Metapopulation Dynamics of Bobolinks Occupying Agricultural Grasslands in the Midwestern United States

3 authors, including:

John B. Dunning
Purdue University
71 PUBLICATIONS   **5,084** CITATIONS

SEE PROFILE

Kimberly A. With
Kansas State University
97 PUBLICATIONS   **8,677** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project   Behavioral Landscape Ecology: Individual Movement Responses to Landscape Structure View project

Project   Essentials of Landscape Ecology View project

Metapopulation Dynamics of Bobolinks Occupying Agricultural Grasslands in the Midwestern United States

DANIEL M. SCHEIMAN[1] AND JOHN B. DUNNING, JR.

Department of Forestry and Natural Resources, 195 Marsteller St., Purdue University, West Lafayette, Indiana 47907

AND

KIMBERLY A. WITH

Division of Biology, Kansas State University, Manhattan 66506

ABSTRACT.—A metapopulation is any set of populations that are patchily distributed and potentially connected by dispersal. This broad definition includes classical, mainland-island, source-sink, patchy and non-equilibrium metapopulations. To ensure long-term regional population viability in a fragmented landscape we need a better understanding of metapopulation dynamics. To determine which metapopulation model applies to a given species, Stith *et al.* (1996) developed a classification scheme using species-specific estimates of dispersal distance and local extinction risk. We used this scheme to classify bobolink (*Dolichonyx oryzivorus*) populations occupying fragmented, agricultural grasslands in the Midwestern United States. We estimated the distribution of dispersal distances using mark-recapture techniques and calculated local extinction risk. Dispersal rate and turnover were high, indicating that populations were highly connected. Local extinction probability was 4%, indicating that populations were ''midlands'' and vulnerable to extinction. Well-connected populations constitute a patchy metapopulation according to Stith *et al.*'s (1996) scheme. Bobolink dispersal ability was sufficient to overcome habitat fragmentation. Our research showed that the Stith *et al.* (1996) classification can be applied to a migratory species, but should be expanded to the metalandscape scale.

INTRODUCTION

A classical metapopulation is a collection of populations that are spatially divided by a matrix of unsuitable habitat but are connected through dispersal (Levins, 1969). Metapopulation persistence is maintained by the balance between local extinction and recolonization. Critical evaluation of classical metapopulation model assumptions and predictions has concluded that this balance is probably unrealistic for most real-world systems (Harrison, 1991). Thus, the metapopulation framework has been redefined broadly to describe any set of populations that are patchily distributed across a landscape and are actually or potentially connected by dispersal (Wiens, 1996). In addition to the classical metapopulation model, other models have been used to describe the dynamics of spatially subdivided populations: mainland-island, source-sink, patchy and nonequilibrium meta-populations (Harrison, 1991).

High variation in patch size and hence population size characterizes the mainland-island model (Harrison, 1991). The mainland population is large enough to resist local extinction effectively, and supplies smaller, more extinction-prone island populations with colonists. In this case, not all populations are subject to extinction. The source-sink model is conceptually similar to the mainland-island model, but in the case of source-sink dynamics, variation in patch quality, not necessarily size, affects local extinction probability (Harrison,

---

[1] Corresponding author present address: Audubon Arkansas, 201 East Markham St., Suite 450, Little Rock, Arkansas 72201; e-mail: dscheiman@audubon.org

1991). High quality sources are unlikely to suffer local extinction and supply low quality sinks with colonists. In the case of a patchy metapopulation, a high dispersal rate effectively prevents local extinctions. Individuals disperse so frequently that spatially separated groups of individuals are members of a single functional population (Harrison, 1991). Non-equilibrium dynamics occur when dispersal rate is so low that local extinction rate is greater than recolonization rate. Thus, the regional population is declining, not stable as in the other metapopulation models (Harrison, 1991).

Different management strategies are required for different types of metapopulations (Wiens, 1996; Hanski, 1999). For example, large habitat patches containing relatively large populations should be preserved in any system because these mainlands ensure continued persistence. Maintaining connectivity will be important for classical metapopulations to increase the chance that recolonization follows local extinction. Habitat restoration may be required for nonequilibrium systems to reverse the decline in abundance (Stith *et al.*, 1996). Therefore, appropriate conservation strategies stem from an accurate understanding of metapopulation dynamics.

To classify population dynamics and determine which metapopulation model applies to a particular species in a given area, Stith *et al.* (1996) made use of the empirically supported idea that colonization rate decreases with increasing population isolation and extinction rate decreases with increasing population size. They classified population dynamics using species-specific information on population connectivity and local extinction probabilities (Fig. 1). Specifically, they used the distribution of dispersal distances to delineate two buffers. The inner ''subpopulation buffer'' represents the distance at which local dispersal is common, thus lumping spatially separated groups of individuals into a demographically linked single population. The outer ''metapopulation buffer'' represents the smallest interpatch distance where dispersal rate is effectively zero. Populations within the metapopulation buffer are connected by dispersal to some degree; populations outside this buffer are effectively isolated. Stith *et al.* (1996) quantified extinction probabilities for each local population, and classified populations as extinction-resistant (<2% probability of extinction, termed ''mainlands''), extinction-vulnerable (2–50% probability, ''midlands'') or extinction-prone (>50% probability, ''islands''). The combination of relative population isolation and size can thus be used to classify metapopulations. For example, the classical metapopulation exists as a collection of islands, each separated by a subpopulation buffer, but contained within a single metapopulation buffer.

Stith *et al.* (1996) applied their scheme to the Florida scrub-jay (*Aphelocoma coerulescens*), a permanent resident of southern Florida. Metapopulation theory was originally conceived for and has been most often applied to nonmigratory species. In these species, demographic isolation of populations is often equivalent to geographic isolation (Esler, 2000). Populations of migratory organisms, on the other hand, do not remain in one location throughout the annual cycle. Instead, individuals make long-distance movements between breeding seasons, and these movements may affect their settlement patterns in subsequent years. If migrants settle in different landscapes within a region, they may contribute to a higher level of connectivity than is envisioned by Stith *et al.* (1996).

The bobolink (*Dolichonyx oryzivorus*) makes one of the longest migrations of any North American songbird, a roundtrip of 20,000 km between North and South America (Martin and Gavin, 1995). During migration and on the wintering grounds, birds are gregarious. During the breeding season, however, males become territorial, and the species maintains potentially independent populations on spatially discrete habitat patches (Martin and Gavin, 1995). Decreasing quantity and quality of habitat patches have caused populations to
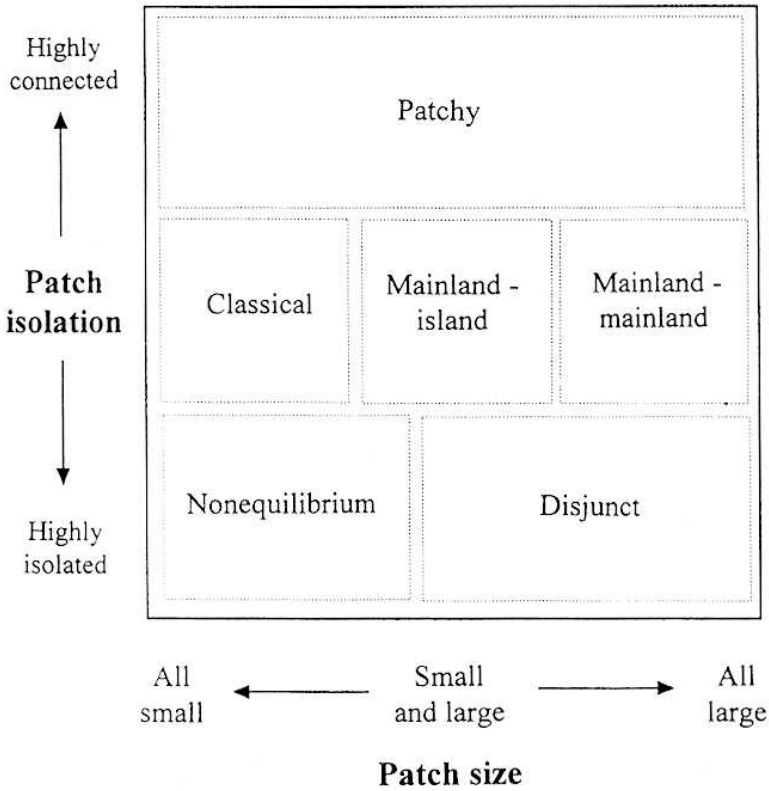
FIG. 1.—Metapopulation classification scheme developed by Stith *et al.* (1996; Fig. 9.3; From ''Classification and conservation of metapopulations: a case study of the Florida scrub-jay'' by Bradley M. Stith, *et al.* Found in Metapopulations and wildlife conservation by Dale R. McCullough, ed. Copyright © 1996 by Island Press. Reproduced by permission of Island Press, Washington, D.C.). This scheme uses species-specific information on dispersal rates and local extinction rates to assess relative patch isolation and size, respectively

decline throughout the species' breeding range (-1.8% change/y, 1966–2005), including Indiana (-7.1% change/y, 1966–2005; Sauer *et al.*, 2005). Conversion to agriculture has caused the area of tallgrass prairie in the United States to decline 88–99% (Samson and Knopf, 1994). Although the species readily occupies agricultural grasslands such as hayfields and pastures, increased frequency of haying and intensity of grazing has further decreased the availability of suitable nesting and foraging patches (Bollinger and Gavin, 1992; Perlut *et al.*, 2006). To assess long-term regional population viability in a fragmented landscape, and to make appropriate management decisions, we need a better understanding of bobolink metapopulation dynamics. Therefore, our purpose was to use the distribution of dispersal distances and extinction risk to classify the metapopulation dynamics of bobolinks occupying hayfields and pastures in an agricultural landscape of the Midwestern United States. In addition, we assessed the applicability of Stith *et al.*'s (1996) classification scheme to a migratory bird.
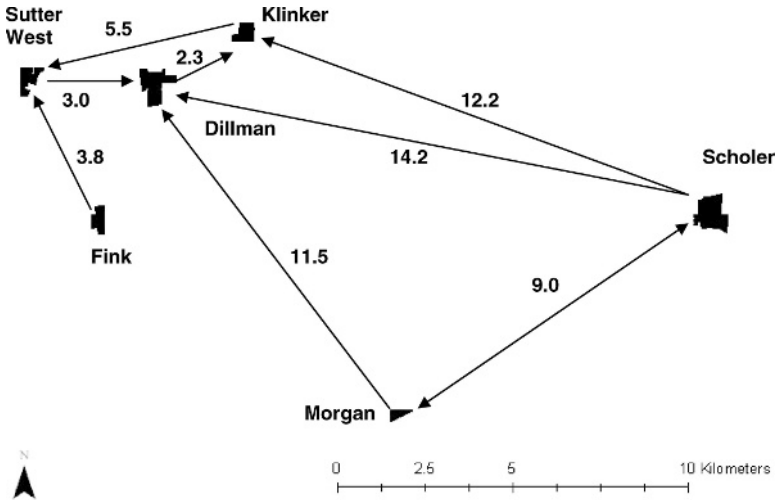
Fig. 2.—Spatial arrangement of six habitat patches occupied by bobolinks in Warren Co., Indiana, during May–Jul. 2001–2004. Dispersal directions and distances (km) are shown for 10 males. Two males dispersed from Fink to Sutter West

METHODS

Study sites.—During May–Jul. 2001–2004, we studied bobolinks on privately owned hayfields and cattle pastures in Warren County, west-central Indiana (Fig. 2). We searched the county (area = 945 km^2) thoroughly to locate all suitable habitat patches. The nearest known occupied habitat patch beyond our study area was 19 km east of Scholer in Tippecanoe County. In a metapopulation framework, populations and habitat patches must be defined independently. We defined a habitat patch as one or a collection of several adjacent hayfields or pastures. A population was the collection of individuals that had a high likelihood of interaction. Therefore, habitat patches were defined by spatial separation, and populations were defined by demographic association. Under the initial naïve assumption that each group of individuals occupying a habitat patch represented an independent population, we delineated six populations occupying six habitat patches ranging in size from 7.8–58.7 ha. Mean interpatch distance was 9.3 km (median = 9.7 km, range = 2.3–17.8 km).

Dispersal.—Throughout each field season we captured adult male and female bobolinks in mist nets. Captured birds were banded with aluminum U.S. Geological Survey bands, as well as three colored leg bands. A unique color combination identified the individual as well as the habitat patch in which the bird was banded. Each habitat patch was systematically searched for banded birds by one or two observers once per week. We analyzed the observations of banded birds as mark-recapture data using a multistate model (Arnason, 1973) in program MARK (version 4.1; White and Burnham, 1999) to obtain estimates of survival, recapture and movement probabilities. Input consisted of only males because of insufficient sample size of females (n = 58 banded, 0 recaptured). Both within and between-year capture occasions were used in the model. To account for the time in between seasons when estimating survival parameters, we specified different lengths for each period between capture occasions: one (~wk) for occasions within a season and 36 (wk) for occasions between seasons. We compared models using Akaike's Information Criterion for small sample size (AIC$_c$), where the model with the lowest AIC$_c$ is considered to be the best model

Table 1.—Values of ΔAIC_c and AIC_c weights for the candidate set of multistate models fitted to mark-recapture data collected on male bobolinks. Models included either a patch (g), constant (.) or other specified effect on survival (S), recapture (p), and movement (Ψ) probabilities

Model	ΔAIC_c	AIC_c weight
$S(g)p(g)\Psi(.)$	0.0	0.98
$S(.)p(g)\Psi(g)$	8.9	0.01
$S(g)p(g)\Psi(\text{patch size})$	9.3	0.01
$S(g)p(g)\Psi(\text{interpatch distance})$	28.9	0.00
$S(g)p(g)\Psi(g)$	36.8	0.00
$S(g)p(.)\Psi(g)$	68.5	0.00

given the data (Akaike, 1973). The set of six candidate models included a group (*i.e.*, patch) effect for survival, recapture and movement probabilities; a constant probability for either survival, recapture, or movement; and an effect of either patch size or interpatch distance on movement probability (Table 1).

<center>Results</center>

Dispersal.—We banded 143 males, and resighted 105 males (73%) at least once during subsequent capture occasions within or between years. Thirty males (21%) survived and were recaptured in subsequent breeding seasons. Twenty-four of these birds (80%) were site faithful. Ten males (9.5% of 105 males resighted) moved up to 14.2 km (mean = 7.4 km, median = 7.3 km) to a different population from the one in which they were banded, either within or between years. The maximum, mean and median observed dispersal distances were less than the maximum (17.8 km), mean (9.3 km) and median (9.7 km) interpatch distances. However, the distributions of dispersal and interpatch distances were not significantly different (Fisher's exact test $\chi^2_4 = 1.2$, P = 0.96). The model with a group effect for survival and recapture, and constant dispersal rate among habitat patches, provided the best fit to the data among candidate models (AIC_c weight = 0.98; Table 1). However, small sample size may have made it difficult to detect an effect of patch, patch size and interpatch distance on movement probability. Adult male survival probability was 0.57–0.90, and recapture probability was 0.21–0.56 among populations. The probability of an individual dispersing from one habitat patch to any other habitat patch during a season was 0.24.

Extinction risk.—We observed one local extinction during the study. In 2001 Fink (Fig. 2) was a hayfield and hosted nesting birds. However, in 2002 and 2003, cattle were introduced and season-long grazing kept the vegetation too short for territory establishment. In 2004 the pasture was converted to row-crop. One extinction event among six populations over 4 y corresponded to a 4% risk of local extinction.

Metapopulation classification.—The relatively high dispersal rate, high survival rate, low recapture rate among years, and constant dispersal probability among habitat patches suggest that dispersal is frequent, thus functionally linking the spatially separated groups of individuals into a single population. Although we did not observe dispersal across the longer interpatch distances, observed dispersal distances were in proportion to available interpatch distances. Furthermore, nearest neighbor distances (mean = 4.9 km, median = 3.3 km, maximum = 9.0 km) were narrower than the range of interpatch distances. Thus, no patch was isolated beyond the maximum observed dispersal distance, and even patches that were farthest apart could be connected in a stepping-stone fashion. In addition, we observed only adult male dispersal. Dispersal tends to be female- and juvenile-biased in songbirds (Greenwood and

Harvey, 1982). Thus, the observed distribution of dispersal distances may be skewed towards the shorter distances more typical of males. Given the evidence, the subpopulation buffer is at least 17.8 km, the maximum interpatch distance, but is probably beyond the radius of our study area. The metapopulation buffer also is located at an unquantified distance beyond our study area. Local extinction risk was 4%, indicating local populations were vulnerable to extinction, *i.e.*, midlands (Stith *et al.*, 1996). A collection of midlands encircled within a metapopulation buffer is a patchy metapopulation; the upper middle section of Fig. 1.

<center>DISCUSSION</center>

Metapopulation dynamics.—Quantification of bobolink breeding dispersal ability and local extinction probability suggested that the initial assumption of demographically indepen-dent populations was incorrect, and that birds occupying spatially discrete habitat patches in Warren County actually constituted a single demographic unit, *i.e.*, a patchy metapopula-tion. Our study sites were privately owned properties that were managed independently for agriculture. Groups of birds that were spatially close could have had their population dynamics independently driven by local agricultural practices. Instead, evidence suggests that dispersal functionally linked these groups despite disturbances at the patch level.

Classification of local populations as midlands based on local extinction risk makes sense in light of field observations. Midlands are characterized by rescue (Brown and Kodric-Brown, 1977) rather than the extinction-recolonization turnover observed on islands (Stith *et al.*, 1996). In a patchy metapopulation consisting of midlands, frequent dispersal should rescue populations from local extinction (Harrison, 1991). Although local extinctions are rare, complete turnover of individuals can occur, as evidenced by studies on marked birds (Stacey and Taper, 1992). We observed one local extinction during the study. We also observed considerable turnover; only 17% of banded birds survived and were site faithful among years. Although we do not know what fraction of banded birds returned but were undetected, male bobolinks are behaviorally conspicuous and tend to be highly detectable when present (Wittenberger, 1978; Fletcher and Koford, 2003). Therefore, we suspect that each year some banded birds permanently emigrated from the study area and were replaced by unmarked immigrants from other metapopulations.

Metapopulation models assume that empty habitat patches remain suitable for recolonization, and regional decline occurs because dispersers fail to reach empty patches (Levins, 1969). Regional declines in the bobolink may not necessarily be the result of metapopulation dynamics failure, but rather a result of the loss of habitat across the species' range (Bollinger and Gavin, 1992). Our observed local extinction resulted from habitat loss rather than a stochastic event that leaves a patch empty, but suitable. In spite of habitat loss, dispersal from within the metapopulation was sufficient to maintain connectivity among habitat patches in the landscape, *i.e.*, landscape connectivity. In addition, observed turnover suggests that the Warren County metapopulation was connected to other metapopulations in the region, *i.e.*, metalandscape connectivity (With *et al.*, 2006). Just as there is a threshold of habitat loss at which a landscape becomes disconnected and metapopulation dynamics disrupted, there is also a threshold of regional habitat loss at which metalandscape connectivity is broken, affecting a species' regional persistence (With *et al.*, 2006). Regional persistence of a variety of migratory birds (*e.g.*, Robinson *et al.*, 1995; Tittler *et al.*, 2006) and probably the bobolink as well, may depend on providing enough habitat to maintain dispersal between source and sink landscapes.

Even in areas where habitat availability remains stable through time, decreased habitat quality through fragmentation and anthropogenic disturbances can decrease the viability of
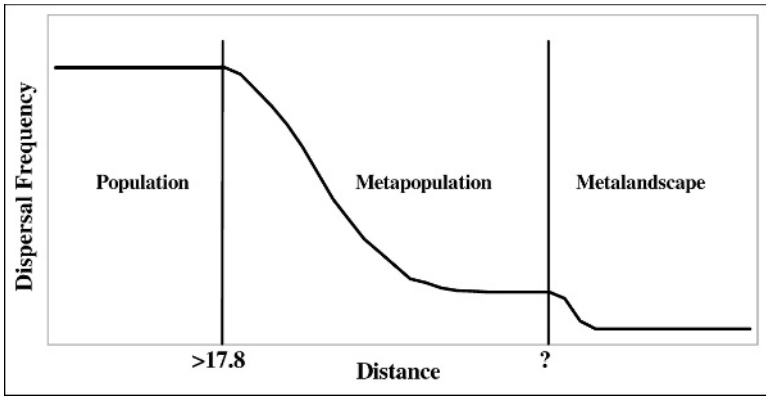
FIG. 3.—Location of subpopulation buffer (left-hand vertical line) and metapopulation buffer (right-hand vertical line) based on the distribution of male bobolink dispersal distances. The metapopulation buffer lies at an undetermined distance >17.8 km. The dispersal frequency curve is hypothetical and based on the assumption that as interpatch distance increases dispersal frequency decreases until it reaches some infinitesimally small rate. The metalandscape domain expands the Stith *et al.* (1996) metapopulation classification scheme to include long-distance dispersal that connects metapopulations across landscapes

a metapopulation. Florida scrub-jay populations have declined in urban areas where habitat fragmentation and the absence of fire cause reduced reproductive success (Breininger, 1999). A metapopulation of bank swallows (*Riparia riparia*) along the Sacramento River, CA, required habitat restoration to reduce the probability of local, *i.e.*, colony, extinction and halt overall metapopulation decline (Moffatt *et al.*, 2005). In the case of bobolinks, fragmentation decreases patch area and increases edge, which leads to increased rates of nest predation and parasitism (Johnson and Temple, 1990). Agricultural practices, such as haying, may not permanently alter habitat quality but can significantly reduce the annual productivity of an entire population (Bollinger and Gavin, 1992). Thus, observed regional declines also could result from a gradual reduction in population abundance, even if habitat is available and dispersal rates are high.

Metapopulation classification scheme.—Stith *et al.* (1996) developed an empirically driven, species-centered method for classifying metapopulations. Their scheme was designed for a permanent resident with a limited geographic range and limited propensity for dispersal. To accommodate a species with a broader range and greater dispersal capability, such as a migratory bird, the model should be expanded to include the metalandscape buffer and domain (Fig. 3). For migratory birds, entire landscapes may be linked by long distance dispersal within or between seasons to produce regional metapopulation dynamics (With *et al.*, 2006). If a metapopulation depends on immigration from other metapopulations to sustain it, understanding local population dynamics will not be sufficient for making inferences about regional persistence. Examination of metalandscape dynamics ultimately may be required to understand the persistence of a species in a particular landscape.

CONCLUSIONS AND RECOMMENDATIONS

Bobolinks in Warren County displayed patchy metapopulation dynamics and appeared to exchange individuals with other metapopulations, suggesting that their dispersal ability was sufficient to overcome current levels of habitat fragmentation. Yet bobolinks are

experiencing range-wide population declines. Management should focus on improving population productivity. Disturbance regime management can enhance patch quality and, hence, nest success (Bollinger and Gavin, 1992; Perlut *et al.*, 2006). Dispersal within and between metapopulations can offset declines and maintain a species' persistence, but will not be sufficient in the face of widespread habitat loss and nest failure (With *et al.*, 2006).

The limit of functional connectivity for bobolinks still is unknown. Future research should expand the spatial scale under consideration to locate the metapopulation and metalandscape buffers. Besides expanding the search radius for banded birds, the use of stable isotope (Hobson *et al.*, 2004) and genetic techniques (Arsenault *et al.*, 2005) may help quantify dispersal ability. Once the buffers have been identified, we will have a better idea of the scale at which bobolinks perceive the landscape and can then focus management efforts accordingly. In the meantime, maintaining interpatch distances of ≤18 km should provide connectivity and allow for rescue. Perhaps more importantly, habitat patch quality must be maintained by adjusting the timing and frequency of disturbances to maintain suitable vegetation structure but prevent widespread nest failure (Perlut *et al.*, 2006).

LITERATURE CITED

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle, p. 267–281. *In:* B. N. Petrov and F. Csaki (eds.). 2nd international symposium on information theory. Akademia Kiado, Budapest, Hungary.

ARNASON, A. N. 1973. The estimation of population size, migration rates and survival in a stratified population. *Res. Popul. Ecol.*, **15**:1–8.

ARSENAULT, D. P., P. B. STACEY AND G. A. HOELZER. 2005. Mark-recapture and DNA fingerprinting data reveal high breeding-site fidelity, low natal philopatry, and low levels of genetic population differentiation in flammulated owls (*Otus flammeolus*). *Auk*, **122**:329–337.

BOLLINGER, E. K. AND T. A. GAVIN. 1992. Eastern bobolink populations: ecology and conservation in an agricultural landscape, p. 497–506. *In:* J. M. Hagan, III and D. W. Johnston (eds.). Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution. Press, Washington, D.C., USA. 610 p.

BREININGER, D. R. 1999. Florida scrub-jay demography and dispersal in a fragmented landscape. *Auk*, **116**:520–527.

BROWN, J. H. AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**:445–449.

ESLER, D. 2000. Applying metapopulation theory to conservation of migratory birds. *Conserv. Biol.*, **14**:366–372.

FLETCHER, R. J. AND R. R. KOFORD. 2003. Spatial responses of bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk*, **120**:799–810.

GREENWOOD, P. J. AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.*, **13**:1–21.

HANSKI, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford, U.K. 313 p.

HARRISON, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biol. J. Linn. Soc.*, **42**:73–88.

HOBSON, K. A., L. I. WASSENAAR AND E. BAYNE. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with ovenbirds and American redstarts. *Condor*, **106**:732–743.

JOHNSON, R. G. AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *J. Wildl. Manage.*, **54**:106–111.

LEVINS, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Ent. Soc. Amer.*, **15**:237–240.

MARTIN, S. G. AND T. A. GAVIN. 1995. Bobolink (*Dolichonyx oryzivorus*). *In:* A. Poole and F. Gill (eds.). The birds of North America, no. 176. Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C., USA.

MOFFATT, K. C., E. E. CRONE, K. D. HOLL, R. W. SCHLORFF AND B. A. GARRISON. 2005. Importance of hydrologic and landscape heterogeneity for restoring bank swallow (*Riparia riparia*) colonies along the Sacramento River, California. *Restor. Ecol.*, **13**:391–402.

PERLUT, N. G., A. M. STRONG, T. M. DONOVAN AND N. J. BUCKLEY. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. *Ecol. Applications*, **16**:2235–2247.

ROBINSON, S. K., F. R. THOMPSON, III, T. M. DONOVAN, D. R. WHITEHEAD AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**:1987–1990.

SAMSON, F. AND F. KNOPF. 1994. Prairie conservation in North America. *Bioscience*, **44**:418–421.

SAUER, J. R., J. E. HINES AND J. FALLON. 2005. The North American breeding bird survey, results and analysis 1966–2005. ver. 6.2.2006 U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, U.S.A. [online: http://www.mbr-pwrc.usgs.gov/bbs/].

STACEY, P. B. AND M. TAPER. 1992. Environmental variation and the persistence of small populations. *Ecol. Applications*, **2**:18–29.

STITH, B. M., J. W. FITZPATRICK, G. E. WOOLFENDEN AND B. PRANTY. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub jay, p. 187–215. *In:* D. R. McCullough (ed.). Metapopulations and wildlife conservation. Island Press, Washington, D.C., USA. 439 p.

TITTLER, R., L. FAHRIG AND M. VILLARD. 2006. Evidence of large-scale source-sink dynamics and long-distance dispersal among wood thrush populations. *Ecology*, **87**:3029–3036.

WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, (suppl.): 120–138.

WIENS, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management, p. 53–84. *In:* D. R. McCullough (ed.). Metapopulations and wildlife conservation. Island Press, Washington, D.C., USA. 439 p.

WITH, K. A., G. R. SCHROTT AND A. W. KING. 2006. The implications of metalandscape connectivity for population viability in migratory songbirds. *Landscape Ecol.*, **21**:157–167.

WITTENBERGER, J. F. 1978. The breeding biology of an isolated bobolink population in Oregon. *Condor*, **80**:355–371.