

Oak Ridge National Laboratory
Environmental Sciences Division

**Assessing the Persistence of an Avian Population
in a Managed Landscape: A Case Study With
Henslow's Sparrow at Fort Knox, Kentucky**

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ABSTRACT

We describe a model of how the spatial distribution of nesting habitat affects the reproductive success of territorial migrant bird species breeding in fragmented landscapes. The model combines a landscape perspective with conventional avian demographic modeling to provide a tool for the assessment of how land-use change might impact the persistence of avian populations. Nesting habitat is mapped with a regular grid of square cells. Neighboring cells are aggregated to form patches. Territories are distributed among patches using logistic regressions describing the relationship between species' occurrence and patch area. Nesting success in each patch is a function of the patches edge:area ratio, reflecting the association of edge with increased risk of predation and brood parasitism. The number of female fledglings produced by all patches is used to calculate the expected number of female fledglings per female. This demographic variable, an explicit consequence of landscape structure, is combined with survivorship in a life-table model to calculate the demographic indices of net lifetime maternity and the finite rate of increase. These indices provide a simple characterization of the landscape as a population source or sink. We describe an implementation of the model for Henslow's sparrow (*Ammodramus henslowii*) at the Fort Knox Military Reservation, Fort Knox, Kentucky. The model indicates that the Fort Knox landscape is a population sink for Henslow's sparrow, with an annual rate of decline of approximately 14%. Analysis of the model results suggest that the prediction of a declining population at Fort Knox is a consequence of too little successful reproduction combined with too low rates of survivorship.

1. INTRODUCTION

Habitat loss and fragmentation have been implicated in the decline of many bird populations in North America and elsewhere (Whitcomb et al. 1981, Wilcove et al. 1986, van Dorp and Opdam 1987, Enoksson et al. 1995, Robinson et al. 1995, Stouffer and Bierregaard 1995). Neotropical migrants and forest-interior species are often the focus of concerns over habitat fragmentation, but short-distance migrants, residents, and grassland species may also be impacted (Herkert 1994, Enoksson et al. 1995). Deforestation, urbanization, and the conversion of native grasslands to pasture and cropland reduce the availability of suitable habitat. The increase in edge habitat that accompanies fragmentation may increase brood parasitism and nest predation and lower reproductive success of interior species (Paton 1994). Isolation, or insularization (Wilcox 1980), can interfere with dispersal and contribute to the decline and extinction of local populations. Fragmented landscapes may function as population sinks where reproduction fails to compensate for mortality (Pulliam 1988, Pulliam and Danielson 1991, Robinson 1992, Donovan et al. 1995). Persistence of a species in sink landscapes requires immigration of individuals from more productive source landscapes. Pulliam (1988) introduced the concept of demographic sources and sinks with reference to “habitat”, or more generally “compartment” (Pulliam 1988, p. 653), but the idea is easily extended to a heterogeneous landscape composed of multiple habitat types (Donovan et al. 1995).

Assessing the persistence of avian populations in fragmented landscapes requires an explicit consideration of the effects of landscape pattern on population dynamics. Compliance with directives for ecosystem management and preservation of biodiversity on public lands (Cooperrider 1991, Salwasser 1991, Petit et al. 1995, Beattie 1996, Dombek 1996, Goodman 1996, Thomas 1996) requires assessment of how landscape pattern and changes in landscape pattern affect bird populations. Land managers need to know whether the landscapes under their purview are functioning as sources or sinks for species of conservation concern, and whether feasible changes in land use and the resulting landscape pattern could shift a landscape from sink to source.

Here we describe a model of spatially structured avian demography. The model combines a landscape perspective with demographic modeling to provide a tool for the assessment of land use and land-use change on the persistence of bird populations in a managed landscape. The version of the model described here applies to territorial migrants. The model assumes that landscape structure only affects female fecundity on the breeding ground. Survivorship is not affected, and the migration and overwintering stages of the annual life cycle are not modeled. Designed explicitly as an assessment tool, the model strives for simplicity and ease of implementation. Accordingly, the model is primarily phenomenological in nature and does not attempt a mechanistic description of avian biology. Model inputs and, just as importantly, the data required to test the model are parameters and variables that can be taken from existing literature, or can reasonably be expected to be collected as part of a landscape assessment.

The model was specifically developed for the assessment of avian demography on Department of Defense (DoD) installations, and we present a case study here of Henslow’s sparrow (*Ammodramus henslowii*) at the Fort Knox Military Reservation, Fort Knox, Kentucky. However, the model’s general structure also applies to other territorial migrants on other landscapes, both public and private.

2. THE MODEL

Consider a landscape of several thousand hectares in the breeding range of a migratory bird species. The species is monogamous on the breeding grounds, and mated pairs establish and defend all-inclusive Type A territories within which nesting and most foraging takes place (Hinde 1956, Morse 1980). The landscape is mapped with a regular grid of square cells. Habitat used for nesting is distinguished from non-nesting habitat. Cells of nesting habitat are aggregated into patches if they are separated by less than the distance the pair will readily cross in using and defending their territory, i.e., their gap-crossing ability (Dale et al. 1994) This gap-crossing ability can be determined from behavioral observations of territory use and defense. A patch so defined by the species' gap-crossing ability is modeled as if it were contiguous homogeneous vegetation or landcover. The individual's gap-crossing integrates the heterogeneous vegetation of the gaps into a territory of effectively homogeneous nesting habitat. This integration defines patches of potential nesting habitat. The matrix between patches is not used for nesting.

Patches of nesting habitat smaller than the species' territory size are not used for nesting. Patches larger than this minimum size are filled with territories (equivalently: nests, breeding pairs, or breeding females) according to an incidence function J_A (Wilcove et al. 1986) which describes the probability of encountering a breeding pair (or territory) at a random point in a patch of area A (Robbins et al. 1989) (Fig. 1). Incidence is calculated with a logistic regression model

$$J_A = \frac{\exp[\beta_0 + \beta_1 \log_{10} A + \beta_2 (\log_{10} A)^2]}{1 + \exp[\beta_0 + \beta_1 \log_{10} A + \beta_2 (\log_{10} A)^2]} \quad 1$$

where β_0, β_1 and β_2 are model (regression) parameters. The probability of occurrence J_A is interpreted as the proportion of the patch occupied, and the number of nests \mathcal{N} in patch i is the occupied area divided by territory size, or

$$\mathcal{N}_i = J_A A_i / A_T \quad 2$$

where A_T is territory size (ha), and \mathcal{N}_i is rounded to the nearest integer. The maximum number of nests in a patch is patch area divided by territory size and occurs when $J_A = 1.0$.

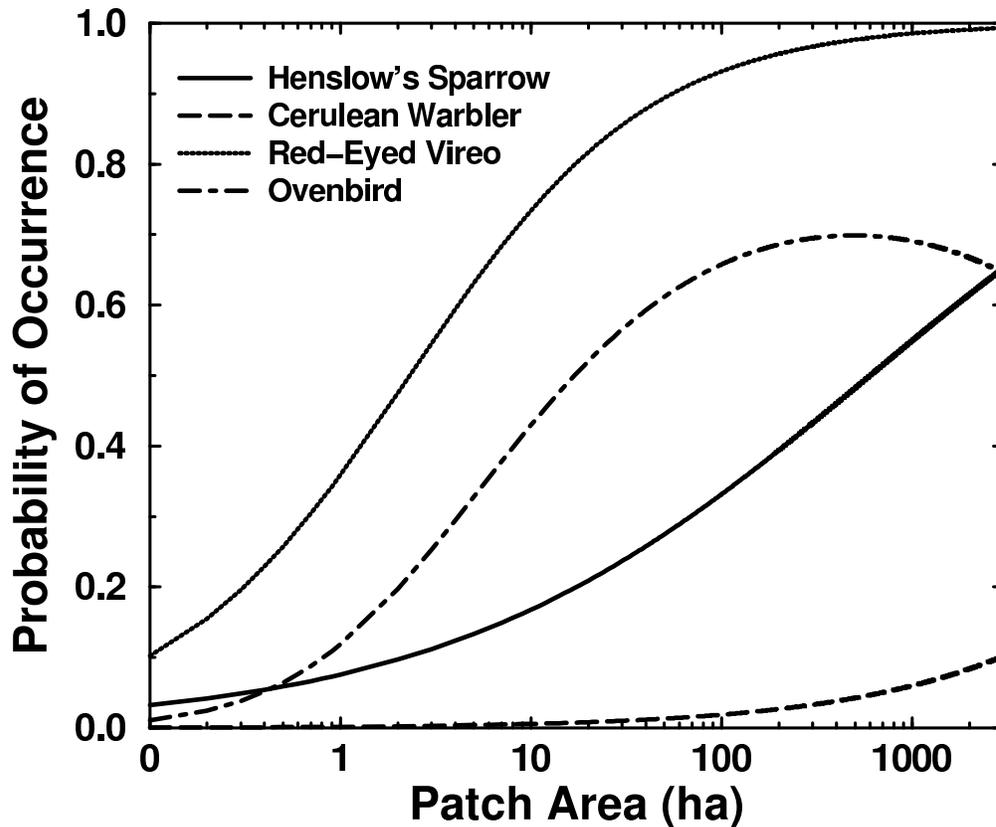


Fig. 1. A sample of incidence functions for different bird species. The curve for Henslow's sparrow is from Herkert (1994); the others are from Robbins et al. (1989).

Each nest in each patch produces a clutch of eggs. Clutch size C for each nest is drawn independently from a species- or population-specific frequency distribution. The clutch size of some species is uniformly distributed between a minimum and maximum; others have a model clutch size. Consequently, clutch size may vary among nests.

Nesting success, the probability that a nest will produce at least one fledgling (Johnson and Temple 1986), is a function of a patch's edge:area ratio. Reflecting the assumption that higher rates of nest predation and parasitism are associated with increased amounts of edge, and edge has a negative affect on nesting success, nesting success is lower in patches with a large edge:area ratio (i.e., those patches with lots of edge per unit area). Maximum nest success occurs in large patches with relatively little edge. The edge:area ratio is normalized by the edge:area ratio of a single square cell, yielding an edge:area index with a maximum value of 1.0 indicating maximum edge per unit area. A value near 0.0 indicates a patch with minimal edge per unit area. The probability of nesting success in patch i , S_i , is given by

$$S_i = S_{\max} \frac{1}{1 + (e_i/k)^\theta} \quad 3$$

where S_{\max} is the maximum probability of nesting success for patches with an edge:area ratio approaching zero, or, equivalently, nesting success in the absence of any edge effect, and e_i is the normalized edge:area index of patch i . The parameter k is the value of e_i where $S_i = 0.5S_{\max}$, and θ is a parameter which determines the rate at which nesting success declines with larger edge:area ratios.

Nesting success in the absence of any edge effect, S_{\max} , will be less than one; some nests will be loss to predation, storms, or other factors, regardless of their proximity to an edge. The probability of nesting success will be less than one even in the largest most contiguous patch of habitat. Some species will be relatively insensitive to edge, at least until patches become mostly edge (i.e., the edge:area index approaches 1). We refer to this pattern as a Type I edge response (Fig. 2). Other species will be very sensitive to edge, and the probability of nesting success will decline very rapidly with an increasing edge:area ratio (a Type III response, Fig. 2). Others will show an intermediate response of more gradual decline with increasing edge per unit area (Type II, Fig. 2) Calibration of the parameters S_{\max} , k , and θ will fit the nesting success curve of Equation 3 to any observed or hypothesized response to edge within this family of response curves.

Nesting success in the model is evaluated stochastically for each nest in a patch. The probability that a nest in patch i fledges no young is $1 - S_i$. Nests which fledge at least one young are assumed to fledge the entire clutch, so F_{ji} , the number of fledglings from nest j in patch i , is C_{ji} (the clutch size of that nest) for successful nests and 0.0 for unsuccessful nests.

The sex of each fledgling is determined stochastically according to the population's fledgling female:male sex ratio. Thus, it is possible for a nest to produce only male or only female fledglings, but cumulatively, across all nests in the landscape, the ratio of female to male fledglings will approach the population's or species' fledgling sex ratio (normally assumed to be 1:1 or 50% females).

Productivity, the number of fledglings (of both sexes) per nest (or territory or pair) for patch i , is

$$P_i = \frac{\sum_{j=1}^{\mathcal{N}_i} F_{ji}}{\mathcal{N}_i} \quad 4$$

where F_{ji} is the number of fledglings in nest j of patch i . Productivity can vary from patch to patch, primarily as a consequence of patch variability in the probability of nesting success, itself a consequence of variability in edge:area among patches. Thus the model reflects variability in patch "quality" and contribution to population dynamics (Pulliam and Danielson 1991) but only that associated with patch size and shape. Productivity for the entire landscape or population, P_L , (not the mean of patch productivity) is

$$P_L = \frac{\sum_{i=1}^m \sum_{j=1}^{\mathcal{N}_i} F_{ji}}{\sum_{i=1}^m \mathcal{N}_i} \quad 5$$

where m is the number of patches. Note that these estimates of productivity incorporate reductions in productivity due to nest failure. The expected productivity of successful pairs (or nests) is the mean clutch size.

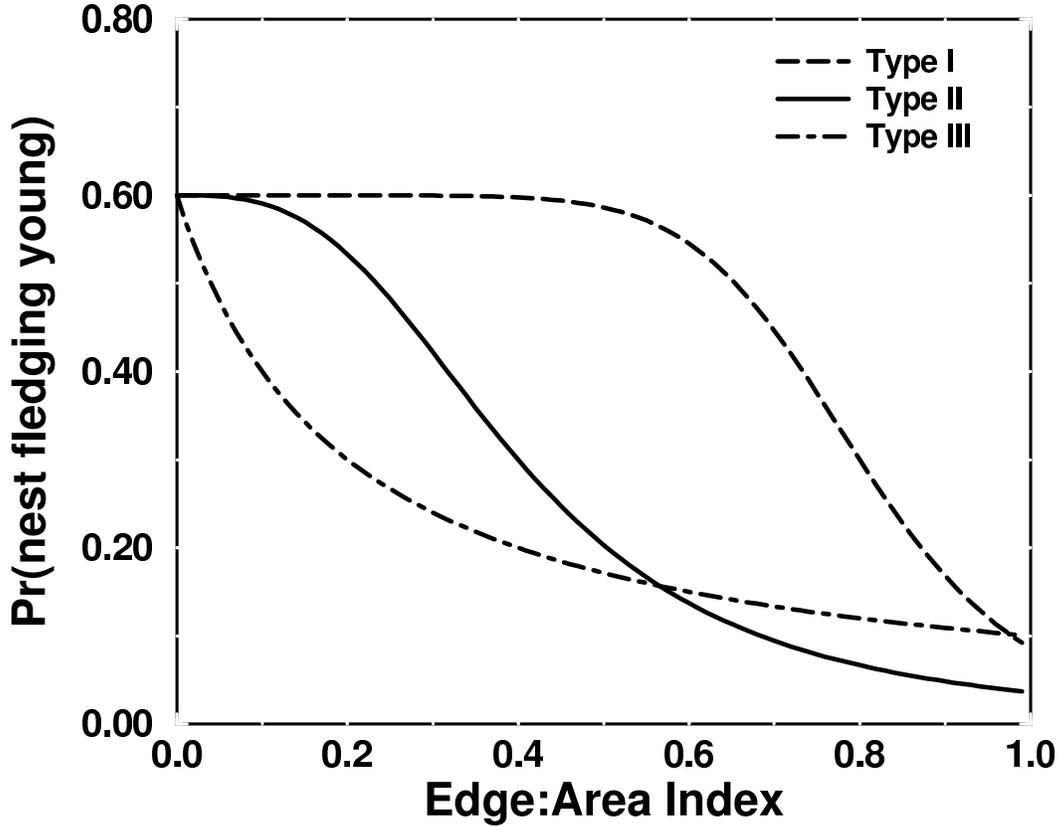


Fig. 2. The relationship between nesting success and the patch edge:area index. The solid curve is parameterized with data from Johnson and Temple (1986); the others are theoretical alternatives.

The demographic parameter b , the expected number of female fledglings produced per female, is

$$b = \frac{\sum_{i=1}^m \sum_{j=1}^{\mathcal{N}_i} F_{ji}^\gamma}{N_a} \quad 6$$

where F_{ji}^γ is the number of female fledglings in nest j of patch i (the γ distinguishes the number of female fledglings from the number of fledglings of both sexes in Equations 4 and 5, and N_a is the total number of adult reproductive females in the landscape population. In determining b , the model assumes that the number of adult females is equivalent to number of territories (i.e., nests or mated pairs) so $N_a = \sum_{i=1}^m \mathcal{N}_i$. Note that this assumption results in a maximum value for b for

6 The Model

a landscape with nesting habitat fully occupied by mated pairs. The presence of non-mated non-nesting females would reduce b .

The model assumes productivity is independent of age after sexual maturity. The maternity function m_x , the number of female fledglings produced by a female of age x , is then $m_x = b$ for all ages x .

The maternity function is combined with age-specific survivorship to create a life table for the landscape's population (Leslie 1966, Mertz 1971, Nichols et al. 1980, Lande 1988, Noon and Biles 1990) (Table 1). Annual survival probabilities are defined for three age classes: juveniles s_0 , subadults s_1 , and adults s . The probability s_0 is the probability of surviving from fledging to age one; s_1 is the annual survival probability for females greater than one year of age but less than breeding age, and s is the annual probability of survival for females of breeding age or older. In many cases, with small passerine neotropical migrants for example, the age of first reproduction occurs at age one (Ricklefs 1973). Consequently, the model default is to set $s_1 = s$.

Table 1. Model generated life history table.

x^1	l_x^2	m_x^3	$l_x m_x^4$
0	1.0	0	0
1	s_0	b	$s_0 b$
2	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 b s$
4	$s_0 s_1 s^2$	b	$s_0 s_1 b s^2$
⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 b s^{x-2}$

¹age in years

²probability of surviving to age x

³female fledglings per female age x

⁴net maternity function

Two demographic indices are calculated from the life table. The first is net lifetime maternity or net reproductive rate:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x = l_{\alpha} b / (1.0 - s) \quad 7$$

where R_0 is the expected lifetime production of females by a female fledgling, l_x is the probability of survivorship to age x , and l_{α} is survivorship to the age of first breeding α (Lande 1988). For a stable age distribution, when $R_0 = 1.0$, a female replaces herself in her lifetime, and the population is stable. If $R_0 < 1.0$ the population is declining, and if $R_0 > 1.0$ the population is increasing.

The second demographic index is the finite rate of increase λ given by the solution of the characteristic equation (Lande 1988):

$$\lambda^\alpha - s\lambda^{\alpha-1} - bl_\alpha = 0 \quad 8$$

where $\alpha \geq 1$ is the age of sexual maturity and $0 < s < 1$. If $\lambda = 1.0$ the population is stable. When $\lambda < 1.0$ the population is declining, and if $\lambda > 1.0$ the population is increasing. The annual rate of change of the population size ($\% \cdot y^{-1}$) is $(\lambda - 1.0) \times 100$.

Equation 8 assumes no reproductive senescence or decline in fecundity with age. This assumption is common to many models of avian demographics (Ricklefs 1973, Nichols et al. 1980, Lande 1988, Noon and Biles 1990).

In addition to the demographic indices of R_0 and λ , the life table parameterizes an age classified matrix population model (Caswell 1989). This Leslie matrix is used to project population numbers forward in time.

Model results with stochastic elements (e.g., b) are reported as the mean (\pm SD). We determined that one hundred runs of the model ($n = 100$) were sufficient to achieve asymptotic means and variances.

3. THE LANDSCAPE

Fort Knox Military Reservation, Fort Knox, Kentucky (hereafter referred to simply as Fort Knox) occupies 44,150 ha of Bullitt, Hardin, and Meade counties in north central Kentucky (Fig. 3). Bordered on the north by the Ohio River, Fort Knox is drained by Otter Creek and by the Salt River and its tributary, the Rolling Fork. Muldraugh's Hill, a steep escarpment, runs northwest to southeast through Fort Knox and roughly divides the reservation into a hilly eastern portion dominated by the Salt River-Rolling Fork watershed and a western karst plateau of rolling uplands and numerous sinkholes (White et al. 1994).

Most of the reservation is covered by second-growth deciduous forest (Fig. 4). Mesophytic forest is found in the lower ravines and in the floodplains of the smaller rivers and creeks. Swamp or bottomland hardwood forest can be found in the larger floodplains, especially adjacent to the Ohio River. Sub-xeric forest occupies the higher ridgetops and is predominant in the southern part of Fort Knox. This part of the reservation is also characterized by the presence of several large limestone slope glades (White et al. 1994). The western uplands of Fort Knox are heavily impacted by human occupation and military training activities. The barren areas on the western edge of Fort Knox (Fig. 4) are largely areas stripped of vegetation by tank and other tracked vehicle traffic. This portion of Fort Knox lies in the northern Elizabethtown Subsection of the Pennyroyal Plain Subsection of the Highland Rim, and historically was considered part of the "Big Barrens," a grass-dominated prairie landscape (Quarterman and Powell 1978, Deselm and Murdock 1993, White et al. 1994). This region is now heavily disturbed, but representatives of the former prairie or grassland flora can still be found in small scattered fragments throughout this portion of Fort Knox. Croplands and pastures dominate the landscape west of the Fort Knox boundary (Fig. 4).

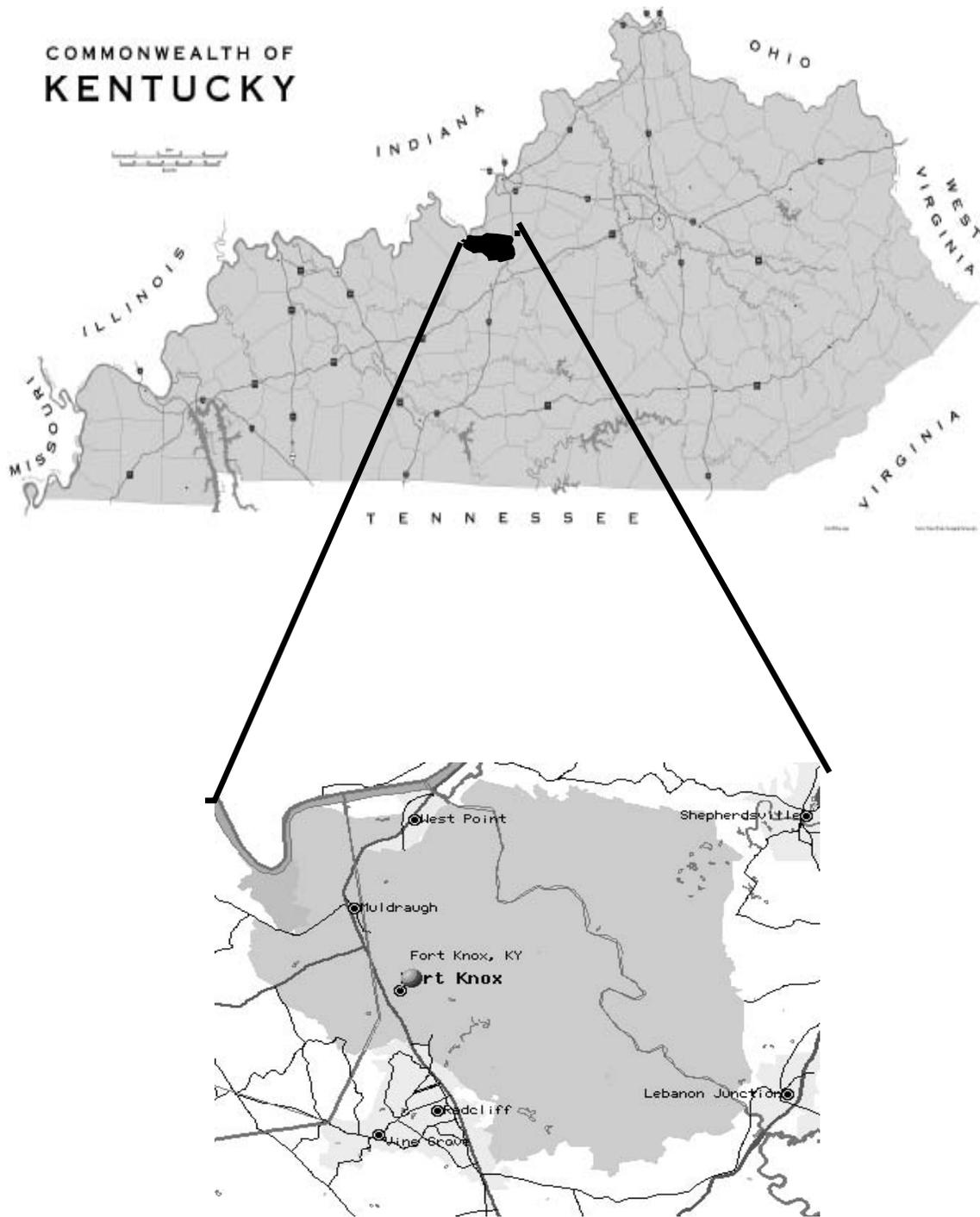


Fig. 3. Location and detail of Fort Knox Military Reservation, Fort Knox, Kentucky.

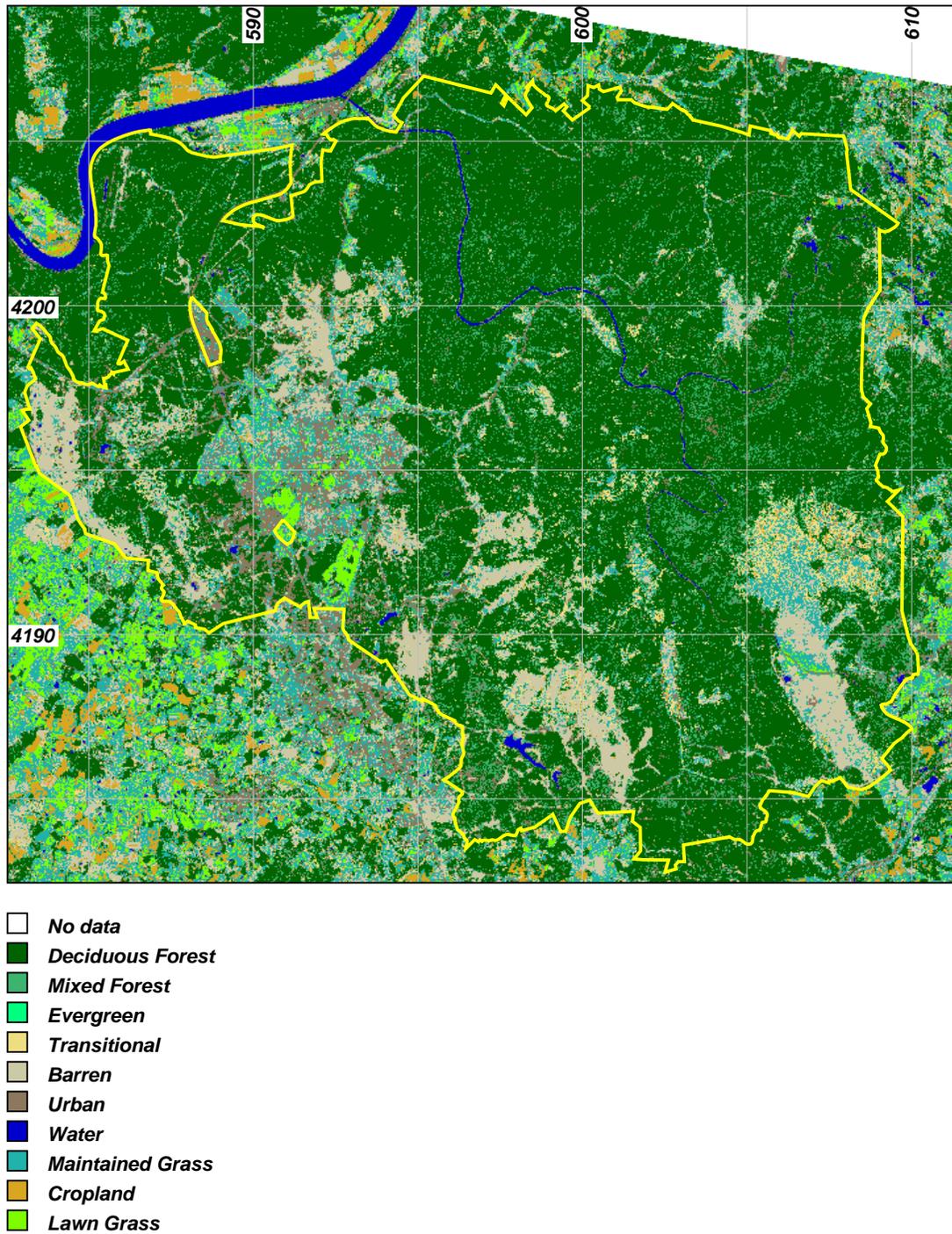


Fig. 4. Landcover map of Fort Knox, Kentucky. Landcover was determined by a supervised classification of Landsat Thematic Mapper (TM) imagery. See Hargrove et al. (unpublished) for details.

4. THE SPECIES

Henslow's sparrow is a small grassland species associated with dense, tall grasslands (including hay fields) that are not mowed or burned annually (Skinner et al. 1984, Zimmerman 1988, Rising 1996). Henslow's sparrow breeds in the northcentral and northeastern United States from South Dakota (east of the Missouri River) and eastern Kansas to New York, Virginia and eastern North Carolina. The northern limit of its range is in central Minnesota, Upper-Peninsular Michigan, and southern Ontario (Beyers et al. 1995, Rising 1996). Northern Kentucky and Fort Knox are on the southern edge of the species' breeding range, and Rising (1996) indicates their occurrence in central and western Kentucky is irregular. Listed by the Kentucky State Nature Preserves Commission as a species of Special Concern (KSNPC 1993), the largest documented summer population in Kentucky is found at Fort Knox where grasslands in the vicinity of Godman Army Airfield are managed as a protected area for Henslow's sparrow (White et al. 1994). A medium distance migrant, the species winters in the coastal plain of the southeastern United States.

Historically, populations of Henslow's sparrow west of the Appalachians were probably most associated with native tallgrass prairies, forest prairie mosaic, and moist grasslands in forest openings (Graber 1968, Zimmerman 1988). The species' gradual but persistent decline has been attributed to decreasing availability of suitable habitat, primarily standing dead vegetation in open grassland (Zimmerman 1988). It is currently thought to be habitat limited because grasslands used by people are usually harvested or burned annually (if not more frequently) (Zimmerman 1988), and in the eastern portions of its range, abandoned fields are rapidly invaded by shrubs and trees. Too frequent burning (e.g., annual) removes the standing dead grass cover preferred by Henslow's sparrow, but the complete suppression of less frequent fires allows the growth of woody vegetation that the species' tends to avoid (Zimmerman 1988). This species is also area-sensitive, preferring patch sizes of 30 ha or more (Zimmerman 1988, Herkert 1994).

The dense grass preferred by Henslow's sparrow only occurs on productive sites with adequate moisture (Robins 1971a, Abrams et al. 1986, Zimmerman 1988, Heikens and Robertson 1995). Native tallgrass prairie meets the habitat requirements of Henslow's sparrow, if it isn't burned every year. In Missouri, for example, Henslow's sparrow occurs only on idle or lightly grazed, unburned prairie (Skinner et al. 1984). The sparrow does not usually nest in sites that are either too wet or too dry, and it prefers sites with little or no woody vegetation (Zimmerman 1988, Hamel 1992). Some of the literature describes fairly wet sites (e.g., of cordgrass, *Spartina pectinata* [Hyde 1939]) where Henslow's sparrow has been observed nesting, but it is more commonly reported in drier prairie-like grassland habitat (Graber 1968, Wiens 1969, Zimmerman 1988, Herkert 1994). Management recommendations include burning every three to four years to eliminate woody vegetation (Zimmerman:88). The resulting suitable habitat should contain no more than about 1 sapling per 100 m² (personal communication, Ken Palmerball, Kentucky Nature Preserves Commission, April, 1996).

Because Henslow's sparrow is a species of conservation concern at Fort Knox (White et al. 1994), and because the nesting habitat of Henslow's sparrow is potentially vulnerable to training activities, we chose to implement the model described above for the Henslow's sparrow population at Fort Knox. This implementation is best considered an example or case study of the model's implementation and use, rather than an analysis of Henslow's sparrow demography *per se*.

5. A HABITAT MODEL

As noted above, a summer population of Henslow's sparrow is known from the Godman Army Airfield at Fort Knox. The presence of singing males suggests that this is a breeding population (White et al. 1994). However, the presence of Henslow's sparrow elsewhere at Fort Knox is not documented, and a map of nesting habitat (one of the model requirements) was not available. Accordingly, we developed a model of Henslow's sparrow nesting habitat to describe the expected spatial distribution of nesting habitat across the Fort Knox landscape.

Two substantially independent lines of reasoning, one deductive and one inductive (Hargrove et al. unpublished), were used to develop predictions for prospective Henslow's sparrow habitat. The intersection of these predictions was used as the final prediction.

Deductive prediction of Henslow's sparrow habitat at Fort Knox was based on identifying 1) sites which were probably prairie prior to extensive agricultural conversion, 2) sites which probably could support prairie or dense grass vegetation, and 3) sites which would be unlikely to support prairie or dense grass vegetation. We assume Henslow's sparrow does not nest in areas frequently flooded or with standing water, but might nest in seasonally wet areas. We also assume that it does not nest in areas too dry or infertile to produce dense grass. Our approach was to combine information from the literature with readily available soil survey interpretations from published Hardin and Bullitt County Soil Surveys (Arms et al. 1979, USDA-SCS 1986) and the draft unpublished Meade County Soil Survey.

Sites which were probably originally prairie are those with soils that are Mollisols. Related soils at Fort Knox that show some properties of Mollisols are mollic Hapludalfs and mollic Paleudalfs (types of Alfisols). These soils probably developed under cane or prairie vegetation or show characteristics transitional to prairie soils (Arms et al. 1979).

Although not under continuous grass or herbaceous vegetation for thousands of years, other soil types at Fort Knox might have also have been prairie vegetation. Soils classified as Alfisols are thought to have developed primarily under forest vegetation, but could also have supported prairie vegetation for periods of time, especially in the prairie transition region in the vicinity of Fort Knox. Many of the Alfisols at Fort Knox are deep and well drained and would support dense grasslands suitable for Henslow's sparrow habitat. Some Alfisols (Aqualfs and Fragiudalfs) have a perched water table less than 3 ft (.91 m) below the surface, but most of these soils are probably dry enough to support wet prairie grasses.

Other soils at Fort Knox which are unlikely to support prairie or dense grass suitable for Henslow's sparrow habitat are too wet, too dry, or unproductive. Aquolls, some of the Alfisols, some of the Inceptisols, and some of the Entisols at Fort Knox have the water table less than one foot below the surface or are frequently flooded; these soils are assumed to be too wet for preferred Henslow's sparrow habitat. Heikens and Robertson (1995) found that soils deeper than 40 inches (1 m) were most likely to support prairies in the loess hills of southern Illinois, while shallower soils were likely to support sparsely vegetated 'glade' vegetation. Therefore, soils less than 1 meter deep at Fort Knox are assumed to be too dry to support the dense vegetation necessary for Henslow's sparrow habitat. Similarly, coarse textured, severely eroded, steep, or gullied land (some Alfisols, Entisols, and Inceptisols), and older, leached soils, developed under forest (Ultisols) would probably not have adequate fertility or moisture to support dense grassland vegetation under

natural conditions, and they were not included in our model of Henslow's sparrow habitat.

Map layers for soils and vegetation land cover (Fig. 4) were combined in a raster Geographical Information System (GIS). Soils identified as potentially suitable to support prairie or dense stands of grass (Table 2) were then compared with land cover. Pixels of either unsuitable soil types (Table 2) or unsuitable land cover (Table 3) were then eliminated as unsuitable as potential Henslow's sparrow habitat.

To further refine (inductively) our prediction of Henslow's sparrow habitat, a 100 m radius circle enclosing the known nesting habitat at Fort Knox's Godman Army AirField (White et al. 1994) was used to identify areas with similar spectral characteristics elsewhere at Fort Knox. Because a single habitat class is not sufficient for discriminating a binary habitat map, a maximum likelihood classification was run with the spectral signature for the known habitat and raw Landsat TM spectral data for Fort Knox (Hargrove et al., unpublished), and a Chi-square test applied to each discriminant result at every cell. The resulting reject threshold map contained the confidence level at which each cell in the map was classified. Cells with < 5% probability of being correctly assigned to the Henslow's sparrow habitat class were defined as not suitable for Henslow's sparrow habitat. A spectral signature was developed for these non-habitat cells, and the maximum likelihood classification repeated to produce a binary habitat-nonhabitat prediction. The intersection of the soil-landcover prediction and the spectral signature prediction of habitat was taken as our prediction of Henslow's sparrow habitat (i.e., cells predicted to be habitat by both methods were defined as nesting habitat).

The resulting map of potential Henslow's sparrow nesting habitat is shown in Figure 5. Characterization of the map's accuracy can be found in (Hargrove et al., unpublished).

Table 2. Suitability of soils at Fort Knox for supporting Henslow's sparrow habitat.

Soil group	Suitable	Unsuitable
Mollisols	Typic Argiudolls	Aquolls (too wet) Lithic Argiudolls, lithic Hapludolls, and other shallow Hapludolls (too shallow to bedrock)
Alfisols	Paleudalfs and mollic Hapludalfs	Lithic and some typic and ultic Hapludalfs (too shallow to bedrock)
	Some typic and ultic Hapludalfs (> 40 inches (1 m) to bedrock)	Severely eroded phases of all soils (too droughty or infertile)
	Fragiudalfs (perched water table > 1 foot (0.3 m) below the surface)	Aqualfs with water table < 1 foot below the surface (too wet)
Ultisols	Some Hapludults (> 40 inches (1 m) to bedrock)	Some Hapludults (too shallow to bedrock)
		Severely eroded phases of all soils (too droughty or infertile)
Inceptisols	Most Eutrochrepts	Dystric Eutrochrepts and lithic Dystrochrepts (too shallow to bedrock)
		Fluventic Eutrochrepts (frequently flooded - too wet)
Entisols	None	Gullied Udorthents (too unproductive)
		Fluvaquents and Udipsamments which are frequently flooded or with water table < 1 foot (0.3 m) below the surface (too wet)

Table 3. Suitability of landcover types at Fort Knox for supporting Henslow’s sparrow habitat.

Landcover type	Suitable	Unsuitable
Deciduous forest		X
Mixed forest		X
Evergreen		X
Transitional	X	
Barren	X	
Urban		X
Water		X
Maintained grass	X	
Cropland	X	
Lawn Grass		X

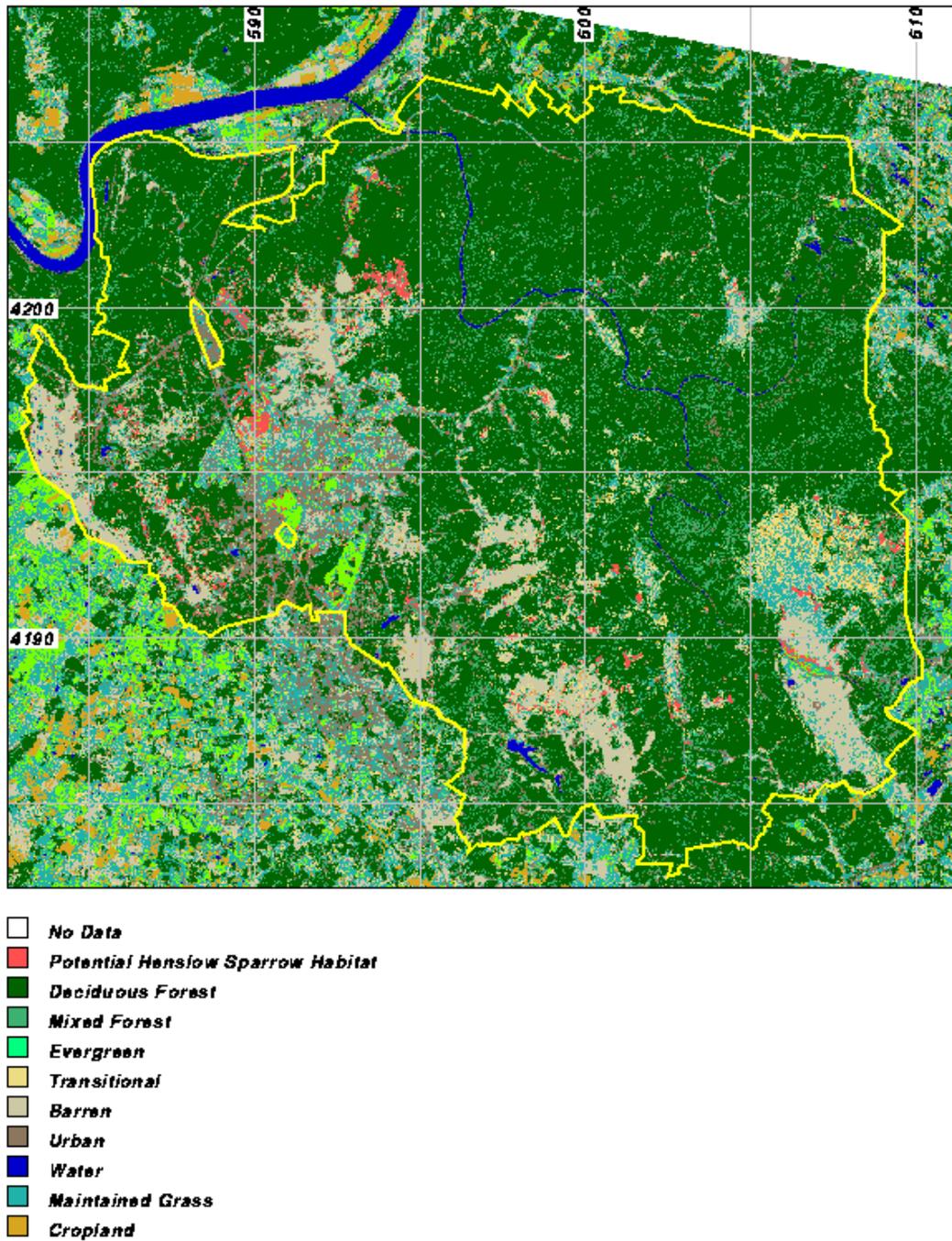


Fig. 5. Predicted distribution of potential Henslow's sparrow nesting habitat at Fort Knox, Kentucky.

6. LIFE HISTORY PARAMETERS

The model's life history parameters for Henslow's sparrow are shown in Table 4. Ideally these parameters would be population specific (i.e., estimated from observations and measurements of Henslow's sparrow at Fort Knox). Those data are not available. We therefore assume that our species-specific estimates for territory and clutch size derived from literature on Henslow's sparrow at other sites (Hyde 1939, Graber 1968, Wiens 1969, Robins 1971a,b, Beyers et al. 1995, Rising 1996) apply to the population at Fort Knox. Similarly, we used the incidence function for Henslow's sparrow from Herkert's (1994) study of grassland bird communities in Illinois (Fig. 1).

Lacking information on survivorship for Henslow's sparrow, we estimated juvenile and adult survivorship from the life table data of the Baker et al. (1981) study of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) in California. These estimates may be too high. The white-crowned sparrow population of Baker et al. (1981) is nonmigratory, and Henslow's sparrow is about half as massive as the white-crowned sparrow (Rising 1996) (survivorship is positively correlated with body mass). Nevertheless, these estimates are consistent with the range of survivorship reported for small migratory passerines (Ricklefs 1992).

We assumed first reproduction at an age of 1 yr. We estimated longevity (Table 4) from the allometric equation of Lindstedt and Calder (1976): $L = 17.6M^{0.20}$, where L is longevity (yr), and M is body mass (kg). We assumed a mass for Henslow's sparrow of 13 g (Rising 1996).

Johnson and Temple (1986) reported fairly low probabilities of nesting success (24–56%) for ground nesting passerines in fragmented tallgrass prairies of western Minnesota, even when nests were far (> 45 m) from a forest edge. We therefore assumed our Type III response to edge for Henslow's sparrow (Fig. 2). Assuming a square patch (Johnson and Temple [1990] describe the patches as compact) we estimated the edge:area index e_i for both their large (130–486 ha, $e_i = 0.0091 - 0.0175$) and small (16–32 ha, $e_i = 0.0357 - 0.05$) patches. We used the higher Johnson and Temple (1986) estimates of nesting success (those from recently burned plots) far from an edge to estimate nesting success for Henslow's sparrow for patches with minimal edge, i.e., those with an edge:area index near 0.0 (Fig. 6). We assumed that the rates of nesting success near to an edge reported by Johnson and Temple (1986) applied to linear patches with edge:area indices ranging from 0.2 - 0.5. Here we also used the highest values from better quality, recently burned, patches (Fig. 6). We assumed a nesting success of 80% in the absence of any edge effect ($S_i = S_{\max} = 0.80$ when $e_i = 0.0$). Arcese et al. (1992) report a minimum nest failure rate of approximately 20% for a song sparrow (*Melospiza melodia*) population on Mandarte Island, British Columbia, Canada. We believe much greater rates of nesting success are highly unlikely. We calibrated the parameters of Equation 3 with these assumptions and estimates to derive an estimate of nesting success response to edge for the Henslow's sparrow population at Fort Knox (Fig. 6).

18 *Life History Parameters*

Table 4. Life history parameters for Henslow's sparrow used as model input.

Parameter	Value
Territory size (A_T)	0.4 ha
Gap crossing ability	< 20 m
Clutch size (C)	4–5 (uniform)
Incidence function parameters	
β_0	-2.55
β_1	0.97
β_2	0.0
Juvenile survivorship (s_0)	0.33
Subadult survivorship (s_1)	0.57
Adult survivorship (s)	0.57
Age of first reproduction (α)	1 yr
Longevity (L)	8 yr
Maximum nesting success (S_{\max})	0.8
Edge:area index where $S_i = 0.5S_{\max}$	0.25
Shape parameter θ (Eq. 3)	0.5

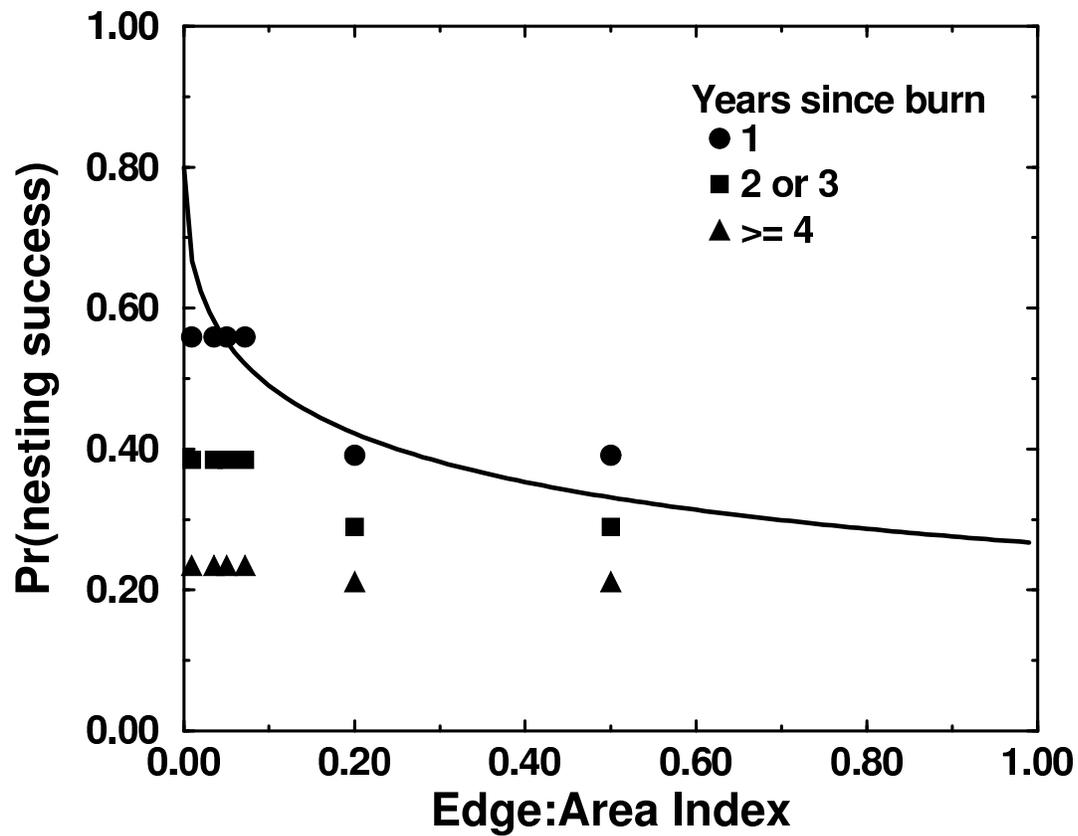


Fig. 6. An estimate of the relationship between nesting success and the patch edge:area index for Henslow's sparrow at Fort Knox. The symbols are estimates derived from data in Johnson and Temple (1986) (see text). The solid curve is the fitted calibration of Equation 3 to the one year since burn points only, and is the relationship used in the model.

7. RESULTS

Our habitat model predicted 859.5 ha of potential Henslow’s sparrow nesting habitat at Fort Knox (Table 5). The model aggregated this area into 3335 patches. However, only 21 (0.6%) of the patches were large enough to support nests (Table 6). The vast majority of the patches were too small for the establishment of territories. Either they were smaller than the territory size (88% of the patches were < 0.4 ha), or, because of the area sensitivity of Henslow’s sparrow (Fig. 1), the patches were unlikely to be occupied. The largest patch was only 51.1 ha. As a result, only 201.4 ha of the potential habitat was utilized.

The 21 utilized patches supported 100 nests and produced 449 ± 4 eggs (Table 5), but only $39 \pm 5\%$ of the nests successfully fledged young, and only $39 \pm 5\%$ of the eggs were fledged. Three patches were responsible for approximately 80% of the fledgling production (Table 6). Productivity was limited to slightly less than 1.8 ± 0.2 fledglings per pair, and $50 \pm 0.03\%$ of the fledglings were female. Rarely, a patch produced only male fledglings. With $b = 0.88 \pm 0.12$ female fledglings per female, the expected net lifetime production of females per female (R_0) is < 1.0 (Table 5) (i.e., less than replacement), and the population’s finite rate of increase (λ) is < 1.0 (Table 5). The landscape’s production of females is insufficient to compensate for mortality reflected in juvenile and adult survivorship, and (in the absence of immigration and assuming constant demographic parameters) the population will decline at an annual rate of approximately $14 \pm 4\%$ (Fig. 7).

Table 5. Model results for Henslow’s sparrow at Fort Knox.

Variable	Value
Total habitat	859.5 ha
Number of patches	3335
Number of patches utilized	21
Area of utilized patches	201.4 ha
Nesting density	0.12 pairs ha ⁻¹ of habitat
Total egg production	449 ± 4
Total fledgling production	175 ± 20
Nesting success	$39 \pm 5\%$
Fledgling success	$39 \pm 5\%$
Productivity (P_L)	1.76 ± 0.21
Female sex ratio	0.50 ± 0.03
b	0.88 ± 0.12
R_0	0.673 ± 0.089
λ	0.859 ± 0.038
Rate of change	$-14.1 \pm 3.8\% \text{ yr}^{-1}$

Table 6. Model patches large enough to support nests.

Patch number	Area (ha)	Edge:area index	Nests	Fledglings	
				Total	Female
167	5.1	0.39	1	1.2 ± 2.1	0.7 ± 1.1
252	5.0	0.42	1	2.0 ± 2.3	1.0 ± 1.3
691	4.2	0.49	1	1.6 ± 2.2	0.8 ± 1.3
734	4.3	0.29	1	1.4 ± 2.1	0.7 ± 1.2
796	4.8	0.36	1	1.6 ± 2.2	0.8 ± 1.3
817	4.5	0.30	1	1.6 ± 2.2	0.9 ± 1.3
838	42.8	0.22	29	55.2 ± 11.9	28.0 ± 7.0
923	4.0	0.34	1	1.4 ± 2.1	0.7 ± 1.2
1051	3.8	0.30	1	1.6 ± 2.2	0.7 ± 1.2
1717	3.6	0.38	1	1.5 ± 2.2	0.7 ± 1.1
1736	8.8	0.35	3	5.8 ± 4.2	2.6 ± 2.3
1865	51.1	0.30	37	63.1 ± 13.2	31.3 ± 7.8
1894	4.2	0.36	1	1.8 ± 2.3	0.9 ± 1.3
2574	3.8	0.39	1	1.4 ± 2.1	0.7 ± 1.1
2874	4.9	0.25	1	1.3 ± 2.0	0.6 ± 1.2
2918	3.5	0.22	1	1.8 ± 2.2	0.9 ± 1.4
2958	4.4	0.39	1	1.9 ± 2.2	0.9 ± 1.3
3155	20.5	0.30	11	19.0 ± 6.9	9.5 ± 4.3
3161	9.6	0.21	4	7.0 ± 4.3	3.5 ± 2.4
3291	3.7	0.27	1	1.8 ± 2.3	0.9 ± 1.4
3306	4.8	0.24	1	1.8 ± 2.2	0.9 ± 1.3

Table 7. Model generated life history table for Henslow's sparrow at Fort Knox with the mean $b = 0.877$.

x	l_x	m_x	$l_x m_x$
0	1.0	0.0	0.0
1	0.330	0.877	0.289
2	0.188	0.877	0.165
3	0.107	0.877	0.094
4	0.061	0.877	0.054
5	0.035	0.877	0.031
6	0.020	0.877	0.017
7	0.011	0.877	0.010
8	0.000	0.000	0.000

$\sum_0^8 l_x m_x = 0.660$

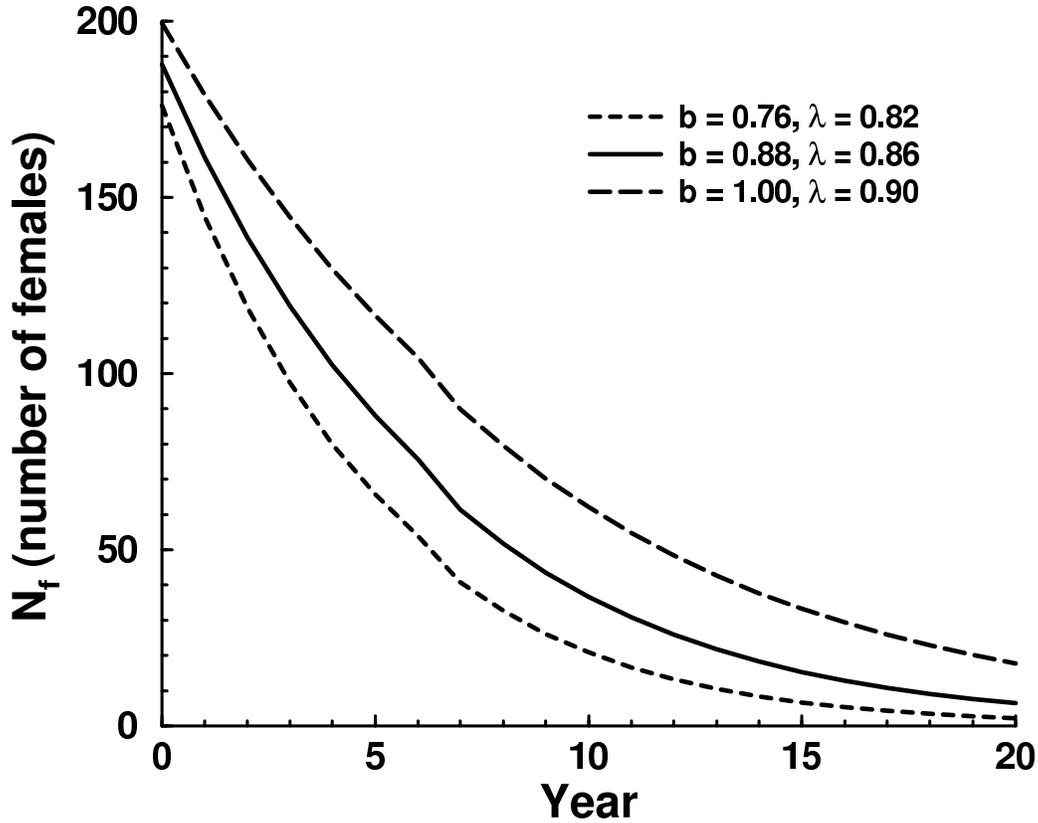


Fig. 7. Model projection of the Henslow's sparrow population at Fort Knox, Kentucky. The solid curve is the model projection for the mean b . The upper broken curve is for the mean plus 1SD; the lower for the mean minus 1SD.

The expected net lifetime maternity R_0 is a consequence of both survivorship and age-specific reproduction (Eq. 7). If more females live longer, lifetime maternity will increase even if age-specific reproduction remains low. Similarly, an increase in age-specific reproduction, perhaps through an increase in nesting success, can increase R_0 for a given survivorship. In Figures 8 and 9 we plot R_0 in the parameter space for maternity b and juvenile (s_0) and adult (s) survivorship, respectively. The shaded region in both Figures indicates the region of parameter space where $R_0 \geq 1.0$. In the shaded region the population will remain at a constant value or increase; elsewhere the population will decline. The filled circles in Figures 8 and 9 indicate the combinations of b and s_0 or s for Henslow's sparrow at Fort Knox.

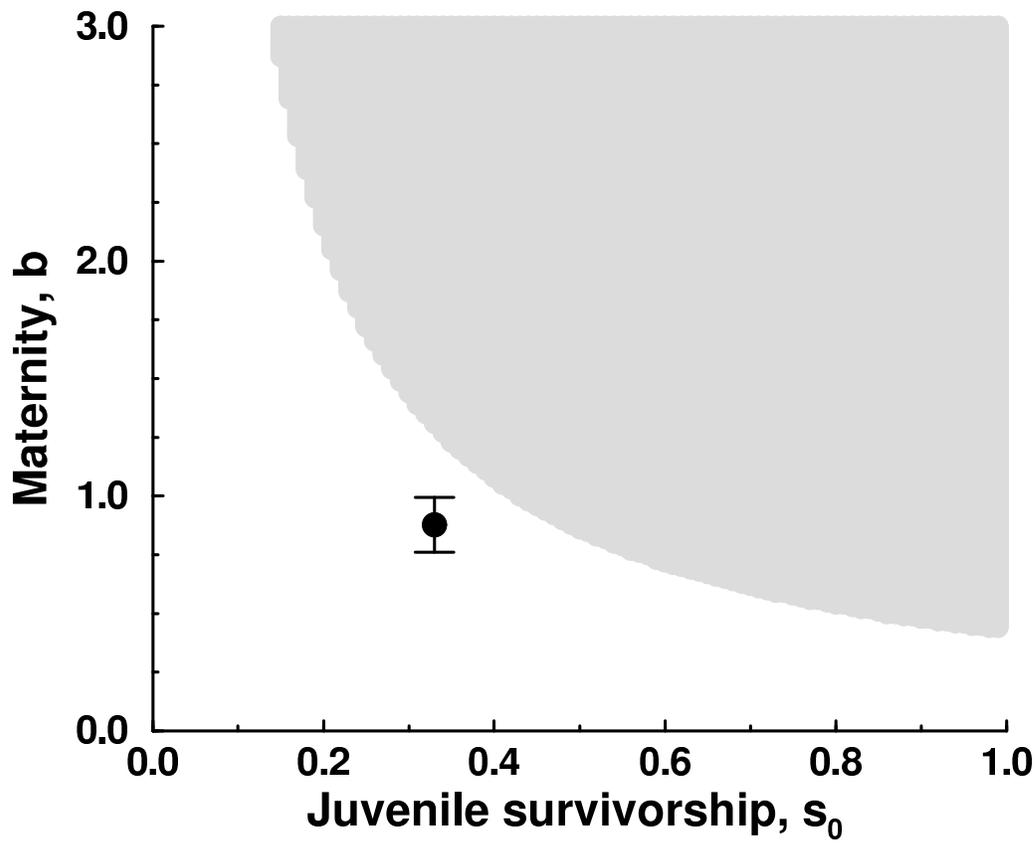


Fig. 8. Net expected lifetime maternity R_0 as a function of age-specific maternity b and juvenile survivorship s_0 . The shaded region indicates where $R_0 \geq 1.0$ and the population is at steady state or increasing. Outside this region the population $R_0 < 1.0$ and the population will decline. The filled circle indicates the combination of parameter values (mean $b \pm \text{SD}$) for Henslow's sparrow at Fort Knox, Kentucky.

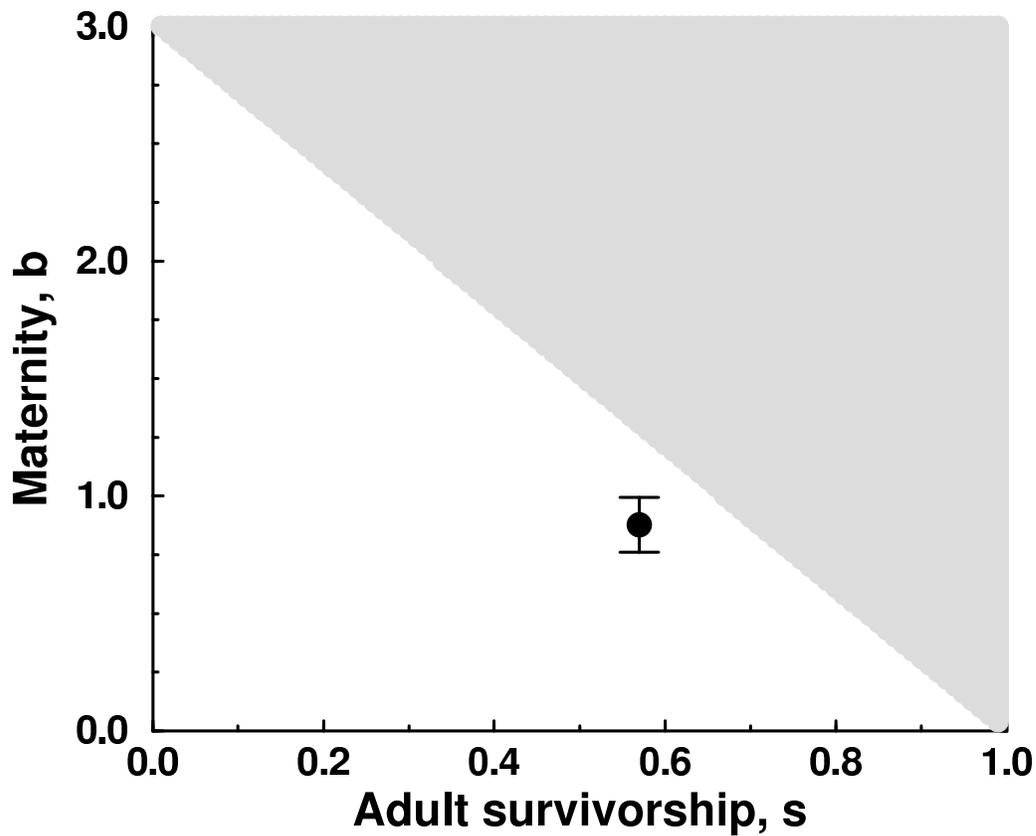


Fig. 9. Net expected lifetime maternity R_0 as a function of age-specific maternity b and adult survivorship s . The shaded region indicates where $R_0 \geq 1.0$ and the population is at steady state or increasing. Outside this region the population $R_0 < 1.0$ and the population will decline. The filled circle indicates the combination of parameter values (mean $b \pm SD$) for Henslow's sparrow at Fort Knox, Kentucky.

The combinations of b and both juvenile (Fig. 8) and adult (Fig. 9) survivorship are insufficient to provide for a steady state or increasing population at Fort Knox. The model's prediction of a declining population at Fort Knox can be attributed to the combination of too little successful reproduction and insufficient rates of survivorship.

8. DISCUSSION

Given the current landscape configuration at Fort Knox, our prediction of Henslow’s sparrow nesting habitat, and our estimates of Henslow’s sparrow life history parameters, the model indicates that the Fort Knox landscape is a population sink for Henslow’s sparrow. The combined values of reproductive output b and survivorship s_0 and s are substantially too low to support either a stable or increasing (i.e., source) population at Fort Knox (Figs. 8 and 9). Persistence of Henslow’s sparrow at Fort Knox requires recruitment of individuals from other parts of the species’ range. This may represent the historical situation at Fort Knox, since the landscape is on the southern edge of the species’ summer range, and may have always represented ‘marginal’ habitat. This hypothesis will require further testing with a map of Henslow’s sparrow nesting habitat thought to approximate potential, pre-European, or pre-agricultural vegetation. It would be premature to ascribe the model’s assessment of the landscape as a sink for Henslow’s sparrow to military activity at Fort Knox. It is just as likely, if not more so, that agriculture outside the Fort Knox Reservation has substantially reduced and fragmented Henslow’s sparrow habitat in the region (see Fig. 4). But here again, it is premature to ascribe culpability.

Nevertheless, the model does suggest a focus for any management intervention to ‘restore’ the viability of the landscape for Henslow’s sparrow or to mitigate the apparent population sink, whatever its origin. Much of the annual mortality of Henslow’s sparrow (especially of juveniles) likely occurs during migration to and from its wintering grounds in the grassland and pine-savannah ecosystems of the southern United States and on the wintering grounds themselves. There is obviously little a land manager in the summer breeding range of the species can do to reduce this overwintering mortality. In any case, shifting the Fort Knox population from a sink to a steady state or source population through changes in survivorship alone, with no change in reproductive output, would require values of juvenile survivorship near 50% (Fig. 8) or adult survivorship near 70% (Fig. 9). These are relatively high survivorship values, and they would probably be difficult to achieve through management intervention.

A land manager at Fort Knox, or elsewhere in the summer range of Henslow’s sparrow, is much more likely to influence the population dynamics of the species by increasing reproductive output (the maternity function b), primarily by manipulations of landscape structure and its influence on nesting success. With juvenile survivorship at 0.33 and adult survivorship at 0.57, an increase in b at Fort Knox from the current estimate of 0.88 ± 0.12 to more than 1.3 female fledglings per female would shift the population into the stable or increasing region of the parameter space for b and s_0 (Fig. 8). Assuming that 50% of the fledglings are female, and that the expected fledgling rate of successful nests is 4.5 fledglings per successful pair, a b of 1.3 would require a nesting success rate for the entire landscape of at least 58%. That is approximately 1.5 times the current assessment’s estimate of landscape-wide nesting success ($39 \pm 5\%$, Table 5), but it is not an impossibly high value. Changes in the spatial configuration of the landscape that would favor higher nesting success (e.g., less edge) might also reduce the expectedly high mortality of fledglings on the breeding ground that occurs prior to their leaving for the winter. Any increase in juvenile survivorship reduces the increase in b needed to shift the population from sink to source (Fig. 8).

We have not pursued it here, but our model could be used to explore the influence of alternative spatial distributions and configurations of Henslow’s sparrow

habitat on b and the net lifetime maternity R_0 . A spatial configuration with larger more contiguous patches with less edge per unit area would likely increase the expected occurrence of Henslow's sparrow in larger patches and increase the landscape wide nesting success. This same conclusion might be reached, without the model, from general principles and expectations of small passerine response to habitat loss and fragmentation; it hardly justifies implementation of the model as an assessment tool. However, the model can do what the general principles cannot. It can provide quantitative estimates of the changes needed to achieve the desired goals—not only that a less fragmented landscape of larger more contiguous patches is desirable, but, how much reproductive output is required for a given estimate of survivorship, and which alternative spatial configurations (planned or proposed) are most likely to achieve that requirement.

Despite the relative simplicity of the model, it does involve a variety of assumptions, and some of the data inputs are highly uncertain, particularly those for the critical variables of nesting success and survivorship. Further development and application of the model as an assessment tool will require more substantial analysis of model sensitivity and uncertainty. The comparisons of b and survivorship in Figures 8 and 9 provide some sense of the model's sensitivity and the importance of uncertainty in model inputs. For example, the prediction of a sink for Henslow's sparrow at Fort Knox is unlikely to be simply a consequence of error or uncertainty in nesting success or survivorship. The change in either needed to alter the models assessment from sink to source is likely larger than even the considerable uncertainty in those model inputs (Fig. 8). Similarly, uncertainty in adult survivorship is unlikely to alter the models assessment of the Fort Knox landscape as a sink for Henslow's sparrow (Fig. 9). On the other hand, if we have overestimated nesting success in the less fragmented patches by assuming the high habitat quality associated with recently burned grasslands (see Fig. 6 and Johnson and Temple [1986]), then we could be overestimating b , and adult survivorship could be a more important parameter (Fig. 9). These results notwithstanding, a more formal error and uncertainty analysis is called for, and the model should incorporate error and uncertainty propagation as an integrated part of its analysis and reporting of model results. The importance of error and uncertainty might not be so 'apparent' when the model is applied to other landscapes or other species, and the difference between a prediction of source or sink might be much more sensitive to model assumptions and data uncertainties.

Demographic models of the type we have presented here are a necessary part of assessing avian response to land use and habitat fragmentation. Population density can be a poor and misleading indicator of habitat and landscape quality (Van Horne 1983, Maurer 1986). Individuals may commonly exist and even breed in regular and substantial numbers in sink habitats, but they will not persist without immigration from source landscapes (Pulliam 1988, Howe et al. 1991, Pulliam and Danielson 1991). Source-sink demographics can interfere with the interpretation of even long-term census (density) data (Brawn and Robinson 1996). Variations in local abundance associated with source-sink dynamics can make the determination of long term trends for the species over its range very difficult, especially if those changes are slow. Sink landscapes may sometimes play an important and positive role in the demography of a metapopulation (or otherwise spatially structured population) with source and sink subpopulations (Howe et al. 1991), but the land managers response to an observed decline in a natural sink landscape is likely to be different than to a similar observation in what had been identified as a source landscape. It is vital that assessments of land use and land-use change on avian pop-

ulations include a quantitative analysis of demographic variables and trends (Van Horne 1983, Maurer 1986). Assessments of the presence of habitat or of density alone are not sufficient. Moreover, because landscape structure can influence key demographic variables, the assessment should include an explicit consideration of spatial pattern and changes in that pattern in response to land use change and land management. We have presented one model designed explicitly for that purpose. Others are available, for example the models of Urban et al. (1988) and Donovan et al. (1995b), and models like them should be incorporated into the ecosystem management of public lands.

9. CONCLUDING REMARKS

We have shown that a relatively simple combination of landscape and demographic modeling can yield an effective assessment tool. It also provides a research tool for investigating the demographic consequences of landscape structure. Elsewhere, the model has been coupled with a neutral landscape model (Gardner et al. 1987) in a theoretical exploration of how changes in the proportion of available habitat shift a population from source to sink (King, unpublished). Feedback from theoretical investigations will improve the model in its more applied assessment applications.

Development and implementation of the model have also emphasized areas where additional empirical and theoretical investigation are needed. For example, models of nest occurrence as a function of patch size (the incidence functions) and estimates of minimum area for breeding merit further attention. How consistent are these relationships from one location to another? How well does an incidence function for Henslow's sparrow in Illinois (Herkert 1994) translate to a Henslow's sparrow population in Kentucky or Kansas? Functional relationships between the probability of nesting success and a patch's edge:area ratio also need further development. The hypothesized relationship between edge:area ratio and nesting success we have developed here needs to be tested, for Henslow's sparrow and Fort Knox in particular, but also to determine its generality. Is knowledge of the edge:area ratio sufficient to predict nesting success, or is a more demanding knowledge of actual distance from edge required? Does the phenomenological representation of nest predation and brood parasitism we use here need to be replaced with more explicit mechanistic models of predation and parasitism?

Finally, the need for basic life history data cannot be overstated, especially for species of conservation concern. In the absence of these data we are forced to extrapolate from other species in other regions that may be only weak ecological analogues. These data can be difficult to obtain (e.g., the low recapture rates of many long distance migrants makes estimating survivorship very difficult), and they can be empirically intensive, requiring long-term multi-year monitoring and many seasons of intensive field work. These data are crucial, however, for accurate and rigorous assessment of avian demographics and persistence in managed landscapes.

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