the expected number of nest initiations to compute the temporal distribution of initiated nests. We then plotted nest survival and expected nest initiations against date of the breeding season for both Clay-colored and Vesper sparrows.

RESULTS

We monitored the fates of 251 Clay-colored and 248 Vesper sparrow nests, resulting in effective sample sizes of 2,459 and 2,729, respectively. Median interval length between nest visits was three days for Clay-colored Sparrows and two days for Vesper Sparrows; 99% of all intervals were less than six days. The global model of nest survival provided an adequate fit for both Clay-colored Sparrows ($\chi^2 = 4.97$, $df = 8$, $P = 0.76$) and Vesper Sparrows ($\chi^2 = 4.29$, $df = 8$, $P = 0.83$).

The best model for both species included only a cubic effect of nest age (Tables 1 and 2). We also found support for models that included both a cubic effect of age and either a linear or a quadratic effect of date. Year effects were not important for either species. Overall, we found little support for models that did not include a cubic effect of age. The two species showed similar patterns in daily survival rates (Fig. 1). Daily survival rates increased from first egg laid to early incubation, but precision of survival rate estimates was low for the first two days of egg laying, especially for Vesper Sparrows. Daily survival decreased during incubation

TABLE 1. Model-selection results for the top six logistic-exposure models of daily survival rate for Clay-colored and Vesper sparrow nests in north-central North Dakota in 1997, 1998, and 2002. Twenty-four candidate models were considered. $\text{Log}_e(L)$ is the value of the maximized log-likelihood function, K is number of parameters in the model, AIC_c is Akaike's Information Criterion for small samples, ΔAIC_c is the scaled value of AIC_c , and w_i is the Akaike weight. AGE^2 = quadratic polynomial effect of age, AGE^3 = cubic polynomial effect of age, DATE = linear effect of date, DATE^2 = quadratic polynomial effect of date, and YEAR = categorical year effect.

Model	$\text{Log}_e(L)$	K	AIC_c	ΔAIC_c	w_i
Clay-colored Sparrow					
AGE^3	-390.1	4	788.3	0.0	0.50
$\text{AGE}^3 + \text{DATE}$	-389.8	5	789.5	1.3	0.27
$\text{AGE}^3 + \text{DATE}^2$	-389.7	6	791.5	3.2	0.10
$\text{AGE}^3 + \text{YEAR}$	-390.0	6	792.1	3.8	0.08
$\text{AGE}^3 + \text{DATE} + \text{YEAR}$	-389.6	7	793.2	5.0	0.04
$\text{AGE}^3 + \text{DATE}^2 + \text{YEAR}$	-389.5	8	795.1	6.8	0.02
Vesper Sparrow					
AGE^3	-334.1	4	676.1	0.0	0.30
$\text{AGE}^3 + \text{DATE}$	-333.2	5	676.3	0.2	0.27
$\text{AGE}^3 + \text{DATE}^2$	-332.9	6	677.8	1.7	0.13
AGE^2	-336.5	3	679.1	3.0	0.07
$\text{AGE}^2 + \text{DATE}$	-335.6	4	679.2	3.0	0.07
$\text{AGE}^3 + \text{YEAR}$	-333.8	6	679.6	3.4	0.05

TABLE 2. Parameter estimates for the two best logistic-exposure models of daily survival rate for Clay-colored and Vesper sparrow nests in north-central North Dakota in 1997, 1998, and 2002.

Parameter	Clay-colored Sparrow		Vesper Sparrow	
	Estimate	95% confidence limits	Estimate	95% confidence limits
Best model				
Intercept	1.050	-0.256 to 2.355	3.139	0.831 to 5.446
AGE	0.818	0.392 to 1.244	0.348	-0.259 to 0.954
AGE^2	-0.087	-0.128 to -0.046	-0.045	-0.094 to 0.004
AGE^3	0.003	0.001 to 0.004	0.001	0 to 0.003
Second-best model				
Intercept	2.054	-0.547 to 4.655	4.657	1.459 to 7.856
AGE	0.812	0.386 to 1.237	0.346	-0.263 to 0.955
AGE^2	-0.086	-0.127 to -0.046	-0.045	-0.094 to 0.004
AGE^3	0.003	0.001 to 0.004	0.001	0 to 0.003
DATE	-0.006	-0.019 to 0.007	-0.009	-0.022 to 0.004

to a low shortly after hatch, then increased throughout brood rearing for both species (Fig. 1). From initiation through mid-brood-rearing, Vesper Sparrow nests had higher daily survival rates than Clay-colored Sparrow nests. The two species had similar daily survival rates during later brood rearing.

The cubic-age model was vastly superior to the model that assumed constant survival within each stage (Clay-colored Sparrow: $\Delta\text{AIC}_c = 21.5$; Vesper Sparrow: $\Delta\text{AIC}_c = 13.3$). However,

estimates of period survival from the cubic-age model and the stage-specific constant-survival model were fairly similar: egg laying (Clay-colored Sparrow: 0.70 vs. 0.80; Vesper Sparrow: 0.86 vs. 0.88), incubation (Clay-colored Sparrow: 0.60 vs. 0.57; Vesper Sparrow: 0.72 vs. 0.71), brood rearing (Clay-colored Sparrow: 0.66 vs. 0.65; Vesper Sparrow: 0.63 vs. 0.65).

The peak of nest initiations occurred during late May to early June for Clay-colored Sparrows (Fig. 2). A broader, less pronounced peak of

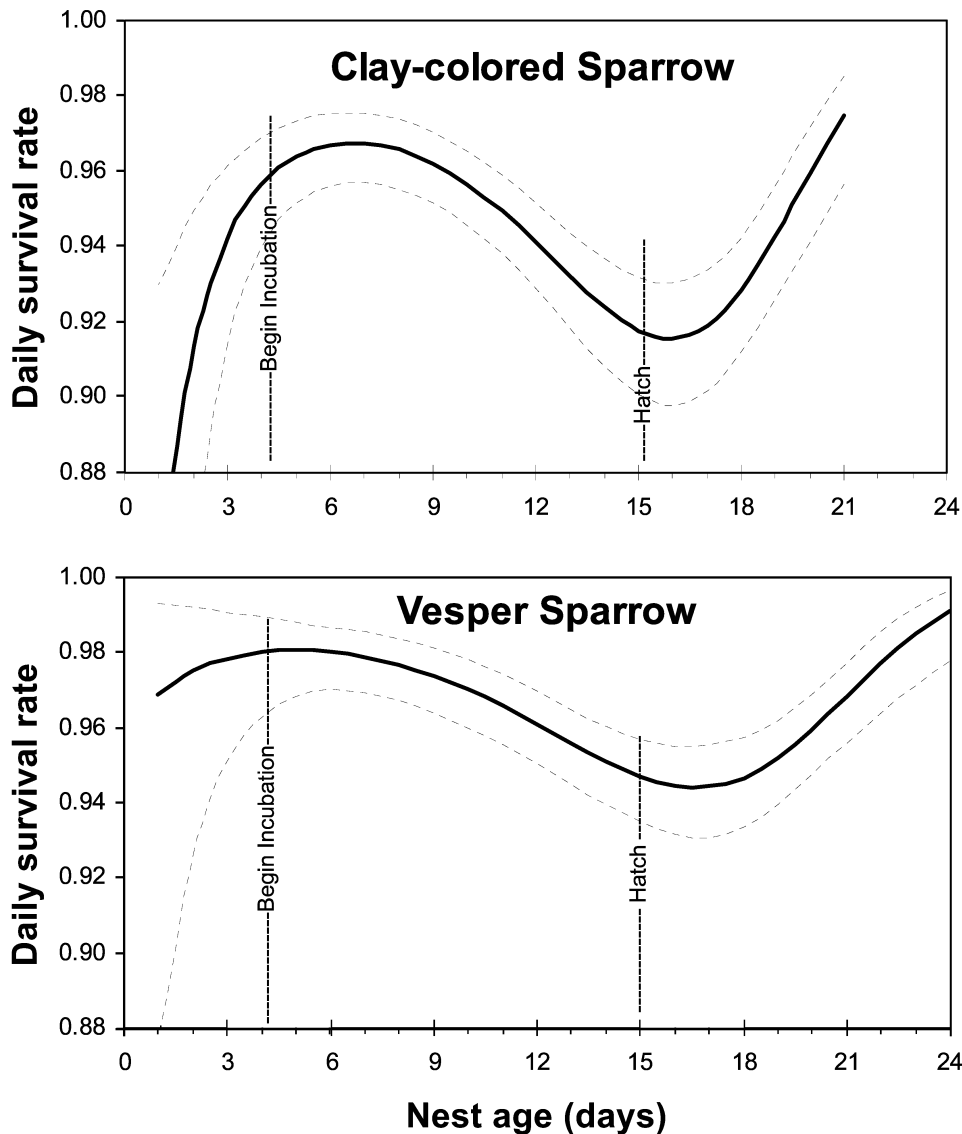


FIG 1. Daily survival rate of Clay-colored and Vesper sparrow nests in relation to nest age (days) in north-central North Dakota in 1997, 1998, and 2002. Dashed lines represent 95% confidence limits for the logistic-exposure model.

initiations occurred about 20–25 days later, presumably reflecting re-nests and second nest attempts. Vesper Sparrows initiated more nests early in the season than Clay-colored Sparrows and exhibited a more prolonged peak of both early and late nest initiations (Fig. 2). Both species initiated more nests early in the season when nest survival rates were highest (Fig. 2).

DISCUSSION

Age-specific nest survival.—Survival was not constant from nest initiation through fledging for either Clay-colored or Vesper sparrows (Fig. 1). Many researchers have calculated daily survival separately during incubation and brood rearing, acknowledging the potential for those

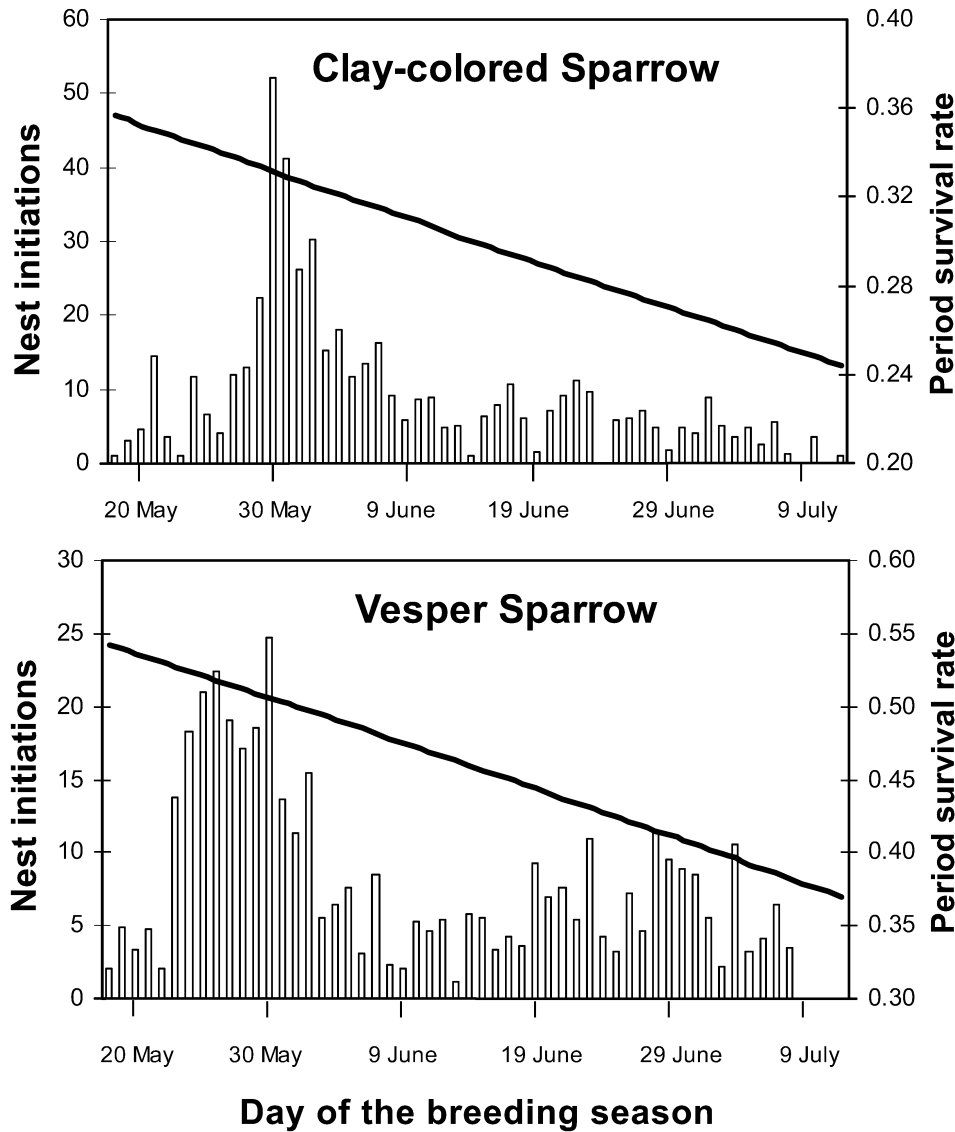


FIG 2. Number of nest initiations and 22-day nest-survival rates for Clay-colored Sparrows and 24-day nest-survival rates for Vesper Sparrows in relation to date in north-central North Dakota in 1997, 1998, and 2002. Solid lines denote the linear effect of date on the probability of a nest surviving until fledge. Shaded bars indicate the expected number of nests initiated on each date. Expected initiations account for nests that did not survive long enough to be found.

stages to have different mortality rates. No obvious mortality patterns have emerged from those stage-specific comparisons. In grassland habitats, for example, some studies report higher mortality during incubation (e.g. Dixon 1978, Knapton 1978, Zimmerman 1984, Winter 1999), whereas other studies report higher mor-

tality during brood rearing (e.g. O'Grady et al. 1996, Patterson and Best 1996, Davis 2003, Lloyd 2003); many studies report no difference in mortality rates between incubation and brood rearing (e.g. Wray et al. 1982, Zimmerman 1984, Hughes et al. 1999, Winter 1999, Pietz and Granfors 2000, Davis 2003).

The lack of consensus among studies may reflect true biological differences (e.g. among species, regions, habitats, or predator communities). In some cases, however, spurious differences could result, or real differences go undetected, if survival varies within nest stages or if small samples limit the power to detect those differences. Mayfield's estimator assumes constant survival within nest stages, and major violations of that assumption can lead to biased estimates (Klett and Johnson 1982). Although nest survival in our study was clearly not constant within laying, incubation, or brood rearing (Fig. 1), estimates of period survival rates derived by assuming constant survival within each stage did not appear to be seriously biased. That may not always be the case. More importantly, survival curves generated for Clay-colored and Vesper sparrows using the logistic-exposure method offer more insight into patterns of nest survival than estimates that assume constant survival.

Several researchers have presented simple, descriptive age-specific survival plots for eggs and nestlings (e.g. Young 1963; Holcomb 1969, 1972; Robertson 1972; Thompson and Nolan 1973; Beaver 1975; Caccamise 1976; Best 1978). Relatively few studies have attempted to examine daily nest survival within nest stages (Willis 1973, Schaub et al. 1992, Morton et al. 1993, Cresswell 1997, Halupka 1998a, Pietz and Granfors 2000). Our use of the cubic function to describe the relationship between nest survival rate and nest age may be unique in the passerine literature. Polynomial models such as our cubic-age model should be considered only when there is a biological basis for doing so (e.g. use of a cubic-age model may not be appropriate for estimating survival of a precocial species or for nests of altricial species that are not monitored beyond hatching). Even then, those models should not be applied without also considering simpler, lower-degree polynomial models. We recommend that investigators carefully evaluate model fit when using higher-order polynomials, such as the cubic function. That can be done by grouping observation intervals on the basis of nest age and visually comparing daily survival rates computed for each age group to fitted values from the polynomial model. We did this for our cubic-age models, and though there was considerable variability, the patterns depicted were similar to those in Figure 1.

Estimated daily survival rates during egg laying were less precise than during incubation and brood rearing (Fig. 1), probably reflecting smaller samples obtained during egg laying. The median age of nests at discovery in our sample was five and six days for Clay-colored and Vesper sparrows, respectively. When age-related survival patterns are complex, the need to locate nests as early as possible during egg laying is clear.

Although nest survival rates of Clay-colored and Vesper sparrows differed in amplitude, the species showed remarkable similarity in the complex pattern between nest survival and nest age. Given that many differences exist between those species (e.g. in nest site selection, overall nest success, egg crypsis, and taxonomy), that similarity suggests that there may be some generalities in the pattern they shared. In the discussion below, we offer some potential explanations for the age-specific pattern of nest survival we observed. Our exploration of the topic is not intended to be exhaustive; we merely highlight some of the many possible mechanisms that might have shaped this pattern of nest survival. Because few studies have examined age effects at such fine temporal scales, much of the following discussion is speculative.

Recall that estimated nest survival rates increased from the first egg laid through early incubation, especially for Clay-colored Sparrows (Fig. 1). Nest losses because of parental abandonment (in response to predators, brood parasites, or other disturbances) are assumed to decrease with greater parental investment (i.e. as more eggs are laid; Sowls 1955, Livezey 1980, Clark and Robertson 1981). Increasing survival through egg laying also may reflect the greater likelihood that eggs will be covered by an adult as the nest approaches clutch completion (Kendeigh 1952). An adult on the nest may provide protection by camouflaging eggs, deterring brood parasites, and defending against nest predators (Klett and Johnson 1982, Sealy et al. 1995).

Daily nest survival rates in our study decreased steadily during incubation (Fig. 1). Analysis of videotapes from camera-monitored nests (Pietz and Granfors 2000) showed that Clay-colored Sparrows increase their frequency of nest visits from early to late incubation (P. J. Pietz unpubl. data). Increased nest visits by

parents may provide cues to predators (Conway and Martin 2000, Martin et al. 2000), making it more likely that a predator will find the nest. Decreased survival through incubation may also reflect an additive exposure to risk. The longer a nest is active, the more likely it will lose eggs to predation, weather, and other factors, and the greater the chance that cumulative losses of individual eggs will result in total nest loss (i.e. no viable eggs remaining). Those cumulative factors should result in a higher rate of nest loss later in incubation. The same argument could apply to nestling losses during brood rearing.

Daily nest survival rates for Clay-colored and Vesper sparrows were lowest shortly after hatch (Fig. 1). That pattern may reflect the sudden increase in visual and auditory cues associated with parental foraging trips; or the increase in visual, auditory, and olfactory cues associated with newly hatched young. Those cues would increase vulnerability to predation and potentially increase the number of predator species capable of detecting the nest.

Nest survival increased throughout brood rearing (Fig. 1), possibly for a number of reasons: (1) Older nestlings are less vulnerable to inclement weather than younger nestlings (e.g. thermoregulatory capabilities and protective feathering increase with age). (2) As nestlings approach fledging age, parents may more vigorously defend them (Montgomerie and Weatherhead 1988), especially if the probability of survival decreases for re-nesting attempts later in the season (Fig. 2). (3) As nestlings grow, fewer predators will be capable of taking all of the young. Some smaller predators either will not attack or will fail in their attacks as nestlings increase in size and strength. (4) Older nestlings sometimes escape predator attacks by prematurely leaving the nest ("forced fledging," *sensu* Pietz and Granfors 2000); thus, the likelihood of predator-induced nest failure (i.e. total brood loss) decreases with nestling age (Halupka 1998b). As a result of forced fledging, even studies that showed an increase in predator attacks later in brood rearing (Halupka 1998a, Pietz and Granfors 2000) did not find an increase in nest failure with nestling age. In fact, the relatively short brood-rearing period of many grassland passerines may be an adaptation to escape late-stage predation (Martin 1995, Yanes and Suarez 1997, Halupka 1998b).

It is likely that multiple factors influence age-specific patterns of nest survival. For any age-specific period, the observed pattern probably represents the net effect of factors that decrease survival and factors that increase survival. For example, forces that increased Clay-colored and Vesper sparrow survival with nestling age were apparently stronger than forces that should have pushed the pattern in the opposite direction. Chief among those opposing forces is activity at the nest. Feeding rate, for example, generally increases as nestlings get older (e.g. Kendeigh 1952, Nolan 1978, Bédard and Meunier 1983, Carey et al. 1994), and increased parental visits to the nest are assumed to increase predation risk (Skutch 1949, Martin et al. 2000). Nestling activity, such as begging, may also increase with nestling age, but its effects on predation risk may be nullified by changes in the behavior of nestlings as they mature (i.e. less uncontrolled movement, cessation of vocalization and movement in the presence of intruders; T. A. Grant and E. M. Madden pers. obs.). Cumulative exposure to risk is another factor that should push nest success in the opposite direction to that which we observed during brood rearing. As nestling age increases, there is more time for nestling attrition to result in loss of the entire brood and for an accumulation of cues to lead to nest discovery by a predator.

Despite the compelling similarity here between Clay-colored and Vesper sparrows' age-specific nest survival, the pattern is unlikely to be universal. Descriptive evidence suggests that different age-specific mortality patterns exist for other species in other locations (e.g. Young 1963; Holcomb 1969, 1972; Robertson 1972; Thompson and Nolan 1973; Caccamise 1976; Nolan 1978). Given the strong influence of predation on nest survival rates (e.g. Ricklefs 1969, Martin 1992), pattern variability may reflect differences in predator types and densities among sites, habitats, and years.

Date-specific patterns of nest initiation and survival.—Effects of date on nest survival have been analyzed in relatively few passerine studies, especially in grasslands (but see Roseberry and Klimstra 1970, Zimmerman 1984, Winter 1999). Some researchers have examined differences among early, middle, and late segments of the breeding season (Burhans et al. 2002) or among 2- to 5-day intervals during the breeding

season (Beaver 1975, Nolan 1978, Zimmerman 1984, Schaub et al. 1992).

In our study, nest survival declined throughout the breeding season for both Clay-colored and Vesper sparrows. Both species initiated most of their nests early in the season, when nest success was relatively high (Fig. 2). Early nesting in the region may be an adaptation to avoid higher predation rates later in the season and may explain why the earlier-nesting Vesper Sparrow had higher overall nest success than the Clay-colored Sparrow. In our study, the decline in nest success with date may correspond to an increase in predator abundance, especially of thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), and an increase in predator movement (post-reproductive adults and dispersing juveniles) later in the season (N. Kadmas, U.S. Fish and Wildlife Service unpubl. data). However, there are other compelling reasons to nest early. For example, the earlier a pair nests, the more time they have to renest if their first nest is destroyed or to raise a second brood if their first nest is successful. Second broods are well documented for both species (Knapton 1994, Jones and Cornely 2002); in northern latitudes, they may nest as soon as insect emergence provides adequate food to support egg production. In Kansas, however, Zimmerman (1984) showed that Dickcissel (*Spiza americana*) nest initiations peaked in mid-season and daily predation rates peaked slightly later. In tallgrass prairie fragments in Missouri, Winter (1999) found no relationship between nest success and date for either Dickcissels or Henslow's Sparrows (*Ammodramus henslowii*). She found markedly different patterns of nest initiation for the two species; Dickcissel nesting peaked in early June, whereas Henslow's Sparrows showed two peaks, one in mid-May and another in late June. In pastures and hay fields in Illinois, Roseberry and Klimstra (1970) observed a pattern of nest initiation for Eastern Meadowlarks (*Sturnella magna*) that was similar to the pattern described for the two sparrows in our study. However, Eastern Meadowlark nest losses to predation appeared to be lower later in the season. In Wisconsin, Lanyon (1957) reported that both Eastern Meadowlarks and Western Meadowlarks (*S. neglecta*) appeared to have greater nest success in the second half of the season, which was possibly related to increased protective cover. Variations in patterns of nest success in relation to date among those studies

may reflect a number of differences among sites, including the composition of predator communities.

Recommendations.—Our data and those of others suggest that researchers should not assume constant survival in relation to nest age or initiation date for any avian species. Some aspects of the patterns that we documented may reflect general, long-term adaptations in passerines; others may reflect species-specific and site-specific adaptations of Clay-colored and Vesper sparrows to local nest predators. By examining age- and date-specific patterns of survival among other passerine species and for other sites, we may gain a better understanding of how widespread or unique those patterns are. We could then formulate biological hypotheses that might help explain those patterns. With these goals in mind, we hope other researchers will examine their nesting data using methods that allow survival rates to be reported as continuous functions of age and date. We strongly encourage researchers to document nest age as precisely as possible (e.g. by candling eggs) and to locate nests early in the egg-laying stage and throughout the breeding season to facilitate time-specific analyses of survival.

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LITERATURE CITED

- BEAVER, D. L. 1975. Breeding success of early- and late-nesting Red-winged Blackbirds in a Michigan oldfield. *Jack-Pine Warbler* 53: 86–94.
- BÉDARD, J., AND M. MEUNIER. 1983. Parental care in the Savannah Sparrow. *Canadian Journal of Zoology* 61:2836–2843.
- BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. *Auk* 95:9–22.
- BURHANS, D. E., D. DEARBORN, F. R. THOMPSON III,

- AND J. FAABORG. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66:240–249.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multimodel Inferences: A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.
- CACCAMISE, D. F. 1976. Nesting mortality in the Red-winged Blackbird. *Auk* 93:517–534.
- CAREY, M., D. E. BURHANS, AND D. A. NELSON. 1994. Field Sparrow (*Spizella pusilla*). In *The Birds of North America*, no. 103 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- CLARK, K. L., AND R. J. ROBERTSON. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. *Wilson Bulletin* 93:249–258.
- CONWAY, C. J., AND T. E. MARTIN. 2000. Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution* 54:670–685.
- CRESSWELL, W. 1997. Nest predation rates and nest detectability in different stages of breeding in blackbirds *Turdus merula*. *Journal of Avian Biology* 28:296–302.
- DAVIS, S. K. 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. *Wilson Bulletin* 115:119–130.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- DIXON, C. L. 1978. Breeding biology of the Savannah Sparrow on Kent Island. *Auk* 95:235–246.
- GRANT, T. A., AND G. B. BERKEY. 1999. Forest area and avian diversity in fragmented aspen woodland of North Dakota. *Wildlife Society Bulletin* 27:904–914.
- HALUPKA, K. 1998a. Nest predation in Meadow Pipits *Anthus pratensis* nesting in natural conditions. *Ornis Fennica* 75:139–143.
- HALUPKA, K. 1998b. Partial nest predation in an altricial bird selects for the accelerated development of young. *Journal of Avian Biology* 29:129–133.
- HOLCOMB, L. C. 1969. Age-specific mortality of American Goldfinch nestlings. *Auk* 86:760–761.
- HOLCOMB, L. C. 1972. Nest success and age-specific mortality in Traill's Flycatchers. *Auk* 89:837–841.
- HOSMER, D. W., AND S. LEMESHOW. 2000. Logistic Regression, 2nd ed. John Wiley and Sons, New York.
- HUGHES, J. P., R. J. ROBEL, K. E. KEMP, AND J. L. ZIMMERMAN. 1999. Effects of habitat on Dickcissel abundance and nest success in Conservation Reserve Program fields in Kansas. *Journal of Wildlife Management* 63:523–529.
- JOHNSON, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96:651–661.
- JONES, S. L., AND J. E. CORNELLY. 2002. Vesper Sparrow. In *The Birds of North America*, no. 624 (A. Poole and F. Gill, Eds.). The Birds of North America, Philadelphia.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. *Illinois Biological Monographs*, no. 22.
- KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77–87.
- KNAPTON, R. W. 1978. Breeding ecology of the Clay-colored Sparrow. *Living Bird* 17:137–158.
- KNAPTON, R. W. 1994. Clay-colored Sparrow. In *The Birds of North America*, no. 120 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. *Publications of the Nuttall Ornithological Club*, no. 1.
- LIVEZEY, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. *Wildlife Society Bulletin* 8:123–128.
- LLOYD, J. D. 2003. Avian life history evolution: Explaining variation among species, populations, and individuals. Ph.D. Dissertation, University of Montana, Missoula.
- LOKEMOEN, J. T., AND R. R. KOFORD. 1996. Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology* 67:660–668.
- MARTIN, T. E. 1992. Breeding productivity considerations: 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. 1995. Avian life history evolution

- in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London, Series B* 269:309–316.
- MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B* 267:2287–2293.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology* 63:167–187.
- MORTON, M. L., K. W. SOCKMAN, AND L. E. PETERSON. 1993. Nest predation in the Mountain White-crowned Sparrow. *Condor* 95:72–82.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs*, no. 26.
- O'GRADY, D. R., D. P. HILL, AND R. M. R. BARCLAY. 1996. Nest visitation by humans does not increase predation on Chestnut-collared Longspur eggs and young. *Journal of Field Ornithology* 67:275–280.
- PATTERSON, M. P., AND L. B. BEST. 1996. Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. *American Midland Naturalist* 135:153–167.
- PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71–87.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, no. 9.
- ROBERTSON, R. J. 1972. Optimal niche space of the Redwinged Blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. *Canadian Journal of Zoology* 50:247–263.
- ROSEBERRY, J. L., AND W. D. KLIMSTRA. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. *Wilson Bulletin* 82:243–267.
- ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187–205.
- SAS INSTITUTE. 1997. SAS/STAT software: Changes and enhancements through release 6.12. SAS Institute, 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.
- SEALY, S. G., D. L. NEUDORF, AND D. P. HILL. 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. *Ibis* 137:76–84.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455.
- SOWLS, L. K. 1955. *Prairie Ducks*. Stackpole Company, Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, D.C.
- THOMPSON, C. F., AND V. NOLAN, JR. 1973. Population biology of the Yellow-breasted Chat (*Icteria virens* L.) in southern Indiana. *Ecological Monographs* 43:145–171.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Academic Press, New York.
- WILLIS, E. O. 1973. Survival rates for visited and unvisited nest of Bicolored Antbirds. *Auk* 90:263–267.
- WINTER, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. *Wilson Bulletin* 111:515–527.
- WRAY, T., II, K. A. STRAIT, AND R. C. WHITMORE. 1982. Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. *Auk* 99:157–164.
- YANES, M., AND F. SUAREZ. 1997. Nest predation and reproductive traits in small passerines: A comparative approach. *Acta Oecologica* 18:413–426.
- YOUNG, H. 1963. Age-specific mortality in the eggs and nestlings of blackbirds. *Auk* 80:145–155.
- ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. *Condor* 86:68–72.

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