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Do Ducks and Songbirds Initiate More Nests When the Probability of Survival is Greater?

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Nesting chronology in grassland birds can vary by species, locality, and year. The date a nest is initiated can influence the subsequent probability of its survival in some grassland bird species. Because predation is the most significant cause of nest loss in grassland birds, we examined the relation between timing of nesting and nest survival. Periods of high nest survival that correspond with the peak of nesting activity might reflect long-term adaptations to specific predation pressures commonly recurring during certain periods of the nesting cycle. We evaluated this theory by comparing timing of nesting with date-specific nest survival rates for several duck and passerine species breeding in north-central North Dakota during 1998–2003. Nest survival decreased seasonally with date for five of the seven species we studied. We found little evidence to support consistent relations between timing of nesting undrest initiations, and nest survival for any species we studied, suggesting that factors other than nest predation may better explain nesting chronology for these species. The apparent mismatch between date-specific patterns of nest survival and nest initiation underscores uncertainty about the process of avian nest site selection driven mainly by predation. Although timing of nesting differed among species, the general nesting period was fairly predictable across all years of study, suggesting the potential for research activities or management actions to be timed to take advantage of known periods when nests are active (or inactive). However, our results do not support the notion that biologists can take advantage of periods when many nests are active and survival is also high.

Key Words: Grassland bird; nest survival; nest initiation; passerine; time-specific survival; waterfowl; Gadwall; Anas strepera; Mallard; Anas platyrhynchos; Blue-winged Teal; Anas discors; Northern Shoveler; Anas clypeata; Clay-colored Sparrow; Spizella pallida; Savannah Sparrow; Passerculus sandwichensis); Bobolink; Dolichonyx oryzivorus; North Dakota

Introduction

Although nesting chronology can vary by year, often in response to weather, nesting periods may be fairly predictable for a given bird species and locality when considered across many years. For many bird species, nest survival can vary with age of the nest, date in the nesting season, or year. Recent studies conducted in the northern Great Plains show that duck and passerine nest survival is influenced by the date a nest is initiated (Emery et al. 2005; Grant et al. 2005; Davis et al. 2006; Kerns et al. 2010; Grant and Shaffer 2012). More specifically, Grant et al. (2005) demonstrated that Claycolored Sparrow (Spizella pallida) and Vesper Sparrow (Pooecetes gramineus) nests initiated early in the season had higher survival rates than nests initiated later in the season. Furthermore, more nests were initiated during periods when survival also was high (see Figure 2 in Grant et al. 2005).

If timing of nesting is adaptive in terms of maximizing breeding success, we would expect that other grassland bird species would also initiate more nests when the probability of survival is greater. Such patterns might reflect long-term adaptations by bird species in response to specific risks of nest predation that recur during certain periods of the nesting cycle. Alternatively, individuals may recognize short-term risks to nest survival, thereby adjusting timing of nesting, perhaps by using environmental cues during the pre-nesting period (e.g., Eichholz and Elmberg 2014).

In this paper, we examine whether more nests are initiated during periods of higher nest survival. We describe patterns of nest initiation among ducks and passerines breeding in the northern mixed-grass prairie of northcentral North Dakota and determine the influence of nest age, nest initiation date, and year on nest survival. We then explore patterns of survival in relation to nest initiation date to determine whether the timing of nesting coincides with periods of higher or lower nest survival in a predictable fashion (Grant *et al.* 2005). We focused on seven common species nesting in North Dakota: Gadwall (*Anas strepera*), Mallard (*Anas platyrhynchos*), Blue-winged Teal (*Anas discors*), Northern Shov-

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eler (*Anas clypeata*), Clay-colored Sparrow, Savannah Sparrow (*Passerculus sandwichensis*), and Bobolink (*Dolichonyx oryzivorus*).

Study Area

Our study was conducted on the 23 900 ha J. Clark Salyer National Wildlife Refuge in Bottineau County, North Dakota (about 48°45'N, 100°50'W). The study site is a 450 ha tract of northern mixed-grass prairie, consisting of a needle grass-wheatgrass (Stipa-Pascopyrum) association intermingled with two exotic grasses, Kentucky Bluegrass (Poa pratensis L.) and Smooth Brome (Bromus inermis Leysser), and variably interspersed with short (< 1.0 m) brush dominated by Western Snowberry (Symphoricarposoccidentalis Hooker). Since the 1960s, prescribed burning of 100-200 ha blocks of the study area has been carried out every 2-12 years. The area is bordered by cropland adjacent to the refuge and by wetland impoundments of the Souris River. Climate is semi-arid to subhumid continental, with average monthly temperatures ranging from -15°C in January to 20°C in July. During our study, annual precipitation was similar to the long-term average of 43 cm.

Methods

Modeling nest survival: the importance of nest initiation date

From mid-April to late July, 1998-2003, we systematically searched for and monitored nests of grassland birds using the methods of Grant and Shaffer (2012). We used the logistic-exposure method for estimating daily nest survival probabilities using nest initiation date and nest age as time-varying explanatory variables (see Shaffer 2004; Grant et al. 2005). Daily nest survival is the probability a nest survives a given day, conditional on it being active at the beginning of that day. A nest survives the interval between visits if at least one egg or nestling is alive on the latter visit or if at least one egg hatched (ducks) or young fledged (passerines) on or before the final visit. For each interval, we assigned midpoint values of nest age and date observed at the beginning of the interval. We used PROC GEN-MOD (SAS Institute Inc., Cary, North Carolina, USA) to fit logistic exposure models following the procedures of Shaffer (2004).

We used an information-theoretic approach and Akaike's information criterion adjusted for sample size (AIC_c) to identify candidate models that best described the data (i.e., those with the lowest AIC_c score; Burnham and Anderson 2002). We also used the Akaike model weight (w_i), which represents evidence in support of a particular model, given the data and the candidate models considered (Burnham and Anderson 2002: 75). We used the effective sample size, *effn* (Rotella *et al.* 2004) to compute AIC_c (where *effn* = total number of days that nests were known to survive + total number of intervals in which a failure occurred).

Following Grant and Shaffer (2012), we considered six basic models when assessing the relation between daily nest survival and nest age (i.e., number of days from laying of the first egg): (1) constant survival, (2) stage-specific constant survival, (3) survival linearly related to age, (4) stage-specific linear survival, (5) survival non-linearly related to age via a quadratic polynomial function, and (6) survival non-linearly related to age via a cubic polynomial function (only for passerines to allow for differential survival during laying, incubation, or brood-rearing periods). We considered three basic models for describing the relation between daily nest survival and date: (1) constant survival, (2) survival linearly related to date, and (3) survival non-linearly (quadratic polynomial) related to date.

We used combinations of the above to assess 15 and 18 candidate models for each duck and passerine species, respectively, using a multi-step process described in Grant and Shaffer (2012: 321). We first determined whether plot and year effects were important (plot effects were relatively unimportant). When year effects were present, we looked to see if age and date patterns were consistent among years. The outcome of our analyses were species-specific daily nest survival models that accounted for effects of nest age, date in the breeding season, plot, and year; we report only the top two models for each species (Table 1).

Although consideration of time-specific effects was not the focus of this paper and these are described elsewhere (Grant and Shaffer 2012), we needed to account for the influence of nest initiation date on nest survival rates. To investigate the relation between nest initiation date (i.e., the date the first egg was laid) and nest survival, we computed "period survival," as the probability a nest survives the period from nest initiation (on any particular date in the nesting cycle) through hatching of the first egg (ducks) or fledging of the first young (passerines). We calculated period survival as the product of daily survival rates for each day in the nest cycle using available literature, where number of days for egg laying, incubation, and/or brood-rearing is known with some certainty. For example, the nesting cycle for Claycolored Sparrow consisted of 4 days egg laying, 11 days incubation, and 7 days brood-rearing (22 days total). When daily survival varies with ordinal date, period survival varies with nest initiation date (Shaffer and Thompson 2007). We used equation 2 in Shaffer and Thompson (2007) to estimate period survival in relation to nest initiation date from model-averaged daily survival rates:

$P_{j} = S_{j1} S_{(j+1)2} \cdots S_{(j+k-1)k},$

where P_j is the period survival rate of a nest initiated on day *j* and S_{ji} is daily survival rate on day *j* of an *i*-day-old nest (i = 1 to *k*).

Estimating the number of nests initiated by date

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To relate timing of nesting to nest survival, we had to depict the temporal distribution of nests initiated

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TABLE 1. Best models ($w_i > 0.10$) that relate daily nest survival to age of the nest, date of the breeding season, and year for
ducks and passerines nesting in North Dakota, 1998–2003. K is number of parameters in the model, $\log_{10}(L)$ is the value of
the maximized log-likelihood function, AIC, is Akaike's information criterion for small samples, ΔAIC , is the scaled value
of AIC, w_i is the Akaike weight, n is the number of nests, and <i>effn</i> is effective sample size.

Model	K	$Log_e(L)$	ΔAIC_{c}	w _i
Gadwall, Anas strepera				
(n = 501, effn = 5805)*				
Year, Date ² , Year×Date ²	18	-552.86	0.00	0.51
Year, Plot, Date ² , Year×Date ²	24	-547.43	1.24	0.27
Mallard, Anas platyrhynchos				
(n = 314, effn = 3033)				
Year, Age ² , Date	9	-304.22	0.00	0.35
Year, Age, Date, Year×Age, Year×Date	18	-295.36	0.46	0.28
Blue-winged Teal, Anas discors				
(n = 622, effn = 7673)				
Year, Date, Year×Date	12	-667.83	0.00	0.61
Year, Age ² , Date, Year×Age ² , Year×Date	24	-667.51	3.48	0.11
Northern Shoveler, Anas clypeata				
(n = 175, effn = 2018)				
Year, Stage-const.	7	-160.15	0.00	0.26
Year, Plot, Stage-const.	13	-154.17	0.17	0.24
Clay-colored Sparrow, Spizella pallida				
(n = 713, effn = 7413)				
Year, Age ³	9	-1095.75	0.00	0.89
Year, Stage-line	11	-1095.84	4.18	0.11
Savannah sparrow, Passerculus sandwichensis				
(n = 635, effn = 5925)				
Year, Age ³ , Date	10	-1107.30	0.00	0.71
Year, Age ³	9	-1109.55	2.49	0.21
Bobolink, Dolichonyx oryzivorus				
(n = 142, effn = 1207)				
Stage-line	6	-220.48	0.00	0.30
Plot, Stage-line	12	-214.90	1.02	0.18

*AIC_c of best models are Gadwall = 1141.83, Mallard = 626.49, Blue-winged Teal = 1379.70, Northern Shoveler = 334.36, Clay-colored Sparrow = 2209.53, Savannah Sparrow = 234.65, and Bobolink = 453.04.

throughout the breeding season. Patterns of nest initiation constructed from samples of nests can be misleading unless they are adjusted for nests that do not survive long enough to be detected (e.g., nests that are depredated during egg laying but before nest searching, where presence of the female is the primary cue for locating nests). We used the Horvitz-Thompson method (Dinsmore *et al.* 2002; Shaffer and Thompson 2007) to account for such nests (see example in Grant *et al.* 2005: 664).

Relating period survival to number of nests

We used the estimates of period survival and number of nest initiations by date as described above to look for relationships by graphically superimposing period survival rates on the number of expected nest initiations by date in the breeding season (e.g., see Figure 2 in Grant *et al.* 2005). If timing of nesting reflected enhanced nest survival based on long-term predator–prey dynamics, we might expect this relation to be consistent across the 6 years we studied and, therefore, evident using simple graphical comparisons. We recognized that number and timing of nest initiations and nest survival rates might vary among years (related to climate, predators, brood parasites, etc.), and that these variations had potential to complicate such simple graphical comparisons, especially when examined across six nesting seasons. In addition, some species might be able to recognize specific risks to survival occurring before nest initiation. In either case, the relation between timing of nesting and nest survival could vary among years. To account for this sort of variation, we calculated Pearson correlation coefficients relating period survival rates to the number of nest initiations for each species—year combination (42 possible combinations). We did not calculate correlation coefficients in cases where survival was not influenced by nest initiation date.

Results

During 1998–2003, we determined the fates of 3102 nests. For all species, survival varied with age of the nest, initiation date, or year (Table 1). Age and year effects were not the primary focus of our analysis and are discussed elsewhere (Grant and Shaffer 2012). The peak of nesting for all duck species was early May to mid-June. For Gadwall, Mallard, and Blue-winged Teal, but not for Northern Shoveler, nest survival declined with initiation date (Figure 1). Mallard and Northern Shoveler initiated nests earlier in the breeding season than Blue-winged Teal and Gadwall. The timing of peak





FIGURE 1. Estimated number of nest initiations and period nest survival rates for (A) Gadwall (*Anas strepera*), (B) Blue-winged Teal (*Anas discors*), (C) Mallard (*Anas platyrhynchos*), and (D) Northern Shoveler (*Anas clypeata*) in relation to ordinal date in North Dakota. Solid circles (with 95% confidence intervals) denote the estimated probability of a nest surviving from laying through hatch when initiated on specific dates that span the nesting period (mean 1998–2003). 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 discovered. Note: The estimated number of Gadwall nests initiated on days 122 and 123 were 875 and 540, respectively.

nest initiations did not correspond to periods of higher or lower survival for Mallard, Blue-winged Teal, or Northern Shoveler (Figure 1), but across all years, Gadwall appeared to initiate more nests during periods when survival also was high (Figure 1). We did not find a single year–species combination for any duck species where number of nest initiations was positively related (P < 0.05) to period survival (Table 2). In contrast, seven cases (three for Blue-winged Teal and two each for Mallard and Gadwall) showed a negative association between number of initiations and period survival.

Survival of Clay-colored Sparrow nests did not vary with initiation date, whereas survival of Savannah Spar-

TABLE 2. Pearson correlation coefficients relating period nest survival and number of nest initiations by date for ducks and passerines nesting in North Dakota, 1998–2003. More nests were initiated during periods of higher nest survival in cases where r > 0 and P < 0.05.

Species (no. nests)	1998	1999	2000	2001	2002	2003			
Gadwall, Anas strepera (501)	-0.50**	-0.25	-0.04	-0.19	-0.65**	-0.32			
Mallard, Anas platyrhynchos (314)	-0.50	-0.19	-0.05	-0.51**	-0.51**	-0.16			
Blue-winged Teal, Anas									
discors (622)	-0.37*	0.05	-0.47 * *	0.30	0.31	-0.35*			
Northern Shoveler, Anas									
clypeata (175)	Survival did not vary with initiation date								
Clay-colored Sparrow,			•						
Spizella pallida (713)	Survival did not vary with initiation date								
Savannah Sparrow,			•						
Passerculus sandwichensis (635)	0.17	0.39**	-0.01	0.22	0.30	0.28			
Bobolink, Dolichonyx									
oryzivorus (142)	0.48	0.14	-0.26	0.38	0.74	0.45			

*P < 0.05.

** P < 0.01.

row nests gradually declined from May through July (Figure 2). We found support for two models depicting decreasing nest survival with initiation date for Bobolink (Table 1). Passerines initiated nests 10-20 days later than ducks. Savannah Sparrow and Clay-colored Sparrow initiated nests earlier in the season than Bobolink (Figure 2). Except for Savannah Sparrow, renesting or second brood periods were not readily apparent. The nesting period for Bobolink started later in the spring and ended earlier in summer than that for either Clay-colored Sparrow or Savannah Sparrow. Savannah Sparrow and, perhaps, Bobolink initiated more nests early in the nesting season when survival was also high, although this relation was not compelling (Figure 2). In contrast to ducks, correlations between number of nest initiations and period survival were generally positive for Bobolink and Savannah Sparrow, although only one species-year combination was significant (Table 2).

Discussion

Nesting chronology

In North Dakota, the nest-initiation period for ducks generally spans 42-52 days (Cowardin et al. 1985; Lokemoen et al. 1990; Krapu 2000) and can be influenced by weather (Hammond and Johnson 1984; Drever and Clark 2007). Renesting among dabbling ducks is common if a first clutch or brood is destroyed; second broods have not been reported. In our study, Mallards initiated first nests in late April and, along with Northern Pintails (Anas acuta), are the first ducks to arrive on breeding sites in North Dakota (Hammond and Johnson 1984; Higgins et al. 1992). The peak of nest initiation for Mallards was 20 days later than reported for nearly the same location during 1936-1968 (Hammond and Johnson 1984). Dubowy (1996) described Northern Shoveler as among the latest of dabbling duck species to arrive on breeding sites. However, we found the timing and pattern of their nest initiations nearly identical to that of Mallards. Blue-winged Teals arrived slightly later than early-nesting dabbling ducks, but the pattern of their nest initiations was bell shaped, similar to that of Mallards and Northern Shovelers, and peaked about 10 days later than reported by Hammond and Johnson (1984). Gadwall is the latest arriving dabbling duck species in our region (Hammond and Johnson 1984; Lokemoen et al. 1990). Although early-season nests were initiated at later dates than other species in our study, Gadwall exhibited a greater proportion of all nests initiated early in the season, gradually declining with date (Figure 1) with the peak date similar to that described for the same location during 1936-1968 (Hammond and Johnson 1984).

The timing of nest initiations for Clay-colored Sparrows, Savannah Sparrows, and Bobolinks generally corroborates findings from recent studies in the northern Great Plains (Davis 2003; Winter *et al.* 2004; Jones *et al.* 2010; B. C. Dale, Canadian Wildlife Service, unpublished data). The Savannah Sparrow is among the



FIGURE 2. Estimated number of nest initiations and period nest survival rates for (A) Savannah Sparrow (*Passerculus* sandwichensis), (B) Clay-colored Sparrow (*Spizella* pallida), and (C) Bobolink (*Dolichonyx oryzivorus*) in relation to ordinal date in North Dakota. Solid circles (with 95% confidence intervals) denote estimated probability of a nest surviving from laying through fledging when initiated on specific dates that span the nesting period (mean 1998–2003). 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 discovered.

first passerine species to arrive on breeding sites and initiate nests in our area, followed about 7–10 days later by the Clay-colored Sparrow. Both species are persistent renesters after nest failure and can raise two clutches per season in the northern Great Plains (Wheelwright and Rising 2008; Grant and Knapton 2012). Despite the fact that individuals were not marked in our study, double-brooding can be inferred by a multimodal peak of nest initiations, clearly evident for the Savannah Sparrow. In contrast, Clay-colored Sparrows do not initiate second nests (after successfully fledging the first brood) every year; this practice depends on arrival dates or other site-specific factors not well understood (Grant and Knapton 2012). This may explain the lack of multimodal pattern of nest initiations across six years in our study. The Bobolink is among the last grassland songbird species to arrive in our area. Bobolinks initiate nests later and have a shorter breeding period (composed of a single concentrated peak of nesting) than either sparrow species. Although replacement clutches are common after nest failures, Bobolinks may be restricted to one brood per season in the northern portion of their range (Gavin 1984; Winter et al. 2004).

Nest survival

Survival can vary with age of the nest and nest initiation date in both grassland passerines and uplandnesting ducks, although time-specific patterns in survival rates are reportedly inconsistent among regions and species (Emery et al. 2005; Grant et al. 2005; Davis et al. 2006; Grant and Shaffer 2012). Survival was highest for nests initiated early in the breeding season for five of the seven species in our study. Nest survival has also been reported to be higher early in the season for ducks and passerines breeding elsewhere (Flint and Grand 1996; Winter et al. 2004; Emery et al. 2005; Thompson et al. 2012). Grant et al. (2005) observed a similar, but more compelling, pattern of survival relative to initiation date for Clay-colored Sparrow and Vesper Sparrow, as did R. K. Murphy (United States Fish and Wildlife Service, unpublished data) for Claycolored Sparrow and Savannah Sparrow nesting in northwestern North Dakota. Early nesting may have conferred survival advantages for grassland species in our study (reviewed in Grant and Shaffer 2012). Fitness may increase for females or broods if higher-quality nests are initiated early in the season (Blums et al. 2005), when the density of nests or nest predators is lower (Nams 1997; Grant et al. 2006) or in cases where predators, such as small mammals, are associated with specific vegetation height and density parameters that change throughout the season (e.g., Dion et al. 2000). For the Clay-colored Sparrow and Savannah Sparrow, early successful nesting increases the probability of double-brooding within the same nesting season. Furthermore, early-hatched offspring may have survival advantages over later-hatched young during both the pre- and post-fledging periods (Rohwer 1992; Amundson and Arnold 2011).

Is timing of nesting adaptive?

An adaptive response (in terms of long-term fitness) could be inferred if patterns of nest initiation corresponded with patterns of nest survival. Grant *et al.*

(2005) demonstrated that more nests were initiated early in the season when nest survival also was high (approximated by a linear decline in survival with date) for Clay-colored and Vesper Sparrows in North Dakota. In our study, Gadwalls and Clay-colored Sparrows initiated more nests early in the season, but evidence was at best equivocal regarding an adaptive response similar to that described by Grant et al. (2005). Alternatively, nest initiation patterns of the Savannah Sparrow, Mallard, Northern Shoveler, Blue-winged Teal, and Bobolink more closely approximated a normal distribution, with a greater proportion of nests initiated midseason. Nesting chronology did not consistently match patterns of nest survival for any species we studied; survival tended to be greater early in the season or was not influenced by date.

We conducted a separate correlation analysis that allowed the relation between timing of nesting and nest survival to vary among years for each species. This analysis reduced potential masking of year-specific relations between survival and initiations that may be meaningful (i.e., when data were considered across all 6 years of study). We found marginal evidence that timing of nesting was positively associated with nest survival, at least during some years, for the Savannah Sparrow and Bobolink but not for other species. In theory, negative correlations between nest initiations and period survival that we observed for ducks may reflect years when nest survival is low and renesting effort is high. When considered across all species-year combinations, this analysis provided scant evidence to suggest that any species we considered initiated more nests during periods when survival was greater.

Although predation was the main cause of nest failure in our study (T. A. G., unpublished data), our results indicate that nest predation was not the primary influence on timing of nesting for the species we considered. The apparent mismatch between date-specific patterns of nest survival and number of nest initiations in our study underscores uncertainty about general processes of avian nest site selection (timing of nesting in our case) as random or non-random events driven by predation risk (e.g., Chalfoun and Schmidt 2012). Given our results, factors other than nest survival may better explain nesting chronology for the species we considered. Chief among these are food availability for females or offspring; predation risk for nesting females, duck broods, or post-fledged passerines; climate effects on brood survival (e.g., heat stress) - factors for which we lack data to address (e.g., Drever and Clark 2007; Dunn et al. 2011). Understanding these relations may be further complicated in highly modified landscapes, such as ours, where evolutionary mechanisms that shaped nest site selection may no longer apply.

Conservation Implications

Few studies have examined factors that affect duck and songbird nesting simultaneously in the same location. Survival decreased with nest initiation date for five of the seven species we studied, and this pattern is also reflected in recent studies across multiple species within the region (Winter *et al.* 2004; Grant *et al.* 2005; Thompson *et al.* 2012; R. K. Murphy United States Fish and Wildlife Service, unpublished data). Although early nesting conveyed survival advantages for several species in our study, patterns of nest initiation did not match patterns of survival in any predictable fashion.

Timing and number of nest initiations in ducks can be partly predictable, based on age of the hen, spring temperatures, precipitation, or wetland availability (Hammond and Johnson 1984; Greenwood *et al.* 1995; Krapu 2000). Similar data for passerines are not available in our region, providing an opportunity and a need for additional study. For some duck species we studied, onset of nesting was later than historic data show for the same location, warranting additional study into the scope and significance of this phenomenon. Ducks initiated nests 10–20 days earlier than passerines, suggesting the potential for spring management activities to affect each taxonomic group differentially.

Knowledge about timing of nesting may allow biologists to identify benefits and consequences of proposed actions. For example, spring grazing or burning can reduce height and density of vegetation used as nesting cover, thereby altering density of bird nests. Furthermore, the presence of cattle during nest initiation can reduce nest densities in some grassland species, suggesting that managers may be able to adjust timing of grazing to reduce avoidance of an area when livestock are present (Bowen and Kruse 1993; Kruse and Bowen 1996). In northwestern North Dakota, grazing during May and June reduced nest densities for latearriving Blue-winged Teals and Gadwalls, but not for early breeding Mallards that initiated many nests before cattle were present (Kruse and Bowen 1996). Our data suggest that grazing could be delayed until after nesting is well underway in June, if bird nesting is the only consideration. Having on National Wildlife Refuges in North Dakota is programmatically delayed until 1 August to protect nesting birds. Based on our data, all duck and Bobolink nests and > 98% of Clay-colored and Savannah Sparrow nests would have been completed by this date.

Population monitoring in general and nest searching activities in particular are expensive and time consuming. We concur with recommendations from Grant *et al.* (2005) to locate nests early in the egg-laying stage and throughout the breeding season to facilitate timespecific analyses of survival. However, if resources are limited and time-specific effects are not of primary interest, monitoring and research activities could target periods when many nests of multiple species are active.

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