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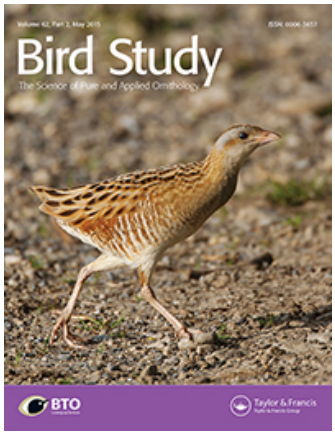


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Tara J. Conkling[a], Jerrold L. Belant[a], Travis L. DeVault[b], Guiming Wang[a] & James A. Martin[a]
[a] Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA
[b] United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Sandusky, OH 44870, USA
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# Assessment of variation of nest survival for grassland birds due to method of nest discovery

TARA J. CONKLING[1]*, JERROLD L. BELANT[1], TRAVIS L. DEVAULT[2], GUIMING WANG[1] and JAMES A. MARTIN[1,†]

[1]*Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA;* [2]*United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Sandusky, OH 44870, USA*

**Capsule** Interpretation of nest survival estimates may be improved by incorporating the search method used to locate nests as a covariate.

**Aims** To compare annual survival estimates for Dickcissel *Spiza americana* nests and determine if incorporating search method (structured, opportunistic, or behavioural searches) improved model fit.

**Methods** Dickcissel nests were located using structured, opportunistic, or behavioural searches over three years (2011–2013) in Mississippi, USA. Models were used to estimate daily survival rates (DSRs) and to analyse factors influencing nest survival.

**Results** DSRs for Dickcissels were best explained by quadratic date, nest age, age found, and year, but incorporating search method improved model fit. Daily survival was 1.51 times greater for nests located using opportunistic search methods relative to structured searches, but was not significantly different between structured and behavioural searches.

**Conclusions** Survival estimates varied by search method, specifically between structured searches and opportunistically located nests. This might have arisen because heterogeneity in nest placement or parental behaviour may influence the sample of nests located with a given search method. Researchers may be able to account for this potential source of bias by including search method as a model covariate when using standard survey designs or modelling approaches.

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Nest success is a central metric of many ornithological studies, and estimating nest survival is a well-studied statistical problem for ecologists (Mayfield 1975, Dinsmore *et al.* 2002). Accurate estimates of nest success are important for understanding population responses to habitat management, predation risk, and other perturbations. Researchers often assume (albeit implicitly) that estimates of nest success derived from the sample approximate the true population parameter that occurred during the study. This assumption is not testable under most circumstances, thus the 'true' population parameter (i.e. nest success) is only approximated through proper sampling and experimental design (Dinsmore *et al.* 2002, Shaffer & Thompson 2007). However, even in field studies using sound methodology, sources of heterogeneity influencing nest survival estimates can occur, including vegetation concealment, temporal and spatial variation in nest initiation dates or nest sites, and variation in the observer's ability to locate nests (Winter *et al.* 2000, 2006, Dinsmore *et al.* 2002, Rodewald 2004, Johnson 2007).

Detection of nests for grassland birds relies mainly on flushing incubating or brooding adults; heterogeneity in nest placement or parental behaviour in the presence of perceived predators may affect the probability of nests being detected (Burhans & Thompson 2001, Ghalambor & Martin 2001, Albrecht & Klvaňa 2004). Research on other taxa has demonstrated capture heterogeneity when sampling animal populations, most commonly with mark-recapture studies (Young *et al.* 1952, Carothers 1973, Williams

*Correspondence author. Email: tjc191@msstate.edu
†Present address: Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA.

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& Braun 1983, Pledger & Efford 1998, Fletcher *et al.* 2012, Biro 2013). Although current methods for calculating nest success can control for factors such as nest age, date, and nest site characteristics, capture bias has rarely been applied to nest searching (Daw *et al.* 1998, Rodewald 2004, Powell *et al.* 2005), especially when calculating survival estimates on nests obtained with multiple sampling methods.

Three common nest search methods often used in conjunction are behavioural cues of adults (hereafter 'behavioural'), haphazard or incidental flush (hereafter 'opportunistic') searches (Martin & Geupel 1993), and systematically conducted (hereafter 'structured') searches (Klett *et al.* 1986, Winter *et al.* 2003). Structured nest searches are considered the best measure to obtain representative samples of nests, especially in grasslands (Winter *et al.* 2003), because they allocate search efforts over an entire sample area through the use of equipment such as handheld sticks or a rope with attached noisemakers to disturb the vegetation and flush nesting birds (Klett *et al.* 1986, Winter *et al.* 2003, Conover 2009). In contrast, opportunistic searches are defined as those where the observer is conducting activities other than nest searching and nests are located incidentally by flushing birds in close proximity (Martin & Geupel 1993). Behavioural searches use observations such as nest material being carried during construction, females vocalizing, or adults carrying food to nestlings to identify nest location (Martin 1993).

Fates of opportunistically or behaviourally located nests may vary from the segment of the population detected using a structured search design due to differences in search procedures, observers (Rodewald 2004), or heterogeneity among incubating adults or nests found with each method. Birds that detect predators (or nest searchers) early may escape or rely on cryptic camouflage and remain at the nest (Lima & Dill 1990). Flush distance from a nest may have implications not only for nest detection, but also for the resulting nest fate if flushing activities also attract potential predators (Burhans & Thompson 2001). For clutches with a greater probability of hatching, individual birds may increase duration of risky incubation bouts to balance the risk of revealing nest location with adult survival (Albrecht & Klvaňa 2004, Osiejuk & Kuczynski 2007). Incubating and brooding birds with increased nest attentiveness (proportion of time on the nest) can reduce activity and the resulting potential to attract visually orientated predators to a nest (Skutch 1949, Andersson *et al.* 1980, Montgomerie & Weatherhead 1988, Martin 2002).

Observers can differ in their nest-searching strategies (e.g. behavioural vs. substrate searchers) and nests located by observers using behavioural cues such as flushing may fail more frequently (Rodewald 2004). This potential difference in nest survival may result from observers using the same behavioural cues attracting nest predators. Additionally, heterogeneity in nest activity or nest location may result in varying nest survival estimates based on the order nests are found. Nests found earlier in the nesting cycle may be more prone to failure as they may also be found more easily by predators than nests with more cryptic vegetation or adult behaviours (Willis 1973, Cresswell 1997).

Combining nests located by different search methods into a single data set for analysis may obscure potential differences in the resulting demographic inferences (Pollock & Raveling 1982). If all search methods find representative samples of available nests drawn from the same population, then we would expect derived estimates of nest success from all samples to be equal (Shaffer 2004). However, if each search method sampled a different segment of the population, we would expect nest survival estimates between the three methods to differ. We modelled daily nest survival of Dickcissel *Spiza americana* nests detected using structured, opportunistic, or behavioural searches of the same population to analyse the influence of search method on the resulting survival estimates.

## METHODS

### Study system

The Dickcissel is a polygynous grassland-specialist of conservation concern (Temple 2002) showing population declines in the Eastern United States similar to declines in other grassland species, with an overall decline of 0.5% in annual indices from 1966 to 2011 (Sauer *et al.* 2012); they were the most frequently encountered breeding bird at our study area. Commonly, nests are constructed by females in dense grass, forbs, or low woody vegetation, usually with overhead vegetative cover (Blankspoor 1970, Temple 2002). Dickcissels are a good model species to compare nest survey methods for grassland birds because previous research on this species has successfully located nests with all three search methods (Jensen & Finck 2004, Conover *et al.* 2011, Sousa 2012).

We conducted the study on eight adjacent 8-ha (range:7.58–8.41) plots of semi-natural grassland

located in the Black Prairie region of Mississippi, USA, 33°39′N, 88°33′W (Barone 2005). The region experiences monthly mean precipitation of 7.8 cm and average daily temperatures of 25.3°C during May–August (National Weather Service, College Park, Maryland, USA). The warm-season grassland plots were established in 2010 with species including Big Bluestem *Andropogon gerardii*, Little Bluestem *Schizachyrium scoparium*, Indian Grass *Sorghastrum nutans*, Tickseed Sunflower *Bidens aristosa*, and Illinois Bundleflower *Desmanthus illinoensis*. Additional species prevalent in the existing seed bank included Annual Ragweed *Ambrosia artemisiifolia* and *Sesbania* spp.

## Nest searching

We located and monitored nests during 1 May–9 August 2011 to 2013 using structured (either systematic rope-dragging or walking), opportunistic, and behavioural searches (Martin & Geupel 1993, Winter *et al.* 2003). For structured searches, 3–5 technicians searched the entire study area bi-weekly for nests by disturbing vegetation with a rope or handheld sticks to flush nesting birds. We used systematic walking on all plots in 2011 when existing vegetation (primarily *Sesbania* spp. > 2m in height) restricted the effectiveness of rope-dragging. In 2012 we mowed all plots to ~16 cm prior to the arrival of Dickcissels to remove existing biomass as part of a concurrent study to examine the influence of biomass harvest for energy production on wildlife habitat use (Roth *et al.* 2005, Adler *et al.* 2006, Robertson *et al.* 2011). Removal of dead vegetation allowed us to use rope-dragging on all plots in 2012 and 2013. Vegetation removal did not influence territory establishment or nest initiation dates (T. Conkling unpubl. data). Additionally, four plots were harvested annually in mid-June 2012 and 2013; we excluded all nests that failed as a result of biomass harvest and any subsequent nests in these plots from analyses.

For rope-dragging, a 3-person team used a 25-m rope with attached noisemakers (0.6-L plastic bottles filled with several rocks at 2-m intervals) held 1–1.5 m above the ground, with the third person walking along behind the midpoint of the rope; otherwise, technicians walked 2–4 m apart and systematically disturbed vegetation with 2-m PVC pipes (2.5-cm diameter). For opportunistic and behavioural searches, 2–3 technicians visited all plots every 3–10 days while conducting other activities such as vegetation sampling, nest checks, and behavioural monitoring of territorial Dickcissels which resulted in incidental flushing of adults, visually observing a nest without adult cues, or observation of behavioural cues.

With all methods, once a bird was flushed, observers searched the vegetation for ≤10 minutes to locate the nest. We included nests located with behavioural cues other than incidental flushes (e.g. nest material or food carries) in this study, but analysed them as a separate search method category instead of incorporating them with the other opportunistic nests. The flush response of the adult birds is assumed to be comparable between both structured and opportunistic search types, as opposed to behavioural cues that do not rely solely on flush observations. However, as most grassland bird studies also use nests located with behavioural cues (Winter *et al.* 2003), incorporating this search method as a separate category allowed us to determine if differences existed with survival estimates using structured searches relative to the other two methods.

We recorded nest locations with a handheld GPS unit and marked nests with flagging 5–10 m north of each nest. We monitored all nests every 2–6 days until young fledged or the nest failed and we checked all nests with the same frequency, regardless of treatment type. We aged nests based on observed nest contents and back-dated to estimate initiation date (i.e. 2–4 days laying, depending on clutch size, because incubation began with the penultimate egg, 12 days incubation, and 9 days for nestling stage) and used progression of physical development to age nests found after hatch date (Temple 2002). For nests we found after incubation had commenced but failed before hatching, we estimated initiation date by assuming the nest to be halfway through incubation (6 days old) at the midpoint of available nest check dates (Sousa & Westneat 2013). From these estimates, we restricted our analyses of opportunistic and behavioural nests to those nests that were active (but not found) during a previous structured search at that site and located opportunistically or behaviourally on a subsequent visit. Thus, all opportunistic and behavioural cue nests were initially 'available' to be located throughout the period of structured searches, and represented nests available for survival estimates that were missed by a structured search.

We collected vegetation measurements at each nest 12–18 days following estimated hatch date (when nests were no longer active) to minimize disturbance. We measured nest height and mean height of visual obstruction 4 m from the nest in each cardinal

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direction using a Robel pole (Robel *et al.* 1970) and calculated distance to nearest edge of grassland habitat using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). We calculated visible height as the difference between nest height and mean height of visual obstruction. Thus, a nest with a negative visible height value would be visually obstructed by vegetation whereas a nest with a positive value was potentially visible from 4 m.

### Statistical analysis

We used R 3.02 (R Development Core Team 2009) to determine mean values (±se) for visible height, nest height, time of day a nest was found (minutes after sunrise), and nest age at initial discovery (hereafter 'age found') by search method and analysis of variance (ANOVA; $\alpha = 0.05$) to compare mean differences between nest characteristics among search methods. We pooled data across years because of small sample sizes of each search method within individual years. We estimated daily survival rate (DSR) using the Nest Survival model in Program MARK 7.1 (White & Burnham 1999, White 2011) and R using package RMark 2.1.7 (Laake 2013). Program MARK uses a maximum-likelihood estimator to calculate daily survival probability and regression coefficients. We grouped nests by search method for analyses. We included year, date (linear and quadratic), nest age, nest height, visual height, and distance to edge as covariates based on previous literature (Davis 2005, Grant *et al.* 2005). We also included age found to examine if nests located earlier in the nesting cycle were more likely to fail. We standardized date of season using 1 May as the initial date (e.g. 1 May = 1 to 9 Aug = 101).

We used sequential model fitting to examine nest survival while minimizing the number of models used (Dinsmore *et al.* 2002). We controlled for effects of year by including year in all models. We first tested for multicollinearity among covariates by examining variance inflation factors (VIFs; Zuur *et al.* 2009). VIFs for all covariates were < 2.64, suggesting multicollinearity was not an issue; however nest height was positively correlated with nest initiation date ($r = 0.71$), so we removed it from subsequent analyses. We first fitted models that included temporal sources of variation (linear date, quadratic date, and nest age). We then used the best-fitting model to determine if nest site parameters (visual height or distance to edge of habitat) improved model fit. Finally, we used the best model from the previous step to determine if the addition of search method, or interactive effects between search method and age found or significant nest site covariates best explained variation in nest survival.

We ranked models in each step based on small sample size corrected Akaike's Information Criterion ($AIC_c$) values and weights, and considered models similar if $\Delta AIC_c \leq 2$ (Burnham & Anderson 2002), provided that models within 2 $AIC_c$ units did not simply include an additional uninformative parameter (Burnham & Anderson 2002, Arnold 2010). We used model averaging for competing models and examined coefficients with 85% confidence intervals (CIs) for interpretation of important group and covariate effects if intervals excluded zero; this allows for a cautious interpretation of potential informative variables that may be erroneously discarded with 95% CIs (Arnold 2010). We calculated the odds ratio for categorical covariates in the best-fit model by exponentiating the resulting parameter coefficients. We also estimated period nest survival by multiplying DSR estimates generated by 24 days in the nesting period (i.e. egg laying to fledging) (Temple 2002) for nests starting on the median initiation date (18 May).

## RESULTS

We monitored 163 Dickcissel nests (structured: 57 in 2011, 31 in 2012, 14 in 2013; opportunistic: 25 in 2011, 9 in 2012, 8 in 2013; behavioural: 2 in 2011, 12 in 2012, 5 in 2013) which were active during structured searches. Visible height ($\bar{x} = -16.68 \pm 1.95$, $F_{2,160} = 2.1$, $P = 0.13$), nest height ($\bar{x} = 26.59 \pm 1.64$, $F_{2,160} = 1.1$, $P = 0.34$), vegetation obstruction ($\bar{x} = 43.27 \pm 2.30$, $F_{2,160} = 0.2$, $P = 0.80$), distance to edge ($\bar{x} = 37.45 \pm 1.89$, $F_{2,160} = 1.9$, $P = 0.15$), time of day (minutes after sunrise; $\bar{x} = 206 \pm 8.77$, $F_{2,159} = 1.0$, $P = 0.39$), and age found ($\bar{x} = 8.51 \pm 0.44$, $F_{2,160} = 0.7$, $P = 0.50$), were similar among search methods.

Variation in Dickcissel nest survival was best explained by search method, quadratic date, nest age, age found, and year (Table 1). DSR declined with nest age (Fig. 1a) and linear date (Fig. 1b), but increased with age found (Fig. 1c) and all factors in the best-supported model influenced DSR (Table 2). The odds for estimated survival were 1.51 (85% CI: 1.06, 2.16) times greater for opportunistically located nests relative to nests located during structured searches when controlling for all other covariates; there was no

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**Table 1.** Model selection results for Dickcissel *Spiza americana* daily nest survival based on sequential model fitting, Clay County, Mississippi, USA, 2011–2013.

| Model | AICc | ΔAICc[a] | Weight | Deviance | K[b] |
|---|---|---|---|---|---|
| *Temporal Variation* | | | | | |
| Quadratic Date[c] + Nest Age + Year | 513.60 | 2.54 | 0.14 | 501.54 | 6 |
| Nest Age + Year | 533.45 | 22.39 | 0.00 | 525.42 | 4 |
| Quadratic Date[c] + Year | 553.16 | 42.10 | 0.00 | 543.12 | 5 |
| Linear Date + Year | 570.64 | 59.58 | 0.00 | 562.61 | 4 |
| Year (Null) | 574.70 | 63.64 | 0.00 | 568.68 | 3 |
| *Nest Site + Best-fit Temporal Variation* | | | | | |
| Visible Height + Quadratic Date[c] + Nest Age + Year | 514.73 | 3.67 | 0.08 | 500.65 | 7 |
| Distance to Edge + Quadratic Date[c] + Nest Age + Year | 515.11 | 4.05 | 0.06 | 501.04 | 7 |
| *Search Method & Age Found + Best-fit (Nest Site + Temporal Variation)* | | | | | |
| Quadratic Date[c] + Nest Age + Search Method + Age Found + Year | 511.06 | 0.00 | 0.48 | 492.94 | 9 |
| Quadratic Date[c] + Nest Age + Search Method + Year | 513.16 | 2.10 | 0.17 | 497.06 | 8 |
| Quadratic Date[c] + Nest Age + Age Found*Search Method[d] + Year | 516.61 | 3.74 | 0.07 | 496.46 | 11 |

[a]ΔAICc from best-fit model
[b]Number of parameters
[c]Quadratic date includes both linear date and quadratic date coefficients.
[d]For models with interactions, main effects are also included.

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difference between structured search nests relative to nests found with behavioural cues, as the 85% CI for the behavioural search odds ratio overlapped one (85% CI: 0.44, 1.18). The period survival for the 24-day nesting cycle based on median initiation date (18 May) was greatest for opportunistically located nests in all years (2011: $S = 0.204$, 2012: $S = 0.070$, 2013: $S = 0.381$), followed by structured searches (2011: $S = 0.098$, 2012: $S = 0.022$, 2013: $S = 0.240$) and nests located by behavioural cues (2011: $S = 0.045$, 2012: $S = 0.007$, 2013: $S = 0.146$).

## DISCUSSION

We found some evidence to suggest nest survival estimates varied among samples of nests located with different methods of capture, because the best-supported model included search method. Our survival estimates for nests located opportunistically were greater than estimates from structured sampling, however, survival for nests located with behavioural cues was not significantly different. Opportunistic nest searching and use of behavioural cues may allow researchers to encounter nests otherwise missed in study plots due to the increased frequency of visits, bird flush behaviours influenced by the number of surveyors (Geist *et al.* 2005) or the bird's perceived risk of predation at the nest (Lima & Dill 1990, Burhans & Thompson 2001). Although our results have limited statistical support, we suggest they have biological importance. Other studies have suggested that ≥10% reduction in nest survival may be biologically significant for populations (Powell *et al.* 1999, Donovan & Thompson 2001, Campomizzi *et al.* 2009). Our period survival estimates for structured and opportunistic searches differed by 10.6% in 2011, 4.9% in 2012, and 14.2% in 2013. Thus, the search method used to locate nests may also influence biological interpretation of nest survival, which can have implications for conservation planning and other management practices for grassland birds.

Heterogeneity in nest placement or adult behaviours may adversely influence nest detection probabilities, especially when combined with cryptic behaviours of adults to reduce predation risk at the nest (Lima & Dill 1990, Albrecht & Klvaňa 2004, Osiejuk & Kuczynski 2007). Birds may perceive a single observer as less risky than multiple nest searchers dragging a rope, thereby only flushing once an observer is close to the nest. If a bird leaves a nest earlier due to perceived risk from a group of nest searchers, the flush behaviour necessary for observers to locate a nest would be missing. Thus, the same behaviours birds use to avoid predation could also decrease the likelihood of locating nests with structured searches. Birds may also display temporal variation in nest attendance (Davis & Holmes 2012) that could influence the ability of observers to locate nests with flush behaviours. However, the time of day we located nests was similar among search methods, indicating factors other than temporal variation in nest attendance caused our observed differences in DSR. As we found no

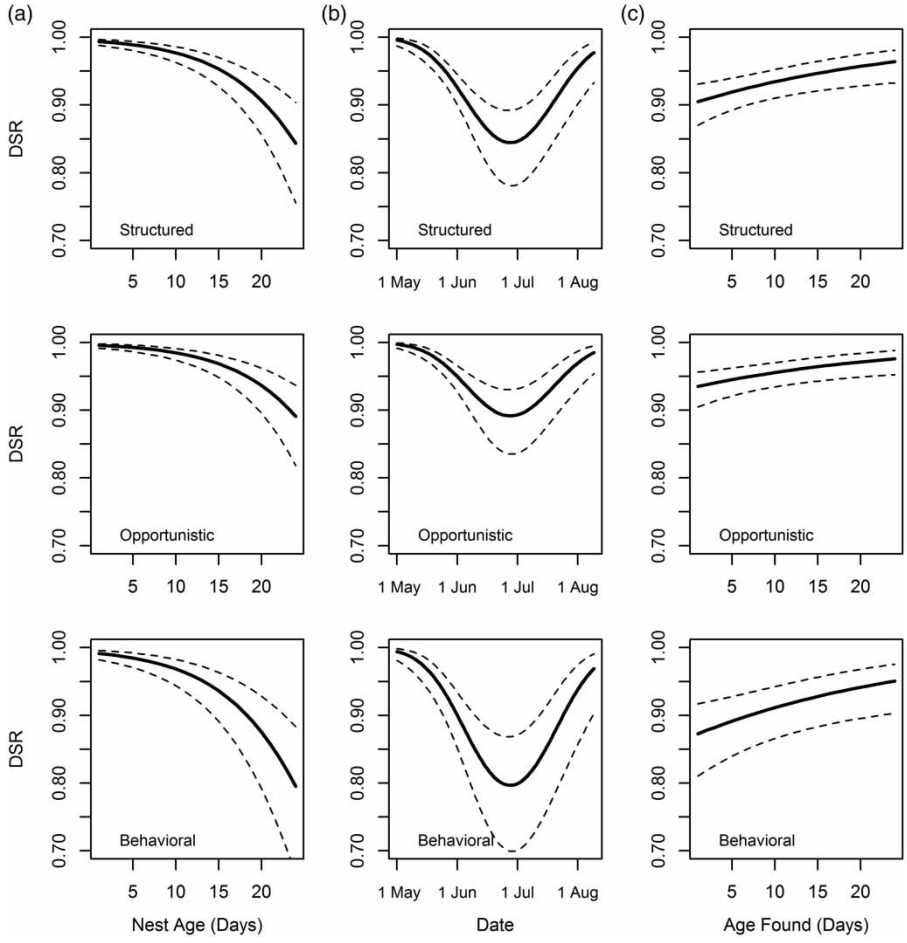


**Figure 1.** DSR and 85% CIs (dashed lines) for Dickcissel *Spiza americana* nests (year = 2012) by search method for: (a) nest age (date held constant at median initiation date (18 May), nest age at initial discovery (age found) held constant at 8.5), (b) date in season (nest age held constant at day 12, age found held constant at 8.5), and (c) age found (nest age held constant at day 12, date held constant at 29 May, corresponding to nests started on median initiation date) using parameter estimates from the best-fit model, Clay County, Mississippi, USA, 2011–2013.

**Table 2.** Model coefficients (±se) and 85% confidence limits for parameters in the best-fit model for Dickcissel *Spiza americana* daily nest survival, Clay County, Mississippi, USA, 2011–2013.

| | | | 85% Confidence Limits | |
|---|---|---|---|---|
| Parameter | Estimate | se | Lower | Upper |
| Intercept | 7.449 | 0.885 | 6.174 | 8.723 |
| Search method (opportunistic)[a] | 0.416 | 0.245 | 0.063 | 0.768 |
| Search method (behavioural)[a] | –0.325 | 0.341 | –0.816 | 0.165 |
| Linear date | –0.135 | 0.035 | –0.186 | –0.085 |
| Quadratic date | 0.001 | 0.000 | 0.001 | 0.002 |
| Nest age | –0.148 | 0.024 | –0.182 | –0.113 |
| Year (2012)[b] | –0.559 | 0.253 | –0.923 | –0.196 |
| Year (2013)[b] | 0.533 | 0.317 | 0.077 | 0.990 |
| Age found | 0.045 | 0.022 | 0.013 | 0.077 |

[a]Systematic searching is the reference condition. Coefficient refers to change in daily nest survival for given search method relative to systematically located nests.
[b]2011 is the reference year. Coefficient refers to change in daily nest survival for given year relative to 2011.



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significant nest site covariates in our best-fitting models and did not quantify adult behaviours at the nest or flush distances, we were unable to identify the mechanism behind observed differences in survival estimates between structured and opportunistic searches.

The presence of behavioural cues useful for locating nests (e.g. females vocalizing, adults carrying nest materials or food for nestlings) allows observers to find nests missed by structured searches, albeit with additional time and effort. Mean age of nests found was similar across search methods, but behavioural searches may also locate more nests in pre-incubation and nestling stages (pre-incubation: 26.3%, nestling: 42.1%, $n = 19$) than structured searches (pre-incubation: 22.5%, nestling: 12.7%, $n = 102$). The 61 opportunistic and behavioural nests were available (but not detected) during structured searches and likely differed by some unidentified factor. Additionally, if observers in other studies find nests at different ages with different search methods, the temporal changes in bird flushing behaviours may produce additional bias between survival estimates. However, as we could not quantify total survey effort for either behavioural or opportunistic search methods, we did not correct for sampling bias or detection probabilities using current survival models.

We recommend structured searches over opportunistic or behavioural searches for locating grassland bird nests because it is best supported by sampling theory; that is, active nests have > 0 probability of being detected with structured searches, whereas, no such probabilities or methods to evaluate validity or reliability of parameter estimates for nest survival apply to opportunistic or behavioural searches under current protocols (Levy & Lemeshow 1999). If researchers want to find an unbiased sample of nests representative of the spatial complexity of the habitat, structured searches are necessary to account for variation in locating nests, such as observers only searching easily accessible locations. Incorporating nest detection probabilities in future research may also improve the accuracy of survival estimates and measures of nest density by accounting for variations in bird behaviours that reduce searchers' abilities to locate nests (Lima 2009, Blumstein 2010, Giovanni *et al.* 2011).

Although the 85% CI of the parameter estimate for nests located behaviourally overlapped zero and our sample size of behavioural nests was small ($n = 19$) compared to nests located with other search methods, our model results (Table 2, Fig. 1a, b) and period survival estimates indicate that nests located using active adult behaviours may have lower nest survival rates. However, if major Dickcissel nest predators such as snakes (Klug *et al.* 2010) use visual cues of adult behaviour to locate nests (as we did), vegetative concealment around the nest may not limit a predator's ability to find a nest. We found a weak positive effect of age found on DSR (Table 2, Fig. 1c), suggesting that nests located earlier in the nesting cycle may have decreased survival; however, there was no interaction between search method and age found. Structured searches missed nests later found using other search methods, but search order alone did not account for the lower nest survival of structured searches relative to opportunistically located nests.

The influence of age found on nest survival provides support that some unidentified factor may leave some nests more vulnerable to early detection by potential predators. If structured searches found nests easier for observers (and presumably also predators) to locate, we would expect to find these nests earlier in the nesting cycle; however, mean age found did not differ among search methods. After nests were located initially, further detections of that nest during subsequent searches of other methods were not recorded; however, future studies quantifying adult flushing behaviours or incorporating repeated searches of systematically located nests to determine detection probability (Giovanni *et al.* 2011) would be beneficial.

Negative influences of both date and nest age on nest survival were similar to findings from previous research (Grant *et al.* 2005). Winter *et al.* (2000) suggested close proximity to habitat edge may reduce nest survival for grassland birds, but we observed no difference in survival based on distance to edge. Additionally, visible height (i.e. nest concealment) was not important in predicting nest survival. However, in situations where location influences nest success, disturbance from observers conducting adjacent structured survey passes could prematurely flush breeding birds, making it difficult to subsequently locate those nests and potentially biasing DSR estimates. Nest searchers can reduce location bias by alternating search order in relation to habitat features (e.g. proximity to edge). Period survival estimates were lower than previous research on Dickcissels in the region based on structured searches in Clay County, Mississippi (27.9%; Adams *et al.* 2013), and the Mississippi Alluvial Valley (12.9% and 19.1%; Conover *et al.* 2011). However, Conover *et al.* (2011) derived estimates based on a 20-day nesting cycle, and

the initiation dates used for both studies were earlier than our data, which could account for differences in survival estimates.

We recommend the accepted practice of combining nests located by structured, opportunistic, and behavioural methods to increase sample size only if researchers account for potential effects of search method on survival estimates, because combining multiple methods may introduce biases. Structured searches allocate survey effort equally across the study area, providing each nest with a probability $> 0$ of being located and accounting for variation in search intensity or effort; this is not plausible for incidentally located nests. We encourage other researchers to assess this potential source of variation (i.e. nest search method) when designing experiments and to more explicitly state how they locate nests and to include search method as a covariate when analysing data to improve interpretation of results.

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