Research Article

Critical Demographic Parameters for Declining Songbirds Breeding in Restored Grasslands

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Abstract

Land area occupied by tallgrass prairie has declined throughout the midcontinental United States during the past 2 centuries, and migratory birds breeding in these habitats have also experienced precipitous population declines. State and federal agencies have responded by restoring and reconstructing grassland habitats. To understand consequences of restoration for grassland bird populations, we combined demographic data collected over 4 breeding seasons (1999–2002) in northern Iowa, USA, with population projection models to estimate population growth rates of 2 declining migratory songbirds, dickcissels (Spiza americana) and bobolinks (Dolichonyx oryzivorus). To determine what parameters were critical for conservation of these species, we estimated relative contributions of nest predation, brood parasitism by brown-headed cowbirds (Molothrus ater), annual survival, and renesting to population growth using elasticity analysis. Based on model simulations, the population growth rate for dickcissels was not high enough to be stable without immigration into the area ($\lambda < 1$). For bobolinks, populations could only be stable ($\lambda = 1$) if annual survival was relatively high (adult survival >0.7, with juvenile survival between 0.2 and 0.5). Population growth rates were most sensitive to adult survival across a wide range of parameter estimates, whereas sensitivity to brood parasitism and renesting were consistently low. Elasticities associated with nest predation were highly variable and dependent on survival estimates. In the absence of changes in other demographic parameters, eliminating brood parasitism would not be enough to ensure stable populations of either species. Only management focused on increasing adult survival or decreasing nest predation could produce stable populations. Our results underscore the need for reliable adult survival estimates and conservation strategies focused throughout all phases of the annual cycle. In addition, our modeling approach provides an effective framework for investigating the importance of demographic parameters to population growth rates of birds that are influenced by nest predation, brood parasitism, and renesting. Although habitat restoration is one of the few alternatives for conserving communities in threatened landscapes, restoration strategies also need to have positive effects on population dynamics for species of concern, which has not been demonstrated in this grassland system. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):145–157; 2006)

Key words

Brood parasitism, elasticity, grassland birds, habitat restoration, nest predation, population projection models, renesting, survival.

Over 99% of native tallgrass prairie in the midcontinental United States has been developed or converted to agricultural use during the past 2 centuries (Samson and Knopf 1994). Many migratory bird species using these habitats have also experienced consistent, widespread declines throughout the United States (Herkert 1995, Igl and Johnson 1997, Peterjohn and Sauer 1999, Fletcher and Koford 2003). Because of this severe habitat loss, habitat restoration is the key to conservation of grassland ecosystems (Herkert et al. 1996). Restoration could have diverse consequences for birds by influencing many aspects of population dynamics, which can complicate evaluation of restoration efforts.

Restoration generally refers to altering an ecosystem back to its initial or original state (Meffe and Carroll 1994). Yet grassland restoration and reconstruction efforts in the Midwest typically include planting areas with few species of grasses and forbs, some of which are not endemic to the area (Fletcher and Koford 2003). These areas do not achieve the diversity and structure of native prairies, but some ecological functions are restored. Therefore, we refer to these plantings as restored grasslands (sensu Johnson and Igl 2001, Fletcher and Koford 2002).

Restoration can potentially provide habitat for breeding birds, based on evidence of similar bird communities in restored areas compared with other land uses (Fletcher and Koford 2002, 2003). Because bird abundance or density can be uncorrelated with components of fitness (e.g., Van Horne 1983, Winter and Faaborg 1999), population growth rates are more prudent measures of the efficacy of restoration. Population growth rates are useful for evaluating whether breeding areas are population sources or sinks (sensu Pulliam 1988), providing insight on the viability of populations within breeding areas (Donovan et al. 1995, McCoy et al. 1999). Yet simply documenting growth rates is not enough for prescribing sound conservation strategies. Instead, biologists need to identify demographic parameters that contribute most to population growth rates and subsequently implement strategies that positively impact these parameters (assuming that these factors are responsive to management; Benton and Grant 1999, Mills et al. 1999). For example, demographic analyses on a population of loggerhead sea turtles (*Caretta caretta*) revealed that management strategies were focused on the life-history stage that was least responsive for increasing the population growth rate (the egg stage), whereas other stages (particularly juvenile survival) were more likely to influence changes in population growth (Crouse et al. 1987).

Similar misdirected management could be occurring with some migratory songbirds. Many studies have focused on various direct and indirect attempts to manage for the detrimental effects of

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predation on nests (reviewed in Heske et al. 2001) or brood parasitism by brown-headed cowbirds (*Molothrus ater*; e.g., Smith et al. 2002) without determining what parameters are most responsive for increasing population growth rates. Although nest predation and brood parasitism both have negative impacts on seasonal fecundity, or the number of fledglings produced/female/year (Pease and Grzybowski 1995), these parameters operate in disparate ways. Nest predation typically results in complete failure (but see Ackerman et al. 2003), yet individuals can potentially renest following failure. Brood parasitism does not usually cause complete failure, but instead individuals continue to raise cowbird young and a diminished number of host young. Furthermore, conservation strategies may ultimately differ for ameliorating detrimental effects of nest predators and brood parasites. While some attempts have been made to determine the relative importance of nest predation and brood parasitism on seasonal fecundity (e.g., Pease and Grzybowski 1995, Schmidt and Whelan 1999), only Woodworth (1999) attempted to partition the importance of these parameters on avian population growth rates.

We combined demographic data on 2 declining migratory songbirds, dickcissels and bobolinks (Peterjohn and Sauer 1999, Fletcher and Koford 2003), breeding in restored grasslands of northern Iowa with population projection models to estimate population growth rates (Caswell 2001). We then determined the relative contribution of nest predation, brood parasitism, annual survival, and renesting to the population growth rates of these species.

Methods

Focal Species and Study Area

We focused on 2 declining, single-brooded neotropical migrants that breed in temperate grasslands of the United States: the dickcissel and the bobolink. We chose these species for 3 primary reasons: 1) both exhibited population declines throughout the continental United States (Peterjohn and Sauer 1999) and in this region during the period of habitat restoration we investigated (Fletcher and Koford 2003); 2) both were large enough to attach radiotransmitters that could last for most of the breeding season, which facilitated estimating seasonal fecundity; and 3) both were common in our study area (Fletcher and Koford 2002).

We collected demographic data on all restored grasslands >10 ha within the Eagle Lake Wetland Complex ($n = 10$; 590 ha), located in Hancock and Winnebago counties, north-central Iowa (43°N94°W; Fletcher 2003). The Eagle Lake Wetland Complex encompassed approximately 162 km^2, and contained a complex of waterfowl production areas and wildlife management areas situated in an agricultural landscape. Grasslands were restored primarily from rowcrop areas, using warm-season (27.5%) and cool-season grass (72.5%) plantings (see Fletcher and Koford 2003). Warm-season plantings were typically switchgrass (*Panicum virgatum*) or big bluestem (*Andropogon gerardii*) mixtures, whereas cool-season plantings were typically smooth brome (*Bromus inermis*) or grass/alfalfa (*Medicago sativa*) mixtures. Plantings were often heterogeneous within sites, with most sites containing >1 planting type ($n = 6$). We pooled information across planting types because both species commonly nest in cool-season and warm-season plantings and because we were interested in population-level dynamics. However, we tested for planting-type effects on nest predation (see below). Elsewhere, we estimate the influence of fine-scale habitat selection and its implications for these species (R. J. Fletcher and R. R. Koford, Iowa State University, unpublished data).

Estimating Breeding Parameters for Seasonal Fecundity

We collected data on all parameters required to estimate seasonal fecundity (sensu Schmidt and Whelan 1999) between 1999 and 2002. All parameters except for information on renesting were estimated using standard nest finding and monitoring methods (e.g., Martin and Geupel 1993); renesting data were collected via radiotelemetry (see below). We used a combination of systematic searching and observing female behavior to find nests (see Martin and Geupel 1993, Pietz and Granfors 2000). We visited nests every 2–4 days to determine the fate of each nest. To minimize problems of assigning uncertain nest fates (Manolis et al. 2000), we considered nests successful and stopped counting nest exposure days if at least 1 host nestling remained in the nest at day 7–8 (approx 1 day before the earliest fledging dates for these species; Martin and Gavin 1995, Temple 2002). To partition components of nest success, we estimated daily predation rates and daily failure rates (from sources other than predation) using the Mayfield method (Johnson 1979, Heisey and Fuller 1985). We subsequently estimated predation and failure rates by exponentially expanding daily estimates to number of days in the nesting cycle (laying, incubation, and nestling stages; dickcissels: 24 days [Temple 2002]; bobolinks: 26 days [Martin and Gavin 1995]).

To estimate renesting probabilities, we radiomarked adult, female dickcissels and bobolinks in each of the study sites during the 2000 breeding season. We attached radios ($\overline{x} = 0.94$ g, range: 0.63–1.10 g; Advanced Telemetry Systems, a modified A1000, and Holohil Systems, Ltd. BD-2) using a leg-loop harness (Rappole and Tipton 1991), which was successfully used on other breeding passerines (e.g., Powell et al. 2000, Walk et al. 2004). These radios typically last between 35 to 50 days. We attempted to radiomark females prior to or during their first breeding attempt. We opened 4 mist net lines (4 nets/line) from approximately 0510–0800 at each site (once between 22 May–8 Jun, and again between 14–28 Jun) to passively catch birds. We distributed nets during the first visit to target bobolinks, and we distributed nets during the second visit to target dickcissels. We supplemented this approach by trapping females at known nest sites. We banded all individuals with a unique combination of 3 plastic color bands and 1 U.S. Fish and Wildlife Service aluminum band. We only attached radios to females with brood patches or if the female was known to be nesting. We located and monitored females once daily using hand-held and vehicle-mounted telemetry systems via homing until battery failure or emigration from the study area (see also Kershner et al. 2004). However, we only approached nests every 2–4 days. We also tracked lost birds from a plane weekly by flying transects at regular intervals in and around the study area, searching >8 km surrounding each site (Fletcher 2003). From planes, signals from radiomarked birds could be heard regularly from 3 to 5 km. Estimates of renesting from radiotelemetry were likely minimum estimates because renesting attempts could be missed, particularly if nests were depredated early in the nesting cycle, and it is possible that radiomarking inhibited renesting. All techniques for handling and marking birds were approved by the

U.S. Fish and Wildlife Service, the Iowa Department of Natural Resources, and the Iowa State Animal Care Committee.

For estimating breeding parameters used in modeling seasonal fecundity, we considered sites to be our sampling unit because nests within these sites were not likely independent. We determined mean estimates for each parameter needed to estimate seasonal fecundity across sites and standard errors using a mixed-model analysis with site as a random effect and year as a repeated measure (Littell et al. 1996). We modeled the repeated measure by specifying 4 potential covariance structures: variance components, autoregressive order 1, compound symmetric, and unstructured covariance (Littell et al. 1996:93–102). We then selected the most parsimonious covariance structure using Akaike's Information Criterion (AIC), adjusted for small sample sizes (AIC_c; Littell et al. 1996; Burnham and Anderson 1998). For nest predation rates and nest failure rates, we used number of nest exposure days per site as a weighting factor to account for differences in sample sizes and precision of estimates for each site (Koford 1999). We compared intercept-only models with models including year to determine whether estimates were consistent across years. In addition, we determined whether pooling estimates for planting types within sites was parsimonious by also comparing models that included the planting type as an explanatory variable. Using 2000 data, we compared nest predation rates of radiomarked nests to unmarked nests to determine whether radiotransmitters influenced nest success of bobolinks and dickcissels by comparing intercept-only models to models including radiomarking as an explanatory variable.

Modeling Seasonal Fecundity

We estimated seasonal fecundity following the analytical, single-brooded model developed by Schmidt and Whelan (1999), modified to incorporate sources of failure other than predation. We chose this model in lieu of other approaches (e.g., Noon and Sauer 1992, Pease and Gryzbowski 1995) because it partitioned effects of nest predation and brood parasitism, and it provided an analytical solution that could be incorporated directly into a population projection matrix. The Schmidt and Whelan (1999) model required determining the total number of potential nesting attempts possible prior to the analysis (see also Donovan et al. 1995, McCoy et al. 1999). For each species, we ran baseline models based on the maximum number of observed nesting attempts by individual females within a season, based on marked birds in the study area (Bobolinks: 2, see also Bollinger and Gavin 1989; Dickcissels: 3, see also McCoy et al. 1999). We also varied the number of renesting attempts because our estimates of renesting were likely minimum estimates (see Model Variations).

Schmidt and Whelan (1999) developed analytical models for estimating seasonal fecundity of single-brooded and double-brooded songbirds; here, we focus on modifying the single-brooded model. The model assumes 4 possible outcomes of a nesting event: 1) successful and unparasitized, 2) successful but parasitized, 3) parasitized and subsequently abandoned, and 4) depredated. Given these possible outcomes, the expected number of young fledged in 1 nesting attempt is:

$$E(1 - P*)(1 - N) + (E - R)(1 - P*)(1 - a^p)N, \qquad (1)$$

where E is the number of host young fledged per successful unparasitized nest, P^* is the probability of nest predation (and other sources of nest failure), N is the probability of brood parasitism, R is the reduction in host young fledged per successful nest due to brood parasitism, and a_p is the probability of abandonment following nest parasitism.

For simplicity, Schmidt and Whelan (1999) considered predation, P^*, to be any source of nest failure other than abandonment from brood parasitism, but predation can be partitioned from other sources of failure (e.g., weather). We assumed predation operates independently of other sources of failure and adjusted equation 1 to:

$$E(1 - P - F)(1 - N) + (E - R)(1 - P - F)(1 - a^p)N, \qquad (2)$$

where P is exclusively the probability of nest predation and F is the probability of nest failure from sources other than predation.

This framework was then extended to estimate seasonal fecundity, given assumptions about the total number of renesting attempts individuals can make. For 2 nesting attempts, an unreduced expression for seasonal fecundity, m, is:

$$\begin{aligned} m = {} & E(1 - P - F)(1 - N) + (E - R)(1 - P - F)(1 - a^p)N \\ & + E(\alpha P)(1 - P - F)(1 - N) \\ & + (E - R)(\alpha P)(1 - P - F)(1 - a^p)N \\ & + E(\alpha F)(1 - P - F)(1 - N) \\ & + (E - R)(\alpha F)(1 - P - F)(1 - a^p)N \\ & + E(\gamma a^p N)(1 - P - F)(1 - N) \\ & + (E - R)(\gamma a^p N)(1 - P - F)(1 - a^p)N, \end{aligned} \qquad (3)$$

where α is the renesting probability after nest failure (either from predation or other sources), and γ is the probability of renesting after abandonment due to brood parasitism (assumed to equal 1 in Schmidt and Whelan [1999]). None of the nests we monitored were abandoned after a parasitism event. Therefore, we assumed $a_p = 0$. Given this assumption, for 2 nesting attempts a reduced expression for seasonal fecundity, m, is:

$$m = (E - NR)(1 - P - F)(1 + \alpha P + \alpha F), \qquad (4)$$

where α is the renesting probability after nest failure. For 3 nesting attempts a reduced solution is:

$$m = (E - NR)(1 - P - F)(1 + \alpha P + \alpha F + \alpha^2(P + F)^2). \qquad (5)$$

And for 4 nesting attempts a reduced solution is:

$$\begin{aligned} m = {} & (E - NR)(1 - P - F)(1 + \alpha P + \alpha F + \alpha^2(P + F)^2 \\ & + \alpha^3(P + F)^3). \end{aligned} \qquad (6)$$

We estimated the sensitivity, S, of seasonal fecundity to each parameter (i.e., proportional change in seasonal fecundity from a proportional change in a parameter) by perturbing the model with small changes (10%) in a single parameter, x, while holding other parameters constant (Jørgensen and Bendoricchio 2001:27, 59–62). In this framework, the sensitivity of seasonal fecundity to parameter x is: $S_x = (x/m) \times (\Delta m/\Delta x)$. We estimated SE for seasonal fecundity using a parametric bootstrap (n = 5,000 replications), by using a beta distribution for all probability parameters (which constrains values to the 0–1 interval), a stretched beta distribution for other parameters (i.e., a beta distribution scaled to observed maxima and minima), and assuming parameters were independent (Morris and Doak 2002:275–282).

Estimating Annual Survival

Between 1999 and 2002, we attempted to estimate apparent annual survival of adult dickcissels and bobolinks using mark–recapture–resighting techniques (Lebreton et al. 1992). In 1999, we opportunistically marked individuals using playback tapes of male songs and by catching males and females at nest sites. From 2000 to 2002, we distributed nets across sites in the same locations each year, as described above for radiotelemetry, and we supplemented that technique by using playback tapes and catching individuals at nest sites. At each site, we resighted color-marked birds opportunistically during visits and also systematically with a spotting-scope approximately once every 2 weeks during the breeding season.

We estimated adult, apparent survival rates with Cormack-Jolly-Seber methods (Lebreton et al. 1992) using program MARK (White and Burnham 1999). Apparent survival rates (ϕ) represent a minimum estimate of survival because estimates do not distinguish permanent emigration from mortality (Lebreton et al. 1992). We compared a series of candidate models to explain apparent survival. We expected that apparent survival (ϕ) and resighting (p) probabilities could differ between sexes (i.e., $\phi[g]$ and $p[g]$; Bollinger and Gavin 1989, Zimmerman and Finck 1989). We also expected that year could influence both parameters if nesting success differed among years (i.e., $\phi[t]$ and $p[t]$) because site fidelity can vary depending on nest success (Bollinger and Gavin 1989). Thus, we compared our global model ($\phi[g \times t]p[g \times t]$) to reduced models using AIC, adjusted for small sample sizes and overdispersion ($QAIC_c$), and Akaike weights (Burnham and Anderson 1998). We assessed goodness-of-fit of global models using the bootstrap procedure implemented in MARK ($n = 1{,}000$ replications; White and Burnham 1999).

Juvenile survival rates are notoriously difficult to estimate in migratory songbirds because juveniles generally do not exhibit natal philopatry (Greenwood and Harvey 1982). No information has been reported on juvenile survival or return rates in dickcissels, but Wittenberger (1978) reported that over 2 years, 41% (7/17) of juvenile bobolinks returned. By combining count data to independently estimate the asymptotic finite rate of increase (λ), juvenile survival was estimated as approximately half of adult survival for some species (Noon and Sauer 1992, Murphy 2001). We used this fraction as a first approximation (see also Donovan et al. 1995, Brawn and Robinson 1996, McCoy et al. 1999), but we varied juvenile survival to determine how our inference might change using different estimates (see Model Variations).S_{ j}

Modeling Population Growth Rates

We used stage-structured, population projection modeling to estimate λ for dickcissels and bobolinks breeding in our study sites (Noon and Sauer 1992, Caswell 2001). Population projection modeling allows for estimating the relative contribution of demographic parameters to λ using proportional sensitivity, or elasticity analysis, which is useful for prescribing conservation strategies focused on increasing population growth rates (Benton and Grant 1999). We used a postbreeding, birth-pulse model to estimate λ (Noon and Sauer 1992):

$$\begin{pmatrix} S_j \times 0.5m & S_a \times 0.5m \\ S_j & S_a \end{pmatrix}, \tag{7}$$

where S_j is juvenile survival, S_a is adult survival (approximated by apparent survival, ϕ), and m is seasonal fecundity. We multiplied seasonal fecundity by the proportion of females fledged (0.5) to focus exclusively on females in the model, assuming a 1:1 sex ratio of fledged young (see also Woodworth 1999). We assumed that seasonal fecundity of second-year birds and after-second-year birds were equal (see also Woodworth 1999). Although components of seasonal fecundity can vary with age (e.g., Bollinger and Gavin 1989), we did not have estimates specific to second-year and after-second-year birds because neither species can be reliably aged based on plumage throughout the breeding season (Pyle 1997:623–626). Using this framework, we estimated λ using the characteristic equation (Caswell 2001:73) and approximated its SE and confidence limits using a parametric bootstrap as described above for seasonal fecundity ($n = 5{,}000$ replications; Caswell 2001:304–317). To do so, we approximated variance for juvenile survival by using the coefficient of variation of adult apparent survival estimates.

We quantified the contribution of demographic parameters to λ using elasticity analyses on both the matrix elements and on lower-level vital rates (e.g., renesting rate), but we focus on elasticities of λ to vital rates. For matrix elements, we estimated the elasticity as (Caswell 2001: 209–226):

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} \times \left(\frac{v_i \times w_i}{v \times w}\right), \tag{8}$$

where $e_{i,j}$ is the elasticity of λ to matrix element $a_{i,j}$, $\partial\lambda/\partial a_{i,j}$ is the sensitivity of λ to matrix element $a_{i,j}$, v is the left eigenvector of the matrix (the stage-specific reproductive value), and w is the right eigenvector of the matrix (the stable stage distribution). However, elasticities of λ to matrix elements do not isolate contributions of specific vital rates. To this end, we estimated the elasticities of λ to lower-level parameters (e_x) as:

$$\frac{x}{\lambda}\frac{\partial \lambda}{\partial x} = \frac{x}{\lambda}\sum_{i,j}\frac{\partial \lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial x}, \tag{9}$$

where x is the vital rate (Caswell 2001:232). Note that elasticities on lower-level vital rates do not sum to 1 (unlike elasticities of matrix elements; Caswell 2001). These elasticities should be interpreted as the proportional change in λ resulting from a proportional change in x. Elasticities can be positive or negative, depending on whether the parameter increases or decreases λ. In addition, we estimated the necessary change in vital rates to achieve stable populations ($\lambda = 1$) using the following equation (Caswell 2001:607):

$$\delta_x = \frac{1}{e_x}\left(\frac{\lambda' - \lambda}{\lambda}\right), \tag{10}$$

where δ_x is the proportional change in vital rate (x) required to change λ to λ' (i.e., $\lambda' = 1$), in the absence of other changes in demographic parameters.

We also estimated the necessary change in vital rates to achieve population growth rates quantified independently from density estimates, D (defined as $\lambda_{\text{ratio}} = D_{t+1}/D_t$; Powell et al. 2000), using Equation 10, where $\lambda' = \lambda_{\text{ratio}}$. We estimated density from point counts conducted in our study area each year using program DISTANCE (Buckland et al. 2001). DISTANCE uses distances from the center point to individuals for calculating detection functions. We surveyed each site ($n = 10$) during 3 periods in each year (20 May–6 Jul) using single observer, 10-min point counts with a 50-m fixed-radius for surveying breeding birds (Ralph et al. 1995). We determined point-count locations using proportional, stratified random sampling within each site, with 3–12 locations at least 150 m apart per site ($n = 102$ point locations). For analyses, we grouped distance estimates into 5 equal intervals (i.e., 0–10 m, 11–20 m, 21–30 m, 31–40 m, 41–50 m). We compared 5 types of models to determine the best estimate of the detection function (see Buckland et al. 2001:45–48). We estimated density for each year using a global detection function across years, and the same count locations and methods were used each year (see Fletcher and Koford [2002] for more details on methods).

Model Variations

We ran a series of model variations to interpret how our conclusions might change given different parameter estimates, and we focused on these model variations for all inferences because elasticities were local estimates (i.e., changing a demographic rate can change the elasticity and rank of elasticities among demographic parameters; Mills et al. 1999) and because we had little to no information on some parameters (e.g., juvenile survival). We considered models that included 1 more nesting attempt than the maximum number we observed with marked individuals (i.e., 4-attempt model for dickcissels and a 3-attempt model for bobolinks). We also considered a 2-attempt model for dickcissels because our radiomarked individuals were only observed to renest once (see Results). In addition to varying the number of nesting attempts, we varied the renesting probability because most other approaches assume renesting will occur if a nest fails before the end of the breeding season (Pease and Gryzbowski 1995). Further, we only estimated renesting probabilities in 2000 and that limits our knowledge on renesting potential in these species, and radiotransmitters can potentially have negative, short-term effects on grassland songbird hormone levels (Suedkamp Wells et al. 2003). We varied adult and juvenile survival because of the difficulty in estimating survival in songbirds. There have been no other studies estimating apparent survival in these species. However, based on return rates for these species (Wittenberger 1978, Bollinger and Gavin 1989, Zimmerman and Finck 1989), we varied juvenile survival between 20 and 50% and adult survival between 40 and 90%. While model perturbations concurrently varying all 4 parameters would illustrate the potentially multiplicative nature of these parameter uncertainties, a full factorial approach would be less tractable. Therefore, we focused perturbations separately on renesting (nesting attempts and renesting probabilities) and survival (juvenile and adult) uncertainties.

Results

Seasonal Fecundity

Over 4 years, we found 200 dickcissel and 237 bobolink nests, of which 77 dickcissel and 114 bobolink nests were successful. For each nesting component, there was no support for year effects in either species (AIC_c for intercept-only models were consistently lower than year-effect models; $\Delta AIC_c > 3.9$), except for the number of young fledged/successful unparasitized nest (E) for dickcissels (AIC_c year-effect models were lower than intercept-only models; dickcissels: $\Delta AIC_c = 14.0$). Therefore, we focused further analyses on mean estimates across years (Table 1), but we

Table 1. Parameter estimates used to model seasonal fecundity and population growth rates of dickcissels and bobolinks breeding in restored grasslands in northern Iowa, USA, 1999–2002. Also, estimated seasonal fecundity and estimated population growth rates from those models.

	Dickcissel		Bobolink	
Parameter	Mean	SE[a]	Mean	SE[a]
Nest predation rate, P	0.756	0.028	0.695	0.039
Nest failure rate, F[b]	0.015	0.002	0.011	0.001
Nest parasitism rate, N	0.187	0.063	0.178	0.028
Number fledged/successful unparasitized nest, E	2.984	0.125	3.990	0.144
Number fledged/successful parasitized nest, $E - R$	1.722	0.266	2.235	0.304
Probability of renesting, α	0.158	0.084	0.129	0.045
Seasonal fecundity, m				
2-Attempt model	0.707	0.105	1.180	0.162
3-Attempt model	0.716	0.111	1.189	0.164
4-Attempt model	0.717	0.113		
Juvenile survival, S_j[c]	0.245		0.360	
Adult survival, S_a[d]	0.490		0.721	0.097
Population growth rate, λ				
2-Attempt model	0.5766	0.0676	0.9334	0.1058
3-Attempt model	0.5777	0.0677	0.9350	0.1060
4-Attempt model	0.5779	0.0678		

[a] For seasonal fecundity and population growth rates, we estimated SE using a parametric bootstrap ($n = 5{,}000$ replications; Caswell 2001:304–317, Morris and Doak 2002: 275–282); we estimated SE for other parameters using generalized linear mixed models (Littell et al. 1996), with site as a random effect and year as a repeated measure.

[b] Failure from sources other than predation (e.g., weather-induced failure).

[c] Juvenile survival was estimated as half of adult survival (see also Donovan et al. 1995, Murphy 2001); therefore, we did not estimate SE. Because of this uncertainty, see Fig. 3 for model perturbations of this parameter.

[d] For dickcissels, we took adult survival from return rates observed in male dickcissels in Kansas (Zimmerman and Finck 1989); therefore, we did not estimate SE. For bobolinks, survival was based on mark–recapture data in Iowa estimated from a constant apparent survival, sex-specific recapture probability (Table 3). Because of these uncertainties, see Fig. 3 for model perturbations of this parameter.

Table 2. Summary of radiotelemetry (totals or means [SD]) used for estimating renesting in dickcissels and bobolinks breeding in restored grasslands in northern Iowa, USA, 2000.

Parameter	Dickcissels	Bobolinks
Individuals radiomarked	25	38
Number of locations/individual	23.0 (12.0)	13.4 (12.6)
Marked females with nests found	20	31
First nest successes	2	9
First nest failures	18	22
Days between nest failure and radio censor[a]	12.0 (12.0)	1 (3.0)
Females renesting	3	2
Renesting interval (days)	6–8	9–10
Second nest successes	1	1
Second nest failures	2	1

[a] For females that did not renest. Censoring could occur from radio failure or emigration from the study area.

investigated how variability in E for dickcissels affected seasonal fecundity and population growth rates. There was also no evidence for the planting type influencing nest predation rates (AIC_c for intercept-only models were lower than planting-type models; $\Delta AIC_c > 8.5$; cf. McCoy et al. 2001).

In 2000, we radiotracked 38 female bobolinks and 25 female dickcissels (Table 2). No confirmed mortalities of radiomarked females occurred during the breeding season. Only 2 female bobolinks and 3 female dickcissels renested after nest failure (Table 2), none of which renested more than once. However, in 2001, we observed a color-marked female dickcissel renest twice after nest failures. Overall, we obtained fewer locations for bobolinks than dickcissels because we tended to lose radio signals of bobolinks immediately after nest failure (Table 2), presumably from individuals emigrating out of the study area. There was no evidence of nest success differing among radiomarked and nonradiomarked females in 2000 (AIC_c for intercept-only models were lower than radio-effect models; $\Delta AIC_c > 3.1$). Only 1 bobolink nest failed within 48 hours of radiomarking (a time of known increases in stress hormones for radiomarked dickcissels; Suedkamp Wells et al. 2003), and the female's radio signal was lost immediately. Renesting (onset of egg-laying) occurred within 6–10 days of nest failure, and distances between successive nesting attempts ranged from 35 to 125 m for dickcissels and 430 to 8,600 m for bobolinks.

Estimates of seasonal fecundity were higher for bobolinks than for dickcissels (Table 1). Surprisingly, estimates were similar among the different models assuming 2–4 possible nesting attempts, probably because of low estimated renesting probabilities (α) and high nest predation rates. Sensitivities of seasonal fecundity to renesting probability were low but did increase with the number of possible nest attempts (Table 3). Sensitivities of seasonal fecundity were highest for nest predation rates (Table 3). Because there was evidence for year effects on E for dickcissels, we estimated fecundity using low (2.4 $\pm$ 0.2 fledglings) and high (3.6 $\pm$ 0.2) annual estimates of E. Overall, m changed approximately 0.13 (0.01 SD) fledglings/female from mean estimates. Increasing α resulted in small increases in seasonal fecundity, but as the number of nesting attempts increased, α had a stronger influence (Fig. 1).

Annual Survival

Between 1999 and 2002, we banded 102 dickcissels (38 females and 64 males) and 268 bobolinks (156 females and 112 males; Table 4). Annual return rates were relatively high for male bobolinks (48.2%; Table 4). Dickcissels and female bobolinks, however, exhibited very low return rates (Table 4; female bobolinks: 4.6%; female dickcissels: 2.9%; male dickcissels: 10.0%), limiting our ability to estimate apparent survival for dickcissels and for female bobolinks. Because dickcissels exhibited low return rates, for further analyses we first approximated $S_a = 0.49$, based on return rates observed by Zimmerman and Finck (1989), but we focus on model variations in survival to make inferences (Figs. 2, 3).

Overall, the global model for bobolinks fit the data relatively well (goodness-of-fit: $P = 0.32$). The best model describing apparent survival was a constant apparent survival rate with a sex-specific resighting probability ($\phi[.]p[g]$; Table 5); however, resighting rates were low for females ($p = 0.044 \pm 0.017$; males: $p = 0.573 \pm 0.108$). We were interested in whether similar apparent survival rates between sexes were reasonable. Fletcher (2003) reanalyzed data from Bollinger and Gavin (1989) and found no evidence for different apparent survival rates between sexes (the only other dataset to our knowledge that allowed for estimating apparent survival in bobolinks), although estimates were lower than estimates from Iowa (New York: $\phi = 0.501 \pm 0.041$; $p = 0.912 \pm 0.057$). Furthermore, a male-only model from the Iowa data set provided a similar estimate ($\phi = 0.702 \pm 0.095$) to the 2-sex model (Table 1), so for projection modeling, we used the estimate from the 2-sex model as a first approximation for S_a.

Table 3. Sensitivity[a] of seasonal fecundity estimates to changes in parameters, based on 3 different models assuming 2–4 potential nesting attempts for dickcissels and bobolinks breeding in restored grasslands in northern Iowa, USA, 1999–2002.

	Dickcissel			Bobolink	
Parameter	2 attempts	3 attempts	4 attempts	2 attempts	3 attempts
Nest predation rate, P	−3.231	−3.211	−3.206	−2.298	−2.287
Nest failure rate, F[b]	−0.066	−0.061	−0.059	−0.036	−0.036
Nest parasitism rate, N	−0.091	−0.086	−0.084	−0.085	−0.085
Number fledged/successful unparasitized nest, E	0.877	0.883	0.885	0.893	0.893
Reduction in number fledged/ successful parasitized nest, R	−0.087	−0.086	−0.085	−0.084	−0.084
Probability of renesting, α	0.103	0.134	0.141	0.085	0.100

[a] Sensitivity estimated by increasing 1 parameter (10%) while holding all other parameters in model constant (i.e., the sensitivity of fecundity to parameter x is: $S_x = [x/m] \times [\Delta m/\Delta x]$).
[b] Failure from sources other than predation (e.g., weather-induced failure).

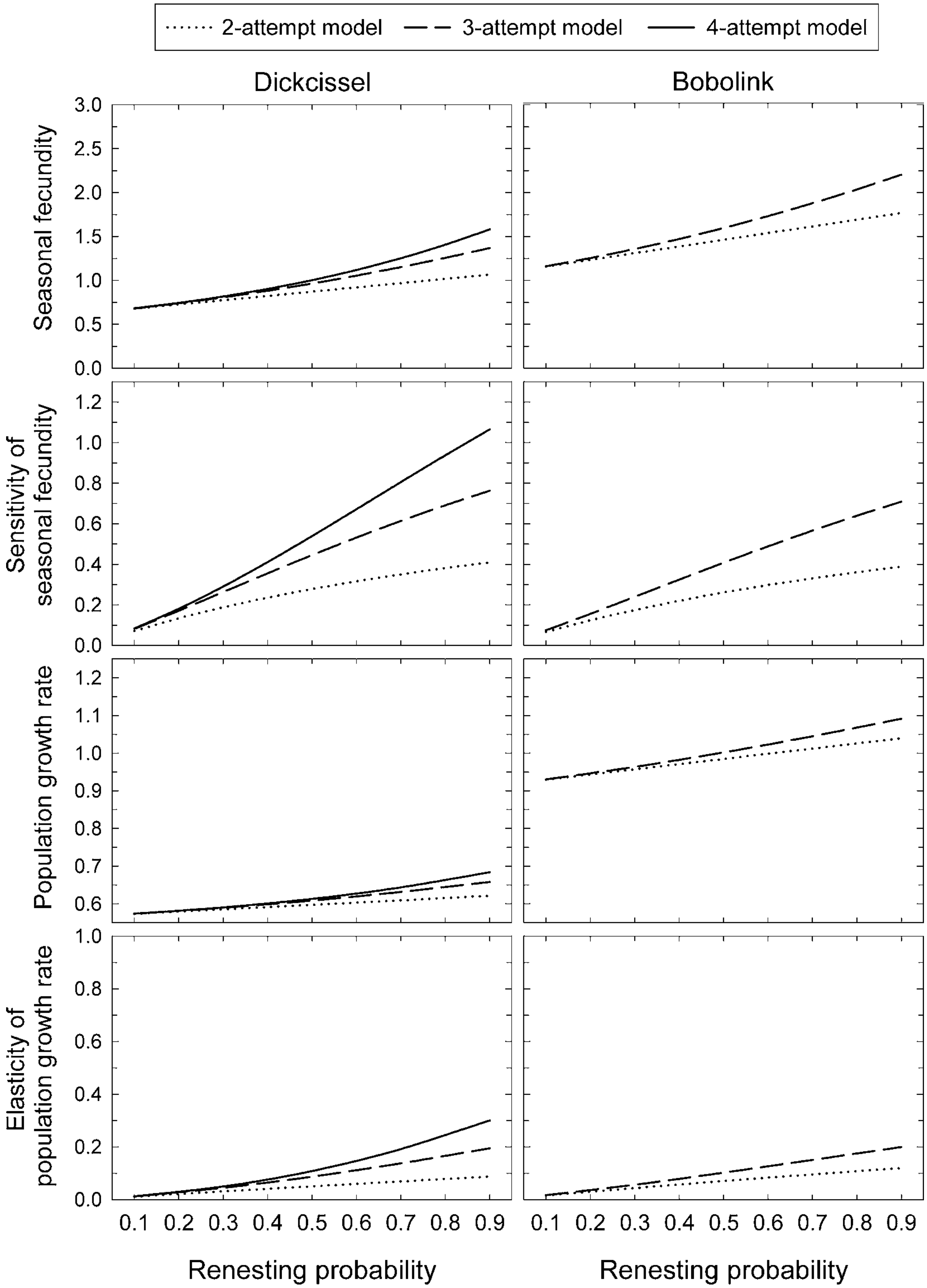

Figure 1. Model variations of renesting probability and its effects on estimates of seasonal fecundity and population growth, and the elasticity of renesting on seasonal fecundity and population growth for dickcissels and bobolinks breeding in northern Iowa, USA, 1999–2002.

Population Growth Rates

For both species, population growth rates were estimated to be <1 (Table 1); confidence limits suggested that the estimated growth rate for dickcissels was significantly <1 (95% CI: 0.443–0.711) but not for bobolinks (95% CI: 0.711–1.122). Uncertainty in population growth estimates was primarily due to uncertainty in survival estimates. When we varied survival estimates to account for this uncertainty, it was apparent that population growth in these areas was not stable for dickcissels and was only stable for bobolinks if juvenile and/or adult survival was relatively high (Fig. 2). Each model type (2–4 nesting attempts) showed similar results.

Matrix-element elasticities for dickcissels from the 3 nesting-attempt model were (Table 1):

Table 4. Summary of mark–recapture data used for estimating apparent annual survival of adult bobolinks in northern Iowa, USA, 1999–2002.

Year released	*R(i)*[a]	Number of recaptures 2000	2001	2002	Total recaptured
Bobolink males					
1999	8	5	0	1	6
2000	50		21	5	26
2001	51			20	20
Bobolink females					
1999	9	1	0	0	1
2000	55		1	3	4
2001	46			0	0

[a] Number of newly marked individuals released in year *i*.

$$e_{ij} = \begin{pmatrix} 0.023 & 0.128 \\ 0.128 & 0.722 \end{pmatrix}.$$

Bobolink matrix-element elasticities from the 2 nesting-attempt model were (Table 1):

$$e_{ij} = \begin{pmatrix} 0.052 & 0.176 \\ 0.176 & 0.597 \end{pmatrix}.$$

For both species, matrix-element elasticities suggested that adult survival had a greater relative contribution to the population growth rate than did seasonal fecundity or juvenile survival. However, matrix-element elasticities do not partition components of seasonal fecundity nor do they isolate demographic parameters (see Equations 7, 8), so we focused on vital rate elasticities. Varying renesting probabilities tended to have small effects on population growth rates of both species (Fig. 1). Elasticity of λ was greatest for adult survival (Table 6). Elasticity associated with nest predation was relatively high but highly dependent on survival estimates (Fig. 3). Elasticity of λ to brood parasitism and renesting were weak (Figs. 1, 3), while elasticity associated with juvenile survival was also relatively weak (Table 6, Fig. 3). Furthermore, even if brood parasitism was reduced to zero, population growth rates would not be stable for either species (in the absence of changes of other parameters; Table 6).

Based on density estimates (Fig. 4), the estimated population growth rates ($\lambda_{\text{ratio}} = D_{t+1}/D_t$) for dickcissels and bobolinks were 1.02 ($\pm$0.49 SD) and 1.18 ($\pm$0.17 SD), respectively. For dickcissels, λ_{ratio} declined for 2 of 3 years, whereas λ_{ratio} was stable or increasing for bobolinks each year. For dickcissels, only increasing adult survival to approximately 90% could result in stable population growth or λ_{ratio} (Table 6). For bobolinks, both lowering nest predation and increasing survival could result in stable population growth or λ_{ratio} (Table 6).

Discussion

Habitat Restoration and Population Growth Rates

Based on our model variations (Fig. 2), we found that restored grasslands in Iowa were likely sink habitats for dickcissels, in which the populations were not sustainable without immigration. McCoy et al. (1999, 2001) also found that dickcissel populations breeding in Conservation Reserve Program fields in Missouri were apparently not self-sustaining. For bobolinks, population growth could only be stable if annual survival was relatively high (Fig. 2, Table 5). No other efforts have been made to estimate population growth rates for bobolinks, so it is unknown how our results compare with population dynamics in other regions.

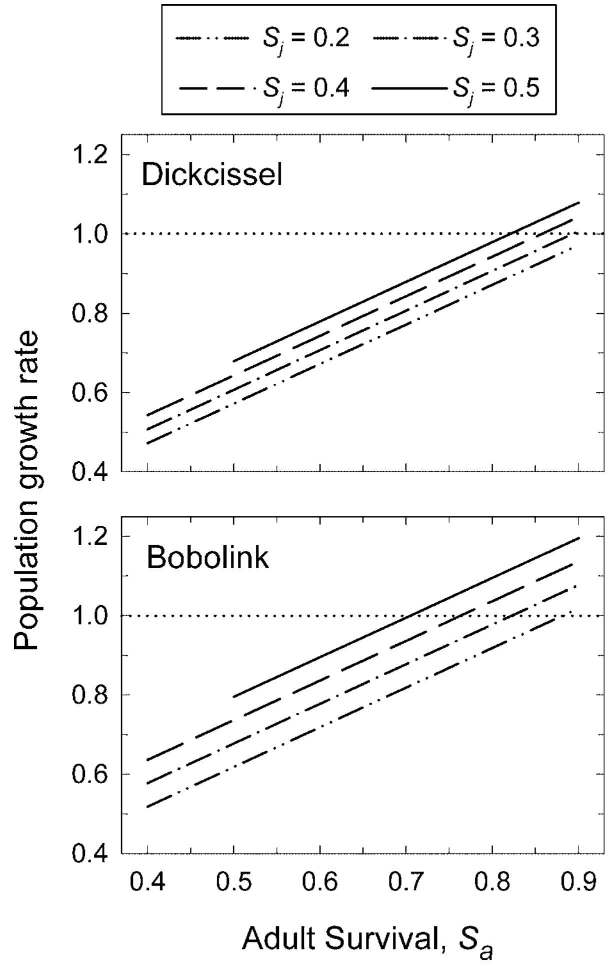

Figure 2. Estimated population growth rates under adult and juvenile survival model variations for dickcissels and bobolinks breeding in northern Iowa, USA, 1999–2002. Seasonal fecundity was held constant and based on the 3 nesting-attempt model for dickcissels and the 2 nesting-attempt model for bobolinks. The dotted line highlights where populations are stable (i.e., $\lambda = 1$).

Estimates of population growth based on demographic data for both species did not match observed estimates of growth based on count data. Two principal explanations for this incongruence are 1) estimates of demographic parameters were biased low, and 2) immigration into the area was counteracting demographic performance. The primary demographic parameters that could be biased include renesting probabilities and survival. Although radiotelemetry might have underestimated renesting probabilities and estimates were based only on 1 year, increasing probabilities had a relatively small effect on population growth (see Fig. 1). Furthermore, synchronous nest initiation dates of unmarked bobolinks in our study area suggest that renesting was probably infrequent for this species (Fletcher 2003; see also Wittenberger 1978). Dickcissels are thought to renest more frequently, with reported renesting probabilities ranging from 27 to 39% (Temple 2002, Walk et al. 2004). Yet even renesting probabilities in this range would not substantially change the relative importance of renesting on population growth (Fig. 1).

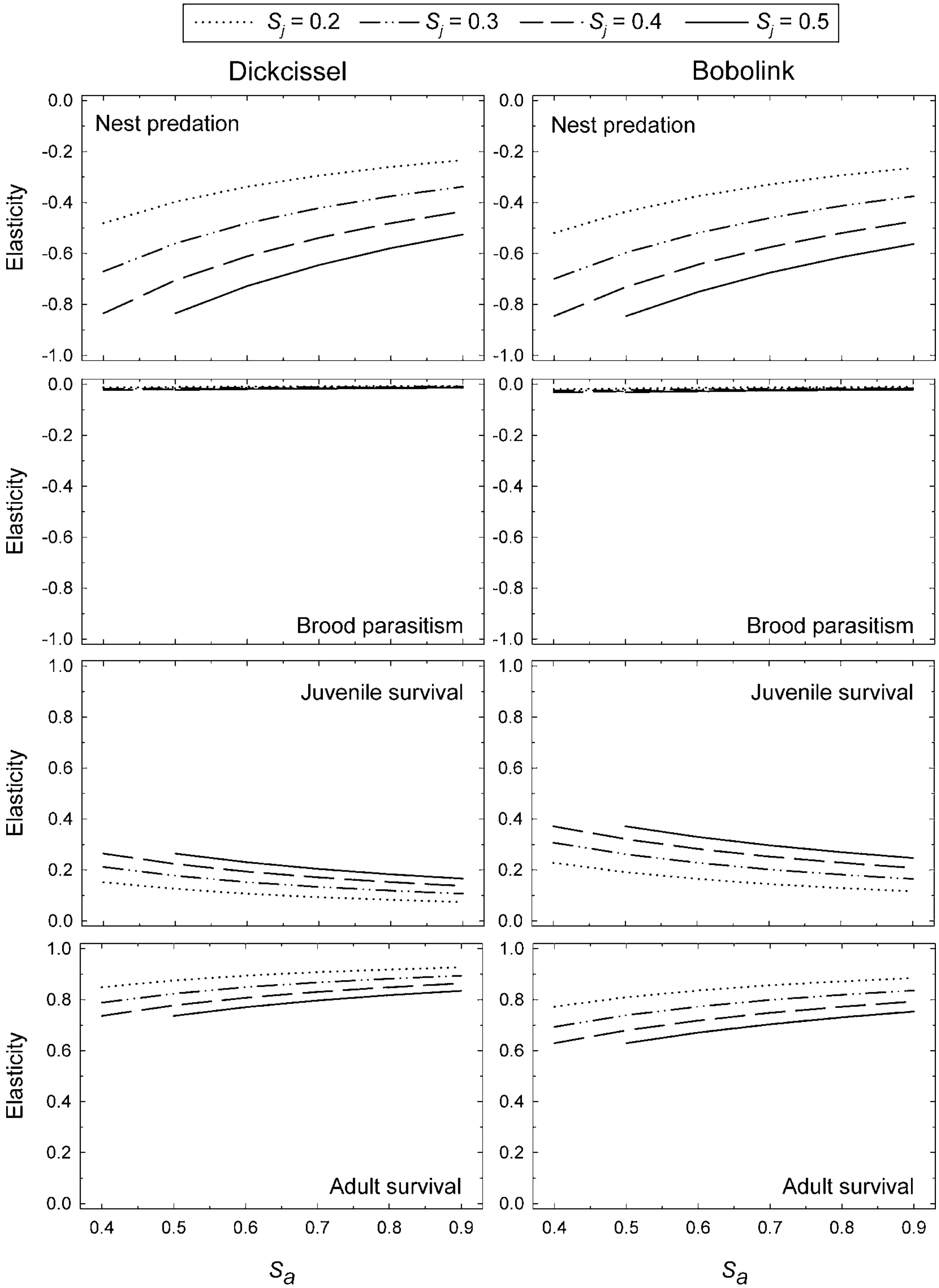

Figure 3. Elasticities of nest predation, brood parasitism, juvenile survival, and adult survival across a wide range of juvenile and adult survival parameter space for dickcissels and bobolinks breeding in northern Iowa, USA, 1999–2002. Seasonal fecundity was held constant and based on the 3 nesting-attempt model for dickcissels and the 2 nesting-attempt model for bobolinks.

We approximated survival with return rates for dickcissels and apparent survival rates for bobolinks, both of which provide minimum estimates of survival because estimates do not distinguish mortality from permanent emigration. Return rates also do not adjust for recapture or resighting probabilities, which tend to bias estimates even more than mark–recapture methods. Using return rates or apparent annual survival in projection matrices typically causes survival to contain a component of movement, whereas fecundity does not (Nichols et al. 2000). One approach that can potentially circumvent this problem is reverse-time mark–recapture modeling (Nichols et al. 2000), which can also estimate the contribution of apparent survival and recruitment to population growth. However, that approach cannot partition contributions of lower-level vital rates, which are important

Table 5. Assessment of candidate models for estimating annual apparent survival of adult bobolinks in northern Iowa, USA, 1999–2002. Models were compared using Akaike's Information Criterion and Akaike weights, adjusted for sample size and overdispersion ($QAIC_c$; Burnham and Anderson 1998). The difference of the model with the lowest $QAIC_c$ and each model candidate model ($\Delta QAIC_c$) are reported as a measure of comparison.

Model[a]	K[b]	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
$\phi(.)p(.)$	2	127.96	24.98	0.00
$\phi(.)p(g)$	3	102.98	0.00	0.46
$\phi(g)p(.)$	3	108.28	5.30	0.03
$\phi(g)p(g)$	4	104.71	1.73	0.19
$\phi(g + t)p(g)$	5	106.24	3.26	0.09
$\phi(g)p(g + t)$	5	105.76	2.78	0.11
$\phi(g)p(t)$	5	111.37	8.39	0.01
$\phi(t)p(g)$	5	106.55	3.57	0.08
$\phi(g + t)p(g + t)$	7	109.85	6.87	0.01
$\phi(t)p(g + t)$	7	110.15	7.17	0.01
$\phi(g \times t)p(g \times t)$	10	115.84	12.86	0.00

[a] Model structure: ϕ = apparent survival, p = recapture probability, g = gender, t = time (year), (.) = constant.
[b] K = Number of estimable parameters.

components of conservation strategies for songbirds. Another approach is to estimate survival during different periods of the annual cycle (Sillett and Holmes 2002) and incorporate these periods into the matrix design, but estimates for different periods are scarce or nonexistent for most songbirds. Finally, multistate mark–recapture models can potentially partition movement among patches from adult mortality (Schwarz et al. 1993), but multistate mark–recapture models are still confounded by permanent emigration outside of a study area (a multistate model for bobolinks provided similar estimates to the CJS model: ϕ = 0.721 $\pm$ 0.098). Yet for both species, model perturbations indicated that increasing survival still could not produce λ similar to those based on count data, except at extremely high survival levels. Immigration into the area is thus a likely factor influencing annual population size. This pattern suggests that grassland bird population dynamics could be operating at very large scales and warrants investigation on dispersal and sources of immigrants (see also Brawn and Robinson 1996). However, we caution that our modeling approach focused primarily on concurrently perturbing only 1–2 parameters to facilitate interpretation of parameter importance, yet concurrently perturbing all parameters might have yielded some different insights.

Because seasonal fecundity and growth rates were low in these areas, a question that immediately arises is whether grassland restoration in rowcrop-dominated landscapes is ultimately bad for breeding grassland birds in this region. Restoration could be increasing the amount of habitat that acts as ecological traps (Schlaepfer et al. 2002) in which individuals prefer settling in habitat that results in lower fitness relative to other, less-preferred habitats. Unfortunately, we were not able to estimate seasonal fecundity and population growth rates in other potentially suitable habitats. Two common approaches for evaluating restoration include comparing bird populations in restored habitat to native habitat or to the previous habitats that were restored (Fletcher and Koford 2002, 2003), yet these approaches were limited for 2 reasons. First, <0.01% of prairies remain in this region (Smith 1998), and those that do remain are widely distributed across the state (see Fletcher and Koford 2002). This distribution makes comparisons difficult because avian demography is likely operating at different spatial scales in remaining isolated prairies than in the restored complex that we investigated. Second, sites in this

Table 6. Elasticities of population growth rates (λ) to demographic parameters and the change in parameters necessary to achieve a stable population ($\lambda = 1$), and population growth based on density estimates (λ_{ratio}) for dickcissels and bobolinks breeding in northern Iowa, USA, 1999–2002.

		Proportional change necessary for λ to equal:		Estimate necessary for λ to equal:[b]	
Species/Parameter	Elasticity[a]	1	λ_{ratio}	1	λ_{ratio}
Dickcissel					
Nest predation rate, P	−0.481	−1.52	−1.61	NP	NP
Nest failure rate, F[c]	−0.009	−79.46	−83.96	NP	NP
Nest parasitism rate, N	−0.013	−56.23	−59.42	NP	NP
Number fledged/successful unparasitized nest, E	0.165	4.43	4.68	NP	NP
Reduction in number fledged/successful parasitized nest, R	−0.013	−56.23	−59.42	NP	NP
Probability of renesting, α	0.020	36.19	38.24	NP	NP
Juvenile survival, S_j	0.152	4.81	5.09	NP	NP
Adult survival, S_a	0.848	0.86	0.91	0.91	0.94
Bobolink					
Nest predation rate, P	−0.519	−0.13	−0.51	0.60	0.34
Nest failure rate, F[c]	−0.009	−8.39	−31.08	NP	NP
Nest parasitism rate, N	−0.019	−3.70	−13.69	NP	NP
Number fledged/successful unparasitized nest, E	0.247	0.29	1.07	5.14	NP
Reduction in number fledged/successful parasitized nest, R	−0.019	−3.70	−13.69	NP	NP
Probability of renesting, α	0.019	3.76	13.91	0.61	NP
Juvenile survival, S_j	0.228	0.31	1.16	0.47	0.78
Adult survival, S_a	0.772	0.09	0.34	0.79	0.97

[a] For elasticity estimates, seasonal fecundity was held constant and based on the 3 nesting-attempt model for dickcissels and the 2 nesting-attempt model for bobolinks (Table 1).
[b] Estimate necessary while holding all other parameters constant, estimated from Equation 10. NP = not possible, or beyond the possible range of parameter values (e.g., negative nest predation rates required).
[c] Failure from sources other than predation (e.g., weather-induced failure).

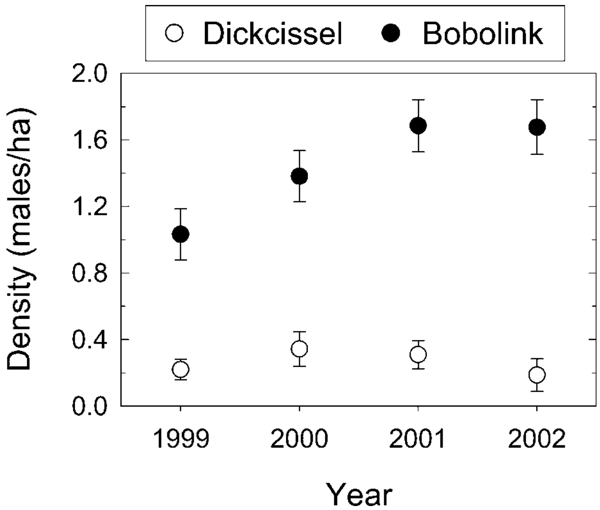

Figure 4. Densities (males/ha; $\bar{x} \pm$ SE) of dickcissels and bobolinks breeding in restored grasslands in northern Iowa, USA, 1999–2002. Densities were estimated using point counts as described by Fletcher and Koford (2002). For both species, a uniform key function with no adjustments was the most parsimonious model to explain detectability within point counts.

complex were restored primarily from rowcrop agriculture, which is not generally used by dickcissels or bobolinks during the breeding season (Fletcher and Koford 2003), and that prevented comparisons of avian demography based on land-use change with restoration. Even if nesting biology was compared among other habitats, the critical issue is arguably whether restored areas can make positive contributions to population dynamics and what demographic parameters ultimately drive population growth rates. Areas with low population growth rates could, however, have positive impacts on population size if movement occurs between these areas and areas with high growth rates (Pulliam and Danielson 1991).

Critical Parameters Contributing to Population Growth Rates

For both species, adult survival consistently had the strongest relative effect on population growth rates. Using a spatially explicit modeling approach, Pulliam et al. (1992) estimated that adult and juvenile survival were the primary parameters influencing growth rates in Bachman's sparrows (*Aimophila aestivalis*). Murphy (2001) found that population growth rates in eastern kingbirds (*Tyrannus tyrannus*) were most sensitive to adult survival, whereas sensitivities to juvenile survival and fecundity were similar and less than half of sensitivities to adult survival. Moreover, a recent review also suggested that adult survival is generally the predominant parameter influencing growth rates across a wide diversity of birds (Sæther and Bakke 2000).

Nest predation tended to have the largest relative effect on seasonal fecundity (see also Schmidt and Whelan 1999), and it had larger relative effects on population growth rates than other breeding parameters. The influence of nest predation was likely conservative in our model as well because our model did not explicitly incorporate partial nest predation (Ackerman et al. 2003); the potential effect of partial nest predation was subsumed within the total number of young fledged/successful nest. The relative importance of nest predation to population growth was greater when assuming high levels of juvenile survival and low levels of adult survival. Nest predation should become relatively more limiting to recruitment if juvenile survival is high, whereas nest predation becomes less limiting with high adult survival because individuals have more breeding opportunities. Sæther and Bakke (2000) also found that the contribution of fecundity to population growth rates decreased with increasing adult survival. These results highlight the need for good estimates of survival, not only for understanding the contribution of survival to population growth but also for interpreting the importance of nest predation to population dynamics.

Perhaps most surprising was the consistently small effect of brood parasitism and relatively small effect of juvenile survival on growth rates of both species. Parasitism rates in our system were moderate compared to other grassland systems (Martin and Gavin 1995, Temple 2002, Herkert et al. 2003). Yet even when parasitism rates are high, high nest predation rates can swamp out detrimental effects of parasitism (Schmidt and Whelan 1999). Although brood parasitism rates had relatively small effects on population growth, our modeling approach and other similar approaches do not incorporate 2 factors that might increase the relative importance of brood parasites to population growth: 1) the positive feedback of cowbirds fledging from host nests, and 2) the impact of nest destruction by cowbirds (Arcese et al. 1996). Modeling the interactions of hosts and parasites could provide a different picture in understanding population dynamics, but in our system, low growth rates of hosts likely had negative effects on parasite dynamics that in turn could further reduce detrimental parasite influence on host growth rates. While brown-headed cowbirds are known to destroy nests (Arcese et al. 1996), this impact is typically not distinguished from nest predation and could lead to underestimating the effect of parasites on population growth rates (Smith et al. 2002).

Recently, attempts were made to estimate post-fledging survival in some migratory songbirds (e.g., Powell et al. 2000). While investigating post-fledging survival provides critical information on a poorly understood period, our results suggest that the importance of post-fledging survival (which is subsumed within S_j in our models) might be less than for some other parameters, such as adult survival and nest predation, influencing population dynamics of these grassland songbirds.

Management Implications

Our results suggest that conservation strategies focused on adult survival during the nonbreeding season might be more fruitful than strategies focused during the breeding season because apparent adult survival in songbirds tends to be lower during that period (Powell et al. 2000, Sillett and Holmes 2002). Indeed, dickcissels and bobolinks are thought to be agricultural pests on much of their wintering grounds in South America, and mortality in these areas could be high (Martin and Gavin 1995, Temple 2002). Yet we caution that when applying elasticity analyses for conservation, one must consider what demographic parameters are amenable to management (Benton and Grant 1999, Mills et al. 1999). While our analysis suggests that adult annual survival is of critical importance to population growth rates of dickcissels and bobolinks, this parameter might be more difficult to manage for than some other demographic parameters.

On the breeding grounds, conservation strategies need to concentrate on ameliorating the detrimental effects of nest predation more than any other demographic parameter for these grassland birds (see also Schmidt and Whelan 1999). However, the predator community affecting grassland birds can be diverse (Pietz and Granfors 2000, Renfrew and Ribic 2003), which makes cookbook prescriptions difficult and limited. One approach that could reduce the overall intensity of nest predation is increasing patch size and the amount of habitat in the landscape (Winter and Faaborg 1999, Heske et al. 2001, Herkert et al. 2003). Yet Herkert et al. (2003) recently found that only in extremely large patches (>1,000 ha) did nest predation consistently decrease for many grassland birds. Nest predation can also increase near edges in grasslands, particularly near woodlands (Johnson and Temple 1990, Bollinger and Gavin 2004). Understanding, and perhaps directly managing, the predator community will certainly be critical for sound conservation strategies focused on breeding grassland songbird populations.

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