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Modeling the Effects of Habitat Fragmentation on Source and Sink Demography of Neotropical Migrant Birds

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Abstract: *Many songbird populations in the midwestern United States are structured as a network of sources and sinks that are linked by dispersal. We used a modeling approach to examine explicitly how populations respond to incremental fragmentation of source habitat and how this response may vary depending upon two life-history attributes: fidelity to natal habitat type and reproductive strength of the source. Fragmentation of source habitat led to a predictable decline in population for both attributes examined, but the manner in which populations declined varied depending upon the reproductive strength of the source and the level of fidelity. When the source was weak and produced few excess individuals, fragmentation of source habitats resulted in a predictable and parallel population decline of adults in both the source and the sink. In this situation high fidelity to natal habitats was important for maintenance of population size and structure. Low fidelity to weak sources resulted in population extinction; populations experienced a demographic cost by dispersing from high quality source habitat to low quality sink habitat. In contrast, when the source was strong and produced many excess individuals, fragmentation of the source led to population declines in both the source and the sink, but this decline was more abrupt in sink habitats. When the source was strong and produced a large excess of individuals, nonfidelity to natal habitats had little effect on metapopulation size and structure.*

Modelación de los efectos de la fragmentación del hábitat sobre la demografía de fuentes y sumideros en aves neomigratorias tropicales

Resumen: *Muchas poblaciones de aves cantoras en el medio-oeste de los Estados Unidos están estructuradas como una red de fuentes ("sources") y sumideros ("sinks"), que se encuentran conectadas por medio de la dispersión. En el presente estudio, usamos una aproximación de modelación para examinar explícitamente como las poblaciones responden al incremento en la fragmentación a del hábitat fuente y como ésta respuesta puede variar dependiendo de dos atributos de la historia de vida: fidelidad al tipo de hábitat nativo y fortaleza reproductiva. La fragmentación del hábitat fuente condujo a una declinación predecible en el tamaño poblacional para ambos atributos examinados, pero la manera en que las poblaciones declinaron varió dependiendo de la fortaleza reproductiva de la fuente y el nivel de fidelidad. Cuando la fuente era débil, y producía un bajo número de individuos excedentes, la fragmentación del hábitat fuente resultó en una predecible y paralela declinación poblacional de los adultos, tanto en la fuente como en el sumidero. En esta situación, una alta fidelidad a los hábitats nativos fue importante para mantener el tamaño y estructura poblacional. La baja fidelidad a fuentes débiles dió como resultado la extinción poblacional, las*

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1396

poblaciones experimentaron un alto costo demográfico al dispersarse de los hábitat fuente de gran calidad a los hábitat sumidero de baja calidad. En forma opuesta, cuando la fuente era robusta, produciendo muchos individuos excedentes, la fragmentación de la fuente condujo a declinaciones poblacionales tanto en la fuente como en los sumideros, pero esta declinación fue más abrupta en los hábitats sumidero. Cuando la fuente era robusta y producía un gran exceso de individuos, la falta de fidelidad hacia los hábitats nativos tuvo poco efecto sobre el tamaño y estructura metapoblacional.

Introduction

Populations of many organisms exist as subpopulations that are linked by dispersal (Harrison 1994). Sources and sinks are one example of subpopulation dynamics where the intrinsic growth rate of subpopulations varies among habitat types (Pulliam 1988). Sources are subpopulations that are demographically viable (juvenile production exceeds adult mortality), whereas sinks are subpopulations that are demographically inviable (juvenile production does not compensate for adult mortality). Sinks will ultimately become extinct unless they receive immigrants from another subpopulation (Brown & Kodric-Brown 1977; Pulliam 1988). Thus, understanding source-sink population dynamics requires knowledge of population demography at the subpopulation level, the habitat conditions responsible for variation in subpopulation demography, and the movement of individuals among source and sink habitat types.

Evidence has accumulated that the viability status of a subpopulation (source or sink) is strongly influenced by habitat size and shape (Harris 1984; Robinson 1992; Lamberson et al. 1994; Hoover et al. in press; Robinson et al. 1995; Donovan et al. 1995). For some species, per capita reproduction is greatest in large, contiguous tracts of interior (core) habitat and reproduction declines as habitats are fragmented (Temple & Cary 1988; Faaborg et al. 1995; Hoover et al. in press; Robinson et al. 1995). In such species large tracts of habitat consist of source subpopulations and fragmented habitats are dominated by sink subpopulations (Robinson 1992; Donovan et al. 1995). In this situation the persistence of sink subpopulations depends upon maintenance of large, intact source habitats (Pulliam 1988; Temple & Cary 1988; Howe et al. 1991).

Because source habitats are vital for population viability and longevity, and in light of increasing anthropogenic habitat alteration and fragmentation, it is important to understand how alteration of source habitats affects the size and structure of the overall population. We develop a baseline source-sink model in which reproduction is a function of percent core habitat, and then we assess the sensitivity of the model to source habitat fragmentation when the reproductive strength of the source and the fidelity of juveniles to their natal habitats are varied. Although many source-sink models have

been developed in recent years (Pulliam 1988; Pulliam & Danielson 1991; Howe et al. 1991; Danielson 1992; Davis & Howe 1992), none have examined explicitly how populations respond to incremental fragmentation of source habitat and how this response may vary depending upon the life-history attributes of a species.

Our objectives were to: (1) develop a baseline source-sink metapopulation model in which some juveniles disperse unidirectionally from an area of high productivity (the source) to an area of low productivity (the sink); (2) modify the baseline model to determine how fragmentation of source habitat affects population size and structure and determine the sensitivity of this response to the reproductive strength of the source, and (3) modify the baseline model so that juvenile dispersal between the source and the sink is bidirectional and determine the model's sensitivity to varying degrees of fidelity to a natal habitat type. We refer to these models as the baseline model, the fragmentation model, and the habitat fidelity model, respectively.

We illustrate the properties of the models with a hypothetical migratory bird species whose reproductive success declines as interior habitats are fragmented. The reproductive traits of this hypothetical species span a range of actual values measured for three avian species in fragmented and contiguous forest habitats in the midwestern United States (Donovan et al. 1995). Migratory birds are excellent organisms for examining source and sink metapopulation dynamics where reproduction is a function of habitat interior (Temple & Cary 1988; Robinson 1992; Hoover et al. in press; Donovan et al. 1995). As North American breeding habitats become fragmented, nest depredation increases (Hoover et al. in press; Robinson et al. in press; Donovan et al. 1995), brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) increases (Robinson et al. 1993), and pairing success decreases (Gibbs & Faaborg 1990; Villard et al. 1993). The result is that fewer young are produced in fragmented forests than contiguous forests. In the midwestern United States the level of nest depredation and parasitism of eight species of forest-nesting, Neotropical migrant birds is significantly and negatively correlated with the amount of forest cover and percentage of forest interior at a 10-km landscape scale (Robinson et al. 1995). Although bird populations may be distributed in habitats that vary in quality, movement of individuals

among source and sink subpopulations is likely because birds are highly vagile organisms (Stacey & Taper 1991; Robinson 1992). Thus, migratory passerines are well suited for investigating how populations respond to incremental fragmentation of source habitat and how this response may vary depending upon the reproductive strength of the source and fidelity of juveniles to their birthplace.

Model Description

The model was programmed in a Microsoft Excel spreadsheet. For all three models we viewed a species' global population as occupying two discrete types of habitat: (1) source habitat, where habitat conditions are favorable for reproduction, and (2) sink habitat, where habitat conditions are less favorable for reproduction (Pulliam 1988). When individuals are surveyed, some fraction of the population is located within source habitat and some fraction is located within sink habitat. The model is not spatially explicit (i.e., it invokes aspects of space but does not consider the actual distribution of source and sink habitat). Thus, we assumed that source and sink habitat is intermingled, where large patches of source habitat are interspersed with and surrounded by an unlimited amount of sink habitat.

In our model a population of a migratory bird species occupies nonbreeding habitat in the winter, then migrates to North American breeding habitat in the spring in year (t). At that time juveniles born in year ($t - 1$) disperse to their first breeding territory in either the source or the sink. In all three models only the female component of the population was modeled, only juveniles disperse, and all dispersal occurs in the spring. Once territories are secured in the source and sink, birds reproduce at habitat-specific rates and populations are censused immediately after fledging. We simulated population growth for 200 years to ensure the population attained equilibrium and discuss all results in terms of equilibrium population size.

In the baseline model we examine the number of individuals within four different classes at equilibrium: adults in the source, juveniles in the source, adults in the sink, and juveniles in the sink. We refer to the combined population of the four habitat/age classes as the metapopulation size (Harrison 1994, who loosely interprets metapopulations as any network of subpopulations linked by dispersal) and the partitioning of individuals among the four habitat/age classes as the metapopulation structure. In the fragmentation and fidelity models we relate the proportion of the adult population located within the source and the sink at equilibrium to source strength and to the degree of habitat fidelity, respectively.

The Baseline Model

In the baseline model juveniles disperse unidirectionally from an area of high productivity (the source) to an area of low productivity (the sink); this dispersal of juveniles from source to sink is dependent on source density. Adults do not disperse. Thus, the censused population size of each habitat/age class in a given year depends on three parameters: class fecundity, class survival rate, and how many juveniles dispersed and established their first breeding territory inside or outside of the class population. We assumed that all adults were habitat faithful regardless of their nesting success in the previous year (i.e., adults in the source in year t will return to the source in year $[t + 1]$, adults in the sink in year $[t]$ will return to the sink in year $[t + 1]$), and that each will be successful in obtaining a breeding territory in their respective habitat type. This assumption is supported by evidence that most dispersal in migratory passerines occurs as natal dispersal (Greenwood & Harvey 1982). Once a breeding territory is secured, adults generally show strong philopatry to a generalized site (Martin & Li 1992; but see Greenwood 1980; Harvey et al. 1980).

We assumed that all juveniles produced in the source seek their first breeding territory in the source and that all juveniles produced in the sink seek their first breeding territory in the sink. Under the guise that sub-optimal habitat is plentiful, we assumed that all individuals seeking a territory in the sink acquired one. (The growth rate for the sink population is by definition less than one so that the population shrinks each year, leaving space for new immigrants). However, we assumed that successful acquisition of a territory in the source is density-dependent, where the probability of acquiring a source territory decreases as the number of individuals seeking a source territory (including last year's adults) increases (Fig. 1). This assumption is supported by evidence that many forest-nesting migrant passerines are territorial and breeding population size may be regulated by the number of territories a habitat possesses (Sherry & Holmes 1989; Newton 1992; Dolman & Sutherland 1994). We used the following equation to describe density dependent dispersal from the source:

$$S = 1 - X^2 / (X^2 + A^2) = A^2 / (A^2 + X^2),$$

where S is the probability of successfully attaining a source territory, X is the total number of individuals seeking a source territory at the time of territory establishment in early spring, and A is a term that varies the success rate of territory acquisition by placing a lid on the number of individuals that occupy the source. The probability of successfully finding a nest site in the source is essentially one if little or no competition occurs (X is very small) but the success rate is reduced by competition following the function previously described. When $A = X$, then 50% of the individuals that

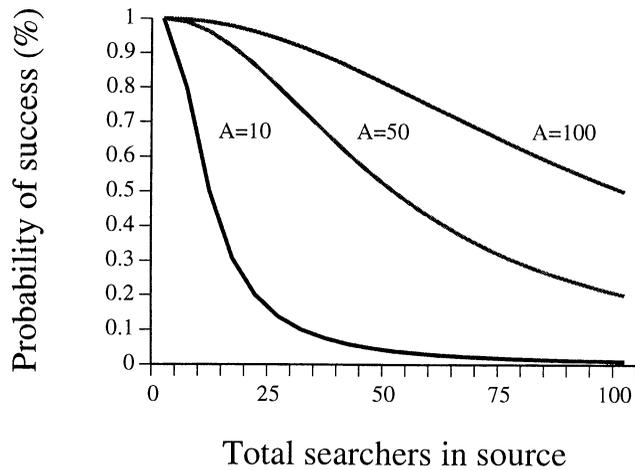


Figure 1. Relationship between the total number of individuals seeking a territory in the source just prior to breeding and the probability of successfully attaining a source territory. Three conditions of A are depicted where A represents the number of individuals that can hold territories in the source habitat.

seek territories in the source will be successful. In other words, if the level of competition for sites in a source region is $X = A$, then 50% of the birds will be discouraged from searching in that area and will disperse to a sink habitat. The total number of individuals seeking a breeding territory in the source year ($t + 1$) consists of

$$(\text{no. of adults in the source in year } (t) \times \text{adult survivorship}) + \text{no. of juvenile searchers}_{(t+1)}$$

In the baseline model, the number of juvenile searchers in year ($t + 1$) consists only of those juveniles produced in the source in year (t). For most of our simulations we arbitrarily set A as 200 individuals in the source. If X is very large relative to A , the probability of a juvenile successfully attaining a source territory is small. All individuals that are not successful in acquiring a source territory disperse to the sink. The effect of A on S and X is shown in Fig. 1.

Next, we assumed that adult and juvenile survival rates were not habitat specific (i.e., the probability that a sink adult survived from year (t) to year ($t + 1$) was the same as that of a source adult). Admittedly, information is lacking to either support or refute this assumption and results must be interpreted with caution. The effects of fragmentation seem to be largely driven by induced declines in fecundity (Robinson et al. 1995); almost nothing is known about how fragmentation affects survival of individuals once they fledge. Birds that fledge from fragments might show decreased yearly survival. However, we elected to use the more conservative assumption of equal survival because: (1) most mortality pressures are constant throughout the year for birds (Ricklefs 1973) and the breeding season represents ap-

proximately one quarter of the annual cycle so that most mortality in birds probably occurs during the nonbreeding season (Greenberg 1980); (2) breeding populations appear to be interspersed during the nonbreeding season (Ramos & Warner 1980), and consequently individuals may be equally exposed to similar mortality threats during that time; and (3) no direct evidence exists that mortality of adult females during the breeding season is higher in fragmented habitats than contiguous habitats. We assumed the survival of juveniles and adults includes any cost of searching for a breeding territory or dispersing from one habitat type to the other, but see Danielson (1992). Realistically, dispersal might involve additional mortality risks, but no evidence exists that this cost is significant in species that annually migrate hundreds of miles between breeding and wintering areas. As such, we included a cost-of-dispersal factor in the model but simply set it to one so it had no effect.

Given these basic model assumptions, we used the following difference equations to describe the population size of each class:

- (1) source adults $_{(t+1)} = (\text{no. source adults}_{(t)} \times \text{adult survival}) + (\text{no. juveniles produced in the source}_{(t)} \times \text{juvenile survival}) \times \text{probability of successfully attaining a source territory}$
- (2) sink adults $_{(t+1)} = (\text{no. sink adults}_{(t)} \times \text{adult survival}) + (\text{no. juveniles produced in the sink}_{(t)} \times \text{juvenile survival}) + (\text{no. juveniles produced in the source}_{(t)} \times \text{juvenile survival}) \times (\text{cost of dispersal}) \times (1 - \text{probability of successfully attaining a source territory})$
- (3) source juveniles $_{(t+1)} = (\text{no. source adults}_{(t+1)} \times \text{source fecundity})$
- (4) sink juveniles $_{(t+1)} = (\text{no. sink adults}_{(t+1)} \times \text{sink fecundity})$.

Model Parameterization

For the generalized migratory passerine species we used the baseline estimates of 0.62 for adult survival and 0.31 for juvenile survival that were derived by Temple and Cary (1988) for a forest interior migrant passerine. These values have been used in modeling migrant bird populations in several studies (Temple & Cary 1988; Howe et al. 1991; Thompson 1993). In the baseline model only we modified adult survival (0.52 and 0.72) to examine the sensitivity of that estimate to the metapopulation size and structure. This range in adult survival (0.52 through 0.72) encompasses most forest-nesting migratory passeriformes (Greenberg 1980; Nichols et al. 1981; Martin & Li 1992). In the fragmentation and fidelity models we used 0.62 for adult survival to focus attention on the risks of habitat fragmentation and straying on metapopulation dynamics. Changing adult survival in these models does not qualitatively affect the results.

We used reproductive data from our fragmentation

studies in Missouri and Minnesota/Wisconsin in which we surveyed birds and monitored reproductive success on fragmented and contiguous forest tracts in each state (Donovan et al. 1995). We located and monitored Ovenbird (*Seiurus aurocapillus*), Red-eyed Vireo (*Vireo olivaceus*), and Wood Thrush (*Hylocichla mustelina*) nests in fragmented and contiguous habitats in Missouri and Wisconsin from 1991 through 1994 (Table 1). Nests were located in 15 fragmented plots that averaged 6% core habitat and 14 contiguous plots that averaged 73% core habitat. We monitored all nests until the fate of the nest was known. To obtain reproductive estimates for each forest-nesting migrant, we pooled all nests through the years and calculated the mean number of female fledglings per adult female per year in both large contiguous forests and forest fragments (Table 1, Donovan et al. 1995). In both Missouri and Wisconsin, reproductive success was significantly lower in fragmented than contiguous habitats; the fragments consisted of population sinks while the contiguous habitats consisted of population sources. To estimate the fecundity of a generalized migrant inhabiting a site with no core, we subsampled our total nest sample by randomly selecting 30 nests known to be located within 250 m of a forest edge and calculated the average number of fledglings for nests located outside core forest habitat (Table 1).

We determined that our fragmented sites averaged 6% core and contiguous sites averaged 73% core in the following manner. For each of our study areas we derived average forest cover landscape statistics from U.S. Geological Survey land use and land cover digital data (Office of Geographic and Cartographic Research, Reston, Virginia). For each plot (15 fragmented plots, 14 contiguous plots) we determined the proportion of forest greater than 250 m from a non-forest edge within a 10-km radius of the plot (Fragstats, Forest Science Department, Oregon State University, Corvallis, Oregon). This radius best explains the distribution of cowbirds in our study sites, and cowbirds directly impact the number of young that fledge from a nest (Donovan et al., in press; Donovan et al. 1995). We refer to this proportion of non-edge forest as core area. We averaged the proportion of core area for fragments and contiguous areas to define the fragmented and contiguous habitats studied (Table 1).

Fragmentation Model

Our objective in developing a fragmentation model was to assess how the metapopulation responds to incremental fragmentation of source habitat and to determine the model's sensitivity to reproductive strength in the source. We examined four functions describing reproductive success across the continuum of fragmentation of source habitat. These functions represent birds that vary in their reproductive response to fragmentation of

source habitats (e.g., reproductive success steeply declines as source habitat is fragmented in one of the functions but only slightly declines in another). All four functions are within the range of observed variation in reproductive success of migrant passerines in source habitats (Donovan et al. 1995). This variation occurs both within a species and among species. For example, we observed that in contiguous habitats Ovenbird populations could function either as strong sources or weak sources (Donovan et al. 1995). We also observed that within the same contiguous habitat, some species produce more offspring per year than others (Donovan et al. 1995). All four functions therefore reflect likely field conditions and were used to assess the model's sensitivity to the reproductive strength of the source. As in the baseline model, all breeding individuals seek a territory in their natal habitat type first, but some disperse from source to sink because success in acquiring a source territory is density dependent.

We describe the fragmentation model below in terms of the function whose reproductive attributes were derived from combined field observations of Ovenbirds, Red-eyed Vireos, and Wood Thrushes in source habitat that was 73% forest interior (core) and in sink habitat that was 6.2% forest interior (core). We later relate how we modified these attributes for the other three functions. We assumed that fecundity is a function of core habitat, defined as the percentage of total area of suitable habitat that is greater than 250 m from a habitat edge (Fig. 2). Core habitat applies to both source and sink habitats, but source habitats for forest migratory birds have a much greater percentage of core habitat compared to sinks (Robinson et al. 1995). As habitats become more fragmented core area is lost and a greater habitat portion is subject to detrimental edge effects or landscape effects, therefore reducing nesting success (Temple & Cary 1988; Paton 1994; Faaborg et al. in press). Thus as core habitat decreases, fecundity decreases. This key assumption is strongly supported by field observations of migratory bird nesting success in forested habitats that vary in the amount of core habitat throughout the midwestern United States (Robinson et al. 1995). We described the relationship between core area and fecundity as

$$\text{fecundity}_{(\text{core percentage})} = M (c + \text{core percentage}) / (b + c + \text{core percentage}),$$

where $\text{fecundity}_{(\text{core percentage})}$ is the mean number of female offspring per adult female per year in a region with the specified core percentage. The parameters M , b , and c were fitted by using the three points based on field observations of three forest-nesting migrants from our fragmentation studies in Missouri and Wisconsin. The points were: average core percentage in the source and average fecundity in the source; average core percentage in

Table 1. Demographic parameters used in baseline and fragmentation models for a generalized forest-nesting, migratory bird.

Landscape	Core habitat (%)	Fecundity		Nest sample size	Adult survival ^a		Juvenile survival
Contiguous	73.12	low	1.2	203	base	0.62	0.31
		observed ^b	1.6 (.37)		low	0.52	
		medium	2.0		high	0.72	
		high	2.4				
Fragmented	6.21	observed	0.66 (.33)	124	base	0.62	0.31
	0% Core	0.00	observed				

^aStarting female adult population was 25 in contiguous and fragmented landscapes.

^bActual observed fecundity in 73% core was 1.7.

the sink and average fecundity in the sink; and no core percentage in the sink and average fecundity at zero percent core (Fig. 2). For example, we observed that fecundity averages 0.66 female offspring per female per year in landscapes that average 6.21% core habitat and 1.6 female offspring in landscapes that average 73.1% core habitat (Table 1).

In addition to reducing female fecundity in source habitat, fragmentation also decreases the probability that a juvenile will successfully attain a territory in the source. In the fragmentation model we considered success in attaining a source territory as a function of percent core by letting $A = \text{percent core in source} \times 200$ in the equation for juvenile success in acquiring a territory

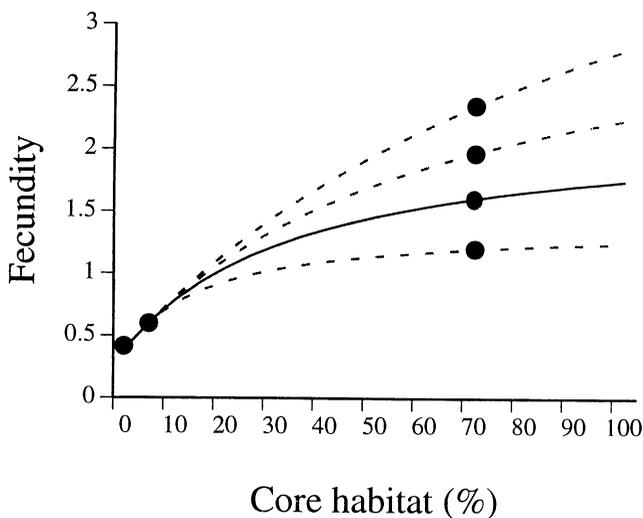


Figure 2. Relationship between fecundity and core habitat percentage for four hypothetical species. The solid curve represents a hypothetical species whose reproductive traits were observed in the field; the three fitted points on the curve depict observed values from our field studies in fragmented and contiguous habitats in Wisconsin/Minnesota and Missouri. The dashed curves represent the relationship between fecundity and core habitat percentage for three additional hypothetical species that vary in their reproductive strength.

in source habitat. Thus, if source core area is reduced from 100% to 50%, then A is reduced from 200 to 100 and the probability that a juvenile will successfully acquire a source territory is decreased (Fig. 1).

Because the fragmentation of core habitat may affect fecundity differently for various species or within a species in different parts of the range (Donovan et al. 1995), we examined three additional functions by varying the fecundity versus core curve previously described. As a result, we were able to determine how fragmentation of source habitats might affect metapopulation size and structure differently depending on the reproductive strength of the source. Only the source fecundity varied. We maintained average sink fecundity (i.e., the percent core in the sink was fixed), and we varied the reproductive strength of the source by changing source fecundity from 1.7 to 1.2 to 2.0, and 2.4 female offspring per adult female per year (Fig. 2). This relationship could be explored by varying sink reproduction as well. However, we chose to vary the reproductive strength of the source and keep the reproductive parameters of the sink constant, simulating further fragmentation of the source because of deforestation. The response of metapopulations to source habitat fragmentation is probably most sensitive to changes in this parameter. In addition, the variation in the number of female offspring per female per year among the three species we studied was greater when some core habitat was present compared to the variation when no core was present (Table 1). Thus biological support exists for varying reproduction in source habitats while keeping reproduction in sink habitats constant.

Habitat Fidelity Model

We assessed the model sensitivity to habitat fidelity of juveniles to their natal habitat type and determined how habitat fidelity affects metapopulation size and structure when the reproductive strength of the source is varied. In source and sink metapopulations the maintenance of sinks depends upon immigrants that dispersed from another subpopulation (Pulliam 1988). Yet as source habitats are fragmented and source productivity is weakened, lack of fidelity to natal habitat type (hereafter,

straying) may have negative connotations for the metapopulation (Davis & Howe 1992).

Most passerine dispersal occurs as a young bird moves from its birthplace to its first breeding territory. Banding studies on passerines have shown that fewer than 1% of all banded nestlings subsequently return as breeding adults to a study area (Greenwood & Harvey 1982; Payne & Payne 1993; Holmes & Sherry 1992). Although these young birds do not exhibit site-fidelity, whether they exhibit some degree of habitat fidelity is not clear. For example, a nestling born in the heavily forested Missouri Ozarks may disperse to an Illinois forest, but whether it will preferentially establish its first breeding territory in a large forest or in a small fragment is not clear. In contrast to juveniles, most adults are faithful to a site after their first breeding territory is secured. If juveniles stray from their natal habitat type, the proportion of the population occupying each habitat is altered and may have profound effects on metapopulation size and structure.

In the baseline model we described a situation where all juveniles return to their natal habitat type. In the habitat-fidelity model we tested six levels of straying to determine model sensitivity to straying. If the natural straying rate (D) is 0.25, then 25% of the individuals born in the source will first seek to establish a breeding territory in the sink and 25% of the individuals born in the sink will first seek to establish a breeding territory in the source; the remaining 75% of individuals will seek a breeding territory in their natal habitat. Similarly, if $D = 0.5$ then the probability an individual will seek a territory in its natal habitat is 50%. The six levels of straying rates that we studied were $D = 0, 0.1, 0.2, 0.3, 0.4,$ and 0.5 . For each level of straying, we examined how the source's reproductive strength influenced the size and proportion of the adult population in the source and the sink.

We modified the basic model difference equations to compute the population size of the adult classes. The juvenile equations are the same as the baseline model:

$$\text{source adults}_{(t+1)} = (\text{no. source adults}_{(t)} \times \text{adult survival}) + [(\text{no. juveniles produced in the source}_{(t)} \text{ that did not disperse to the sink}) + (\text{no. juveniles produced in the sink}_{(t)} \text{ that dispersed from sink to source})] \times (\text{juvenile survival}) \times (\text{probability of successfully attaining a source territory})$$

$$\text{sink adults}_{(t+1)} = (\text{no. sink adults}_{(t)} \times \text{adult survival}) + [(\text{no. juveniles produced in the sink}_{(t)} \text{ that did not disperse to the source}) + (\text{no. juveniles produced in the source}_{(t)} \text{ that disperse from source to sink})] \times (\text{juvenile survival}) + (\text{no. juveniles seeking a territory in the source}) \times (1 - \text{probability of successfully attaining a source territory}) \times (\text{juvenile survival}),$$

where the number of juveniles seeking a territory in the source equals the number of juveniles produced in the

source (t) that did not disperse to the sink added to the number of juveniles produced in the sink (t) that dispersed to the source.

Results

Baseline Model

In all baseline models, the metapopulation stabilized within 20 to 60 years. Metapopulation size and structure at equilibrium were sensitive to changes in adult survival (Fig. 3). When baseline adult survival was 0.62 (Fig. 3a), the majority of the censused population consisted of source juveniles, followed by source adults, sink adults, and sink juveniles. At equilibrium, approximately 78% of the juveniles from year ($t - 1$) that sought a territory in the source habitat were successful, whereas the remainder failed to acquire a source territory and dispersed into the sink (Fig. 3b). This relatively low level of dispersal from source to sink, combined with low reproduction in the sink producing few juveniles from year ($t - 1$) seeking territories in the sink in year t , stabilized the metapopulation so that most of the individuals inhabited source habitat.

This trend was even more apparent when adult survival was reduced to 0.52 (Fig. 3c), such that most juveniles (>90%) produced in year ($t - 1$) that sought a territory in the source were successful (Fig. 3d). Very few juveniles dispersed to the sink; the population size of sink individuals was maintained at low levels by low reproduction in the sink and the few source juveniles that dispersed to the sink. A second consequence of low adult survival was that the metapopulation size at equilibrium was substantially reduced.

In contrast, when adult survival was increased to 0.72, the majority of the census population consisted of sink adults (Fig. 3e). Because the bulk of the adult population was located within the sink, most juvenile production occurred in the sink even though per capita productivity was relatively low. This occurred because we assumed that sink habitat was widely available and that population size in the sink was unlimited. The remainder of the metapopulation at equilibrium consisted of source juveniles and source adults (Fig. 3e). At equilibrium, the number of juveniles from year ($t - 1$) that sought a territory in the source area in year t was high compared with the base adult survival and low adult survival, but only ~58% successfully attained a source territory; 42% dispersed into the sink (Fig. 3f). This relatively high dispersal from source to sink maintained the metapopulation size at high levels and the bulk of the metapopulation occurred in the sink.

Fragmentation Model

Because we considered fecundity a function of core habitat percent, fragmentation of the source area reduced

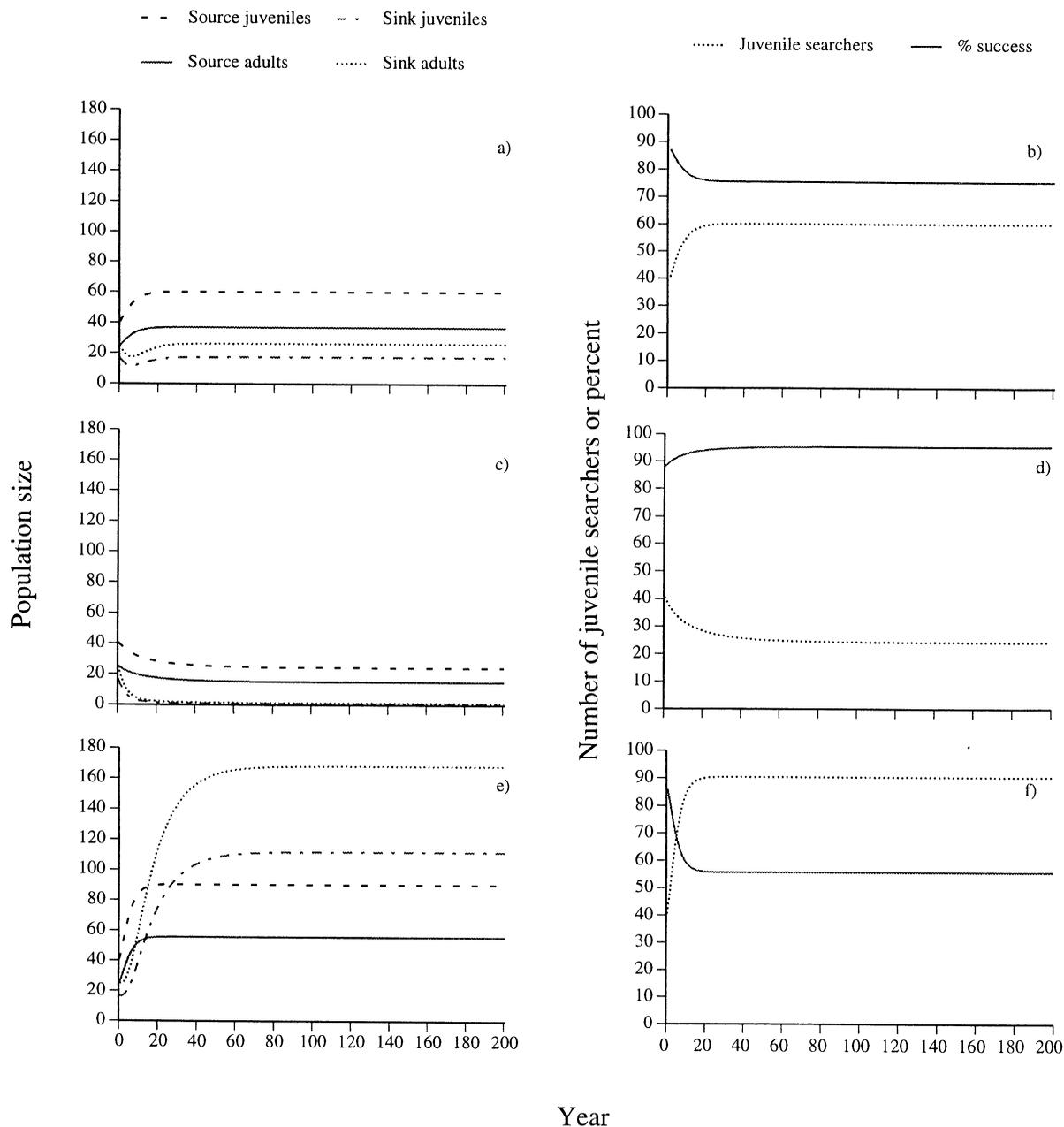


Figure 3. Results of baseline model simulations of a generalized forest-nesting migratory bird in which there is density-dependent dispersal from source to sink: metapopulation size and structure after 200 generations (a, c, and e); and density-dependent dispersal as a function of the number of juveniles from the previous year that seek territories in the source habitat (b, d, and f) (baseline adult survival = 0.62 [a and b], low adult survival = 0.52 [c and d], and high adult survival = 0.72 [e and f]).

metapopulation size and affected metapopulation structure regardless of source strength. However, source strength had a large impact on the manner in which the metapopulation declines. When source reproduction was low, any fragmentation of source habitat resulted in loss of sink populations because source productivity was not sufficient to rescue sinks from extinction (Fig. 4a). For the function in which reproductive traits were

derived from observations (1.62 female offspring per adult female per year at 73% core habitat), fragmentation of the source reduced the equilibrium adult population size in both the source and the sink in a nearly parallel fashion (Fig. 4b). When the source core area was reduced to 25% core area, the metapopulation went extinct because the source was not able to sustain itself or provide immigrants to the sink habitat.

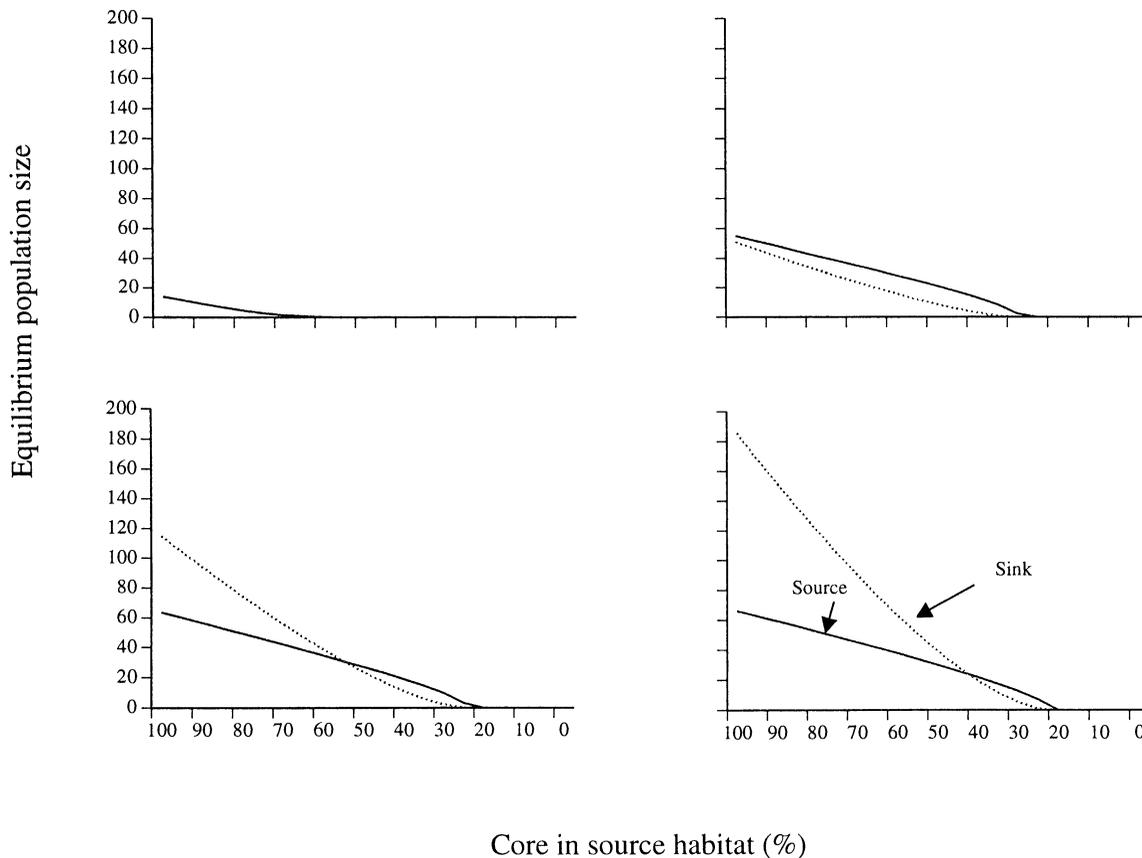


Figure 4. Relationship between equilibrium population size of adults in the source (solid curve) and the sink (dashed curve) and core habitat percent in the source for four hypothetical species whose reproductive response to habitat fragmentation varies: low (a), observed (b), medium (c), and high (d) source fecundity.

When source reproductive strength was moderate to high, incremental fragmentation of the source resulted in a steady decline in source population but the decline in the sink population varied dramatically (Fig. 4). When source fecundity was moderate (2.0 female offspring per adult female per year with 73% core habitat), most of the adult population resided in sink habitat (Fig. 4c). This occurred because increased source fecundity allowed individuals to migrate from the source to the sink, maintaining the metapopulation at higher levels. Fragmentation of source core habitat and concomitant decrease in fecundity of the source resulted in decreased metapopulation size, but this decrease was more readily apparent in the sink than in the source (Fig. 4c). When the source core habitat was reduced to 50%, the number of adults in the source and the sink was approximately equal. Further reduction in source core habitat resulted in a metapopulation where most adults occurred in the source and fewer occurred in the sink.

When source productivity was high (2.4 female offspring per adult female per year at 73% core habitat), the metapopulation size was large compared to the previous examples and fragmentation of the source habitat from 100 to 50% core resulted in a strong reduction of the

sink population whereas the source equilibrium population declines only slightly by comparison (Fig. 4d). When the source core habitat was reduced to 40%, the number of adults in the source and the sink was approximately equal; further fragmentation resulted in a metapopulation where most adults occur in the source.

Habitat Fidelity Model

Model sensitivity to the proportion of juveniles that strayed from their natal habitat type to the other habitat type was dependent upon the reproductive strength of the source (Fig. 5). When source fecundity was high (Fig. 5a), straying had little effect on metapopulation size or structure. When source fecundity was medium, metapopulation size was reduced and high rates of straying ($D = 0.4-0.5$) decreased the number of individuals in both the source and the sink by approximately 10 individuals. When source fecundity matched those based on field observation, high levels of straying sharply reduced the number of individuals in both the source and the sink (Fig. 5c). When D was 0.4, the metapopulation went extinct. When source fecundity was low, the metapopulation size was very small and all individuals were located

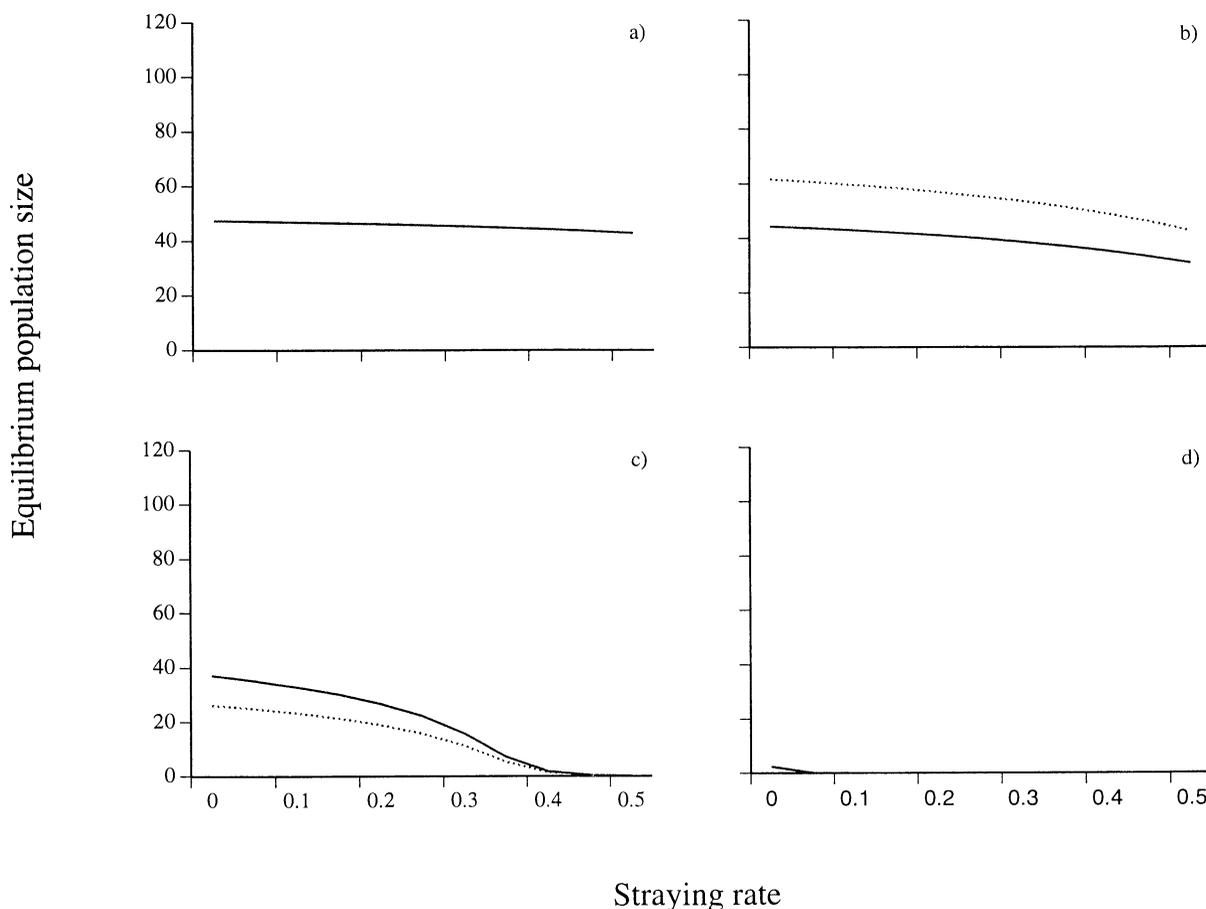


Figure 5. Relationship between equilibrium population size of adults in source (solid curve) and sink (dashed curve) habitats for six hypothetical species that vary in their intrinsic dispersal rate. Source fecundity is reduced from high (a) to medium (b) to observed (c) to low (d) via habitat fragmentation.

in the source. Any straying or nonfidelity resulted in metapopulation extinction (Fig. 5d).

Discussion

Our models show that metapopulations will decline in response to incremental fragmentation of source habitat, but the manner of decline varies depending upon two life-history attributes of a species: the reproductive strength of the source and the degree of habitat philopatry. Fragmentation resulted in rapid metapopulation extinction for species with weak reproduction in the source. For species that produced a large excess of individuals in the source, initial population declines occurred in sink habitats. These results provide important connotations for migratory bird populations.

The widespread decline of some migratory species has been attributed to habitat fragmentation (Temple & Cary 1988; Askins et al. 1990; Faaborg et al. 1995). These studies corroborate that migrant bird population declines are most apparent in small fragmented habitats whereas populations in large, contiguous habitats are

not declining (Askins et al. 1990). Field observations show that population sinks dominate small isolated fragments (Robinson 1992; Donovan et al. 1995). Without immigration, migratory bird populations are expected to decline in fragmented habitats. However, we suggest that fragmentation of source habitats may result in population declines in the sink by decreasing the number of potential immigrants available to rescue sinks from extinction. These declines may occur without concomitant population declines in the source. Thus, the reduction in density of some bird species on fragmented habitats (so-called area-sensitive species) may be the result of two nonexclusive processes: (1) poor reproductive success in fragmented habitats when immigration is negligible (Faaborg et al. 1995) or (2) fragmentation of source habitat, which affects the number of immigrants available to rescue populations on fragments from extinction. Based on these results we reemphasize the need to identify and protect large intact source habitats throughout a species' breeding range to ensure long-term metapopulation survival.

Our fragmentation model is qualitatively different than the fragmentation model developed by Temple and Cary

(1988). First, we conducted a sensitivity analysis to assess how incremental fragmentation differentially affected populations depending on their life history traits; Temple and Cary (1988) demonstrate how the metapopulation of a single migratory bird will respond to three fragmentation scenarios. In this sense, we present a larger picture that enables a more clear interpretation of their results. Second, Temple and Cary (1988) assumed that fecundity is a function of distance-to-edge whereas we assumed that fecundity is a function of habitat core area within 10 km of a particular habitat (Robinson et al. in press). Although edge effects do exist for many species, we suggest that overall landscape quality and pattern governs reproductive success of migratory birds. For example Wood Thrushes nesting in relatively large forest blocks (>1000 ha) but in a highly fragmented landscape in southern Illinois experience the same reduced reproductive success as thrushes nesting on much smaller forests in the same landscape (Robinson, personal communication), the edge effects extend well beyond 200 m. In this situation features of the surrounding landscape may be more important in determining reproductive success than distance-from-edge. For such species examination of core habitat within a given area should more realistically predict population changes with fragmentation (Robinson et al. 1995).

That habitat fragmentation is detrimental for species with limited dispersal capacity has been appreciated for many years (Gilpin 1987). In these species decreased habitat and population size can erode the genetic variability and increase the probability of local extinction (Gilpin 1987). Until recently, habitat fragmentation has not been a major concern in highly vagile species because movement of individuals among sources and sinks can preserve the genetic diversity of the population and rescue subpopulations from local extinction (Brown & Kodric-Brown 1977). Such rescue, however, may be at a cost to the larger global population. Recently developed mathematical models predict that demographic systems driven by frequent extinction and recolonization of subpopulations result in rapid reduction in effective population size and loss of global genetic variation for the species as a whole, even in otherwise abundant species (McCauley 1993). In this scenario interacting sources and sinks may actually lose genetic variation faster than a panmictic population with the same number of individuals.

In addition to a genetic cost of rescue, our results suggest a demographic cost to rescuing sinks from extinction may exist if individuals stray from areas that are favorable for reproduction to less favorable areas. This cost is most pronounced in populations where the reproductive strength of the source is low, and fragmentation of source habitats is one way that reproductive strength of the source is diminished. When reproduction in the source is diminished, metapopulation size de-

clines for species with low habitat-fidelity because individuals tend to stray away from high quality habitats (sources) to low quality habitats; sinks may drain the source population, resulting in population decline in both the source and the sink. By contrast, habitat fragmentation affects species with high habitat fidelity comparatively less because individuals tend to return to habitats where per capita reproduction is the highest (the source). Our results support the hypothesis put forth by Howe et al. (1991) and Davis and Howe (1992) that species with high intrinsic dispersal should be most affected by habitat degradation if they disperse from high quality habitat to low quality habitat.

Although the dynamics within and among subpopulations should be emphasized for maintaining migratory songbird populations (Villard et al. 1992), traditional management practices and the majority of Neotropical migrant bird studies continue to focus on local-scale (or subpopulation) demography. Conservation strategies must acknowledge source-sink population structure and protect regionally important source areas. Future research should encompass a broader landscape perspective and might include, for example, identification of the geographic scale by which populations are dispersally connected or the intrinsic and extrinsic factors that govern dispersal among sources and sinks and how these vary among species. Verification of our model predictions is needed to lend credence to the metapopulation dynamics proposed in our models. Studies of the details of metapopulation dynamics of widespread species are needed to provide critical information necessary for directing long-term conservation efforts.

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