METAPOPULATIONS, SOURCES AND SINKS, AND THE CONSERVATION OF NEOTROPICAL MIGRATORY BIRDS IN THE MIDWEST

Therese M. Donovan[1], Douglas A. Clark[2], Robert W. Howe[3], and Brent J. Danielson[4]

ABSTRACT.—Metapopulation models and source-sink models depict species whose distributions are spatially subdivided at some scale. Although the distribution is spatially subdivided, the subdivided populations (also called subpopulations) are linked to each other when individuals disperse from one location to another. Both models examine the consequences of dispersal among subpopulations and its impact on the survival of the entire population. These models are relevant for migratory bird management because distribution gaps and dispersal are typical of many migratory bird populations; management at the local scale may have limited or perhaps no effect on global populations of priority species.

A metapopulation is a set of connected subpopulations where each subpopulation experiences extinction but is recolonized when individuals disperse from one subpopulation to another. Metapopulation models explain and predict the distribution of occupied and unoccupied habitat patches and factors that affect dispersal between patches and the persistence of the greater metapopulation. In a metapopulation context, critical information consists simply of presence or absence of a species for each patch across time. Factors that influence extinction and recolonization rates are studied to understand their impacts on the spatial distribution and persistence of the populations.

Source-sink models, by contrast, consider both the distribution and size of connected populations, where subpopulations vary in their birth and death rates. Sink subpopulations inhabit relatively poor quality habitat and are not viable without an influx of immigrants. Source subpopulations inhabit relatively high quality habitat in terms of reproduction and survival and are viable without an influx of immigrants; sources can export individuals to sinks. The numbers of individuals located within each subpopulation, the birth and death rates of each subpopulation, and rates of dispersal between subpopulations are critical in determining the size (number) of the entire population.

Although today's theoretical models describe many types of dynamics, their implications for the management of migratory birds are the same: (1) isolated breeding subpopulations are linked by dispersal, which may be critical for the maintenance of regional populations, (2) the spatial scale at which subpopulations interact by dispersal, while typically unknown, defines an appropriate demographic unit for management, (3) in the absence of dispersal data, regional-scale management is preferred over local-scale management, and (4) identifying and maintaining source subpopulations is vital for the persistence of spatially subdivided populations.

[1]*USDA North Central Forest Experiment Station, 1-26 Agriculture Bldg., University of Missouri, Columbia, MO 65211*

[2]*Learning Center Mathematics Division, University of Missouri, Columbia, MO 65211*

[3]*Department of Biology, University of Wisconsin - Green Bay, Green Bay, WI 54311-7001*

[4]*Department of Animal Ecology, Iowa State University, Ames, Iowa, 50011-3221*

INTRODUCTION

Many bird species have distributions that are geographically discontinuous; that is, they consist of multiple populations (Andrewartha and Birch 1954, den Boer 1981). From a management perspective, this discontinuity can influence whether or not a local population and the global population can persist over time. Metapopulation and source-sink models depict local populations (or subpopulations) that vary in longevity and emphasize the importance of dispersal among local populations (Harrison 1994). These models are relevant for migratory bird management because migratory bird populations are often spatially discontinuous but linked by dispersing individuals. Therefore, setting management goals directed solely at the local scale may have limited success because populations may be regulated by events occurring at scales beyond the local scale.

Our objectives are to: (1) briefly review the importance of metapopulation and source-sink concepts, (2) provide empirical evidence that supports or refutes these models, (3) discuss the demographic implications of each model, and (4) provide some general management recommendations in light of current knowledge of these systems. Our intent is to help managers understand the concepts and implications of metapopulation and source-sink theory for the management of migratory bird species. Based on empirical knowledge, managers can apply these concepts and assess appropriate actions on a species-by-species basis.

METAPOPULATIONS: CONCEPTS AND EMPIRICAL EVIDENCE

Metapopulation Concepts

The metapopulation model (Levins 1968, 1969, 1970) was originally devised to describe organisms in spatially discrete habitat patches where local subpopulations periodically go extinct and are recolonized; the persistence of the greater population depends on how the patches interact in terms of dispersal and local extinction (reviewed by Hanski and Gilpin 1991). Levins (1968, 1969, 1970) developed the "classic" metapopulation model to discern how a patchily distributed insect pest population could be controlled when it consisted of multiple populations. His concern was that local populations could be sprayed to extinction with seemingly little effect on the larger population, and thus he pursued the demographic consequences of localized extinction and recolon-ization in a "population of connected subpopulations."

In Levins' metapopulation model, a "metapopulation" exists in a network of habitat patches, some occupied by subpopulations of individuals and some unoccupied (fig. 1). Each subpopulation has a finite lifetime and each has the same probability of extinction. Although any local subpopulation can go extinct, the patch also can be recolonized by individuals dispersing from other subpopulations. Levins' model implicitly assumes that patches are of equal population size and contribute colonists equally. Each unoccupied patch has the same probability of being colonized. At equilibrium, the proportion of patches that are occupied remains constant, although the pattern of occupancy continually shifts as some subpopulations suffer extinction followed by recolonization (fig. 1).

Levins' model was a differential equation that determined the rate of change in the percentage of inhabited patches. There are two key parameters: the local extinction rate and the migration rate of individuals to other patches. The original equation is

$$dp/dt = mp(1-p) - ep,$$

where p is the proportion of inhabited patches, m is the migration rate (the probability that migrants from any given population reach another site), and e is the local extinction rate of inhabited patches. Importantly, there is no mention of within-population dynamics. In this simplistic model, subpopulation size and within subpopulation reproduction and mortality rates are not considered; presence-absence data are sufficient to determine metapopulation structure, assuming that subpopulations are of equal size.

Levins' model has a few take-home points: (1) A metapopulation persists as long as individuals can successfully disperse from one patch to another and this migration rate exceeds the local extinction rate. (2) The pattern of patch occupancy by birds varies with time, but at equilibrium, the proportion of patch occupancy remains constant. The actual equilibrium proportion of occupied patches can be

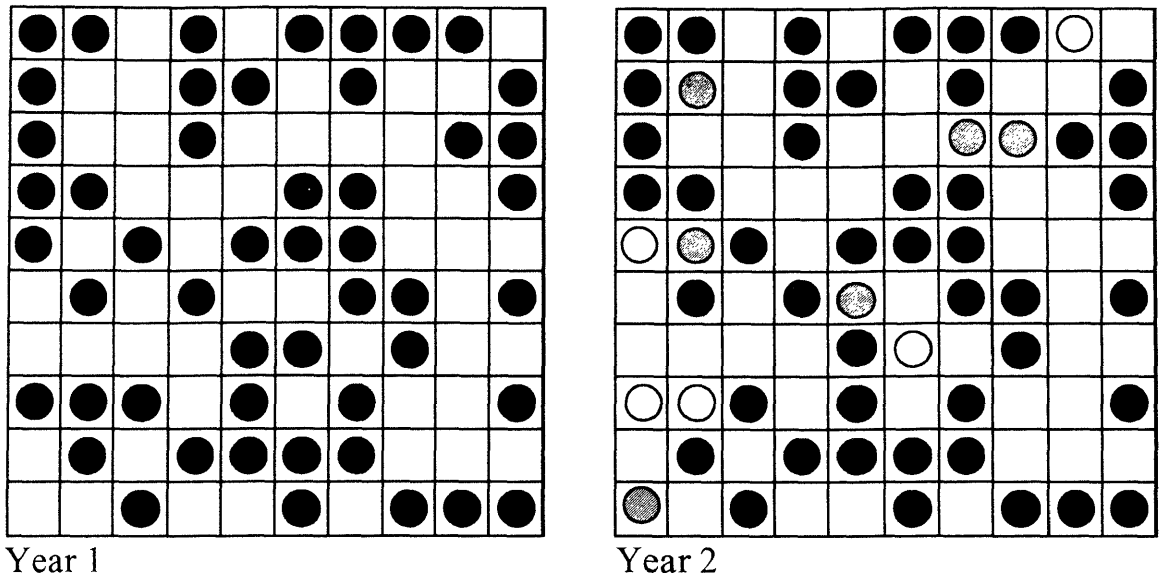

Figure 1.—*Hypothetical example of metapopulation dynamics for a species with 100 suitable habitat patches in two years. Darkened circles represent patches that are occupied in year 1 or year 2. Empty circles in year 2 represent local extinctions, and gray circles represent newly colonized habitat. In year 1 (left),* n_1 *= 50 or 50% of the suitable habitat is occupied, migration rate (m) = 0.225, and extinction rate (e) = 0.1 (estimates derived from Villard* et al. *1992). In year 2 (right),* n_2 *= 51 or 51% of the suitable habitat is occupied; five patches went extinct and six patches were colonized. The equilibrium population size for this metapopulation is 1 - e / m = 1 - (.1/.225) = .56 = 56% of suitable habitat occupied over time.*

large or small, and a metapopulation will persist as long as the migration rate exceeds the extinction rate.

It is fairly easy to see that few real populations satisfy the conditions of Levins' model. Classical (Levins') metapopulation structure has been documented for only a handful of species (Harrison 1994), and these species typically occur in early successional or ephemeral habitat and possess relatively poor dispersal capabilities. Some examples are frogs in temporary ponds (Sjogren 1991) and butterflies in disturbed habitats (Harrison *et al.* 1988, Thomas 1994). Most species, however, do not conform to Levins' assumptions because subpopulations invariably are nonrandomly configured in space and do not have uniform extinction and recolonization probabilities. Numerous spinoffs of Levins' model have been devised in an attempt to incorporate real-world processes. In general, these spinoffs still attempt to explain and predict the spatial distribution of occupied and unoccupied habitat patches.

For birds, metapopulation structure additionally might be obscured by the time scale at which extinction and recolonization occur. If extinction rates are low, for example, but dispersal between subpopulations is high, extinction-colonization episodes will be rare and metapopulation structure will be difficult to recognize. Bird species that appear to consistently occupy the same habitat patch over time might be overlooked as candidates for metapopulation structure since local extinction and local recolonization are necessary components of metapopulation structure. A typical field study may be too brief to detect "classical" metapopulation structure (sensu Levins 1970), even when subpopulation structure is present.

To summarize, metapopulation structure exists when a population of individuals is subdivided into semi-independent breeding populations that are linked by dispersal, but the dynamics of the greater population are driven by local extinction and recolonization that act at the larger spatial scale. Determination of metapopulation structure requires (1) knowledge of

the scale at which subpopulations are linked by dispersal, (2) knowledge of what constitutes "suitable" habitat, and (3) documentation of subpopulation presence or absence across suitable habitats over time. In addition, tests of classic metapopulation structure require that the additional assumption of uniform extinction and recolonization rates be met.

Empirical Evidence of Metapopulation Structure

In North America, evidence that neotropical migratory passerines exist as metapopulations is weak and has only recently become a major research topic (Villard *et al.* 1992). As far as we are aware, in North America, metapopulation structure has been considered only for forest-nesting passerines in highly fragmented landscapes (but see Opdam 1991). Hence, we will use forest-breeding migratory passerines to illustrate the evaluation of metapopulation structure.

First, many species of forest-nesting passerines occur as distinct, spatially separated subpopulations during the breeding season. Ovenbirds, for example, occur only in forests > 300 ha. (Hayden *et al.* 1985). Ovenbird territory size is generally a few hectares or less and ovenbirds hold breeding territories throughout the breeding season (Van Horne and Donovan 1994). Therefore, ovenbirds that populate a particular fragment are effectively isolated from breeding subpopulations in other fragments.

Second, recent studies document the disappearance and re-appearance of some forest-nesting passerines on a local scale (Brawn and Robinson 1996). Thus, local populations experience periodic extinction and recolonization, a condition of classical metapopulation models. In one example, bird populations have been censused since 1927 in Trelease Woods, an isolated woodlot in central Illinois (Kendeigh 1982). In most years, several breeding pairs of wood thrush occurred in the woodlot, but in other years, three extinction events were recorded followed by three colonization events (Brawn and Robinson 1996). During the time of wood thrush absence, Trelease Woods changed relatively little in its vegetation characteristics, and apparently suitable habitat remained unoccupied, another characteristic of metapopulations.

Finally, the only direct field test for metapopulation structure in forest nesting birds demonstrated that extinction and recolonization occurred and met conditions needed for metapopulation structure (Villard *et al.* 1992). Villard *et al.* (1992) studied three forest nesting species (ovenbird, wood thrush, and scarlet tanager) in 71 forest patches within an agricultural matrix near Ottawa, Ontario. Each of the forest patches was surveyed over a 2-year period, and each species was scored as present or absent in the two successive years. Occupied patches in year 1 that became unoccupied in year 2 constituted a local-scale extinction, and unoccupied patches in year 1 that became occupied in year 2 constituted a local-scale recolonization. Although patch occupancy shifted from year 1 to year 2, recolonizations exceeded or equaled local extinctions, a necessary outcome if the metapopulation is to persist (Villard *et al.* 1992). The authors concluded that the relevant demographic unit for these species in fragmented forests consists of a network of interacting patch populations.

Although these studies indicate that some aspects of metapopulation structure are exhibited by North American songbirds, none provide sufficient evidence that populations are structured as metapopulations and that the overall persistence of a species is dictated by a balance of extinction and recolonization of habitat patches. However, these studies force managers to consider patch dynamics for bird species, and metapopulation theory provides impetus for documenting dispersal patterns, the scale at which subpopulations are linked, and the factors that promote or retard dispersal (Villard *et al.* 1995).

Management Implications for Metapopulation Dynamics

Managers must consider several critical issues when evaluating whether metapopulation dynamics pertain to a given bird species, including identifying the effective scale and boundaries of the metapopulation, the definition of subpopulations or suitable habitat patches, and rates of dispersal and local patch occupancy over time (Harrison 1994). First, in defining the boundaries of a metapopulation, managers need to consider the scale at which bird subpopulations interact by dispersal; this scale defines an appropriate demographic unit

for management. For example, if dispersal occurs within a Breeding Bird Survey physiographic region (defined by history, vegetation, and soil characteristics), then all suitable habitat patches should be evaluated in terms of presence and absence within that region to evaluate possible metapopulation structure. Focusing on a smaller region than the actual scale of dispersal could result in misinterpretation of presence and absence patterns and the status of the metapopulation.

Second, once this scale of dispersal is defined, managers should consider the spatial distribution of priority species (its presence and absence in space across time). This includes considering how interbreeding individuals are distributed across habitats to determine what constitutes a subpopulation. For example, ovenbirds in the Midwest that inhabit relatively large (>100 ha) forest patches collectively represent isolated subpopulations during the breeding season; dispersal among patches in successive years occurs when birds disperse from one breeding patch to another or from birth location to the first breeding territory (Martin and Li 1992). By contrast, Baltimore orioles that inhabit relatively small (<10 ha) habitat patches often move from patch to patch within a breeding season (Howe 1979, 1984), and thus an isolated breeding subpopulation may encompass an archipelago of small habitat islands (fig. 2) (Rolstad 1991, Weins 1989). Thus, the definition of a subpopulation in a metapopulation context is likely to be species specific and to depend on species-specific habitat requirements.

Although we do not know the scale of dispersal in most species and are challenged to define what constitutes a subpopulation, metapopulation theory promotes active management at spatial scales larger than the traditionally viewed local scale. One consequence of dispersal among subpopulations is that managers should realize that actions taken at their particular location can influence the dynamics of bird populations some distance from their location. For example, suppose a large forest patch is managed to the detriment of a species. If this large patch is a significant part of the metapopulations habitat, declining habitat quality in this large patch may put subpopulations in other patches at risk as well. In some instances, this could even result in the extinction of the metapopulation. Furthermore, management actions at the local scale contribute to the extinction and recolonization rates of the larger metapopulation and thus can influence population dynamics beyond the local scale. Likewise, management actions that promote the presence of a species at the local scale may be offset by management actions elsewhere that impact the number of colonists available to disperse to their patch (Lande 1991).

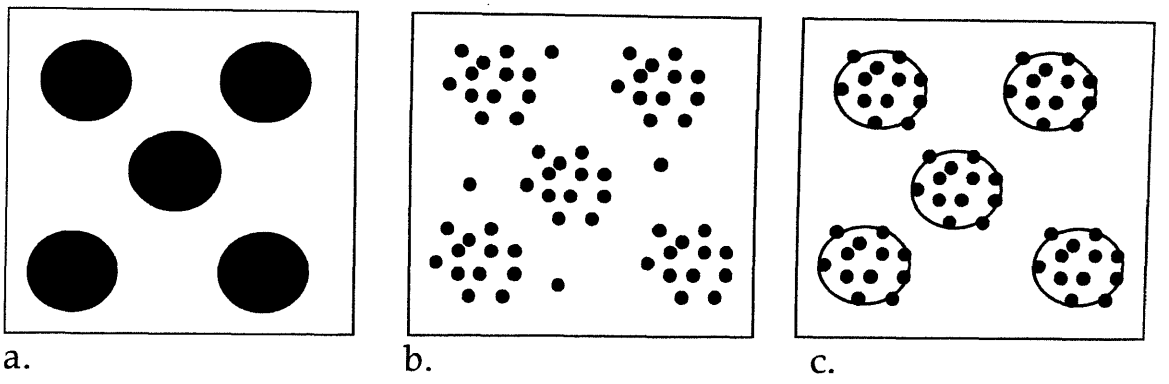

Figure 2.—*Hypothetical example of subpopulation identification: (a) darkened circles represent habitat patches with each patch containing demographically independent subpopulations, (b) darkened circles represent a patchy habitat mosaic over which all individuals move and exchange genes, therefore one population (or subpopulation is depicted); (c) darkened circles represent a patchy habitat mosaic, and although individuals move across habitat patches, demographically independent subpopulations exist because gene exchange is limited within open circles.*

From a management standpoint, the extinction of a subpopulation from apparently suitable habitat is a normal occurrence in metapopulation dynamics. Metapopulation equilibrium focuses on the proportion of patches that are occupied over time. Complete loss of one subpopulation may or may not influence this equilibrium proportion. But this does not imply that local extinctions should be considered lightly (Harrison 1994). If suitable habitat becomes unsuitable, the total number of patches available to the metapopulation is reduced. If equal population size in all patches is assumed, the result is a decline in the total number of individuals in the metapopulation, which in turn influences the pool of migrants that disperse from patch to patch.

SOURCE-SINK DYNAMICS: CONCEPTS AND EMPIRICAL EVIDENCE

Source-Sink Concepts

Resource managers have long recognized that reproductive and mortality rates can vary tremendously across a species range, and there is evidence of this for midwestern neotropical migratory birds (e.g., Robinson *et al.* 1995). Source-sink models were created to describe organisms in spatially discrete and demographically independent subpopulations, similar to the metapopulation models described above. In this situation, however, the key demographic question is how a greater population can persist at equilibrium when its subpopulations vary in their birth and death rates (Pulliam 1988 and references therein). Thus, where metapopulation models assume that subpopulations have equal probability of extinction and recolonization, source-sink models recognize that some subpopulations (sinks) are inviable without constant influx of immigrants from other subpopulations, while others (sources) remain viable without the influx of any immigrants.

Pulliam used "BIDE" models (Cohen 1969, 1971) to determine how a greater population that is comprised of subpopulations varies in number over time. In a BIDE model, B, I, D, and E represent birth, immigration, death, and emigration, respectively. All subpopulations contribute to the equilibrium number. As stated, each subpopulation is an independent demographic unit and has its own bide parameters. A subpopulation is in dynamic equilibrium (not changing) when $b + i - d - e = 0$. At equilibrium, a subpopulation is a source when $b > d$ and $e > i$, and is a sink when $b < d$ and $e < i$. The greater population is at dynamic equilibrium (not changing) when b (all the births) + i (all the immigrants from outside the greater population) - d (all the deaths) - e (all the emigrants that leave the greater population) = 0.

For example, consider a very simplistic global population at equilibrium that consists of 100 individuals, distributed across four discrete patches (fig. 3). Each subpopulation varies in its birth, death, emigration, and immigration rates. The bide parameters represent per capita rates and thus are not area specific. One habitat is a source, with an initial population of 10 breeding adults (5 pairs), where b = 2.5 young per year, d = 0.5 deaths per year, i = 0, and e = 2.0 emigrants per year. (Thus, $b > d$, and $e > i$, but the population overall does not change over time). Three habitats are sinks, where the initial number of individuals is 40, 25, and 25, and in which b = 0.25, 0.4, 0.52, d = 0.5, 0.52, 0.8, and i = 0.25, 0.12, 0.28, and e = 0, 0, 0 respectively. Thus, in all sinks, $b < d$ and $e < i$, but the population numbers of each sink does not change over time. Each subpopulation is in equilibrium, and the overall (global) population is also in equilibrium (b = 0.58, d = 0.58, i = 0, and e = 0).

This example depicts a population at equilibrium (N = 100 individuals). In general, Pulliam considered a species that occurs in both source and sink habitat in which the population size in the source is regulated by some resource that cannot be infinitely subdivided between individuals (e.g., the number of possible breeding territories or nest-hole cavities). Individuals unable to find a breeding site in the source emigrate to the sink because a poor breeding site is better than none at all. If there are many habitats, the total population reaches an equilibrium when the total surplus in all the source habitats equals the total deficit in all the sink habitats.

Some basic take-home points from Pulliam's source-sink model are: (1) At equilibrium, the **number of individuals** in the overall, global population is not changing. This is quite different from the equilibrium point in Levins' metapopulation model, which focuses on the **proportion of occupied patches** over time

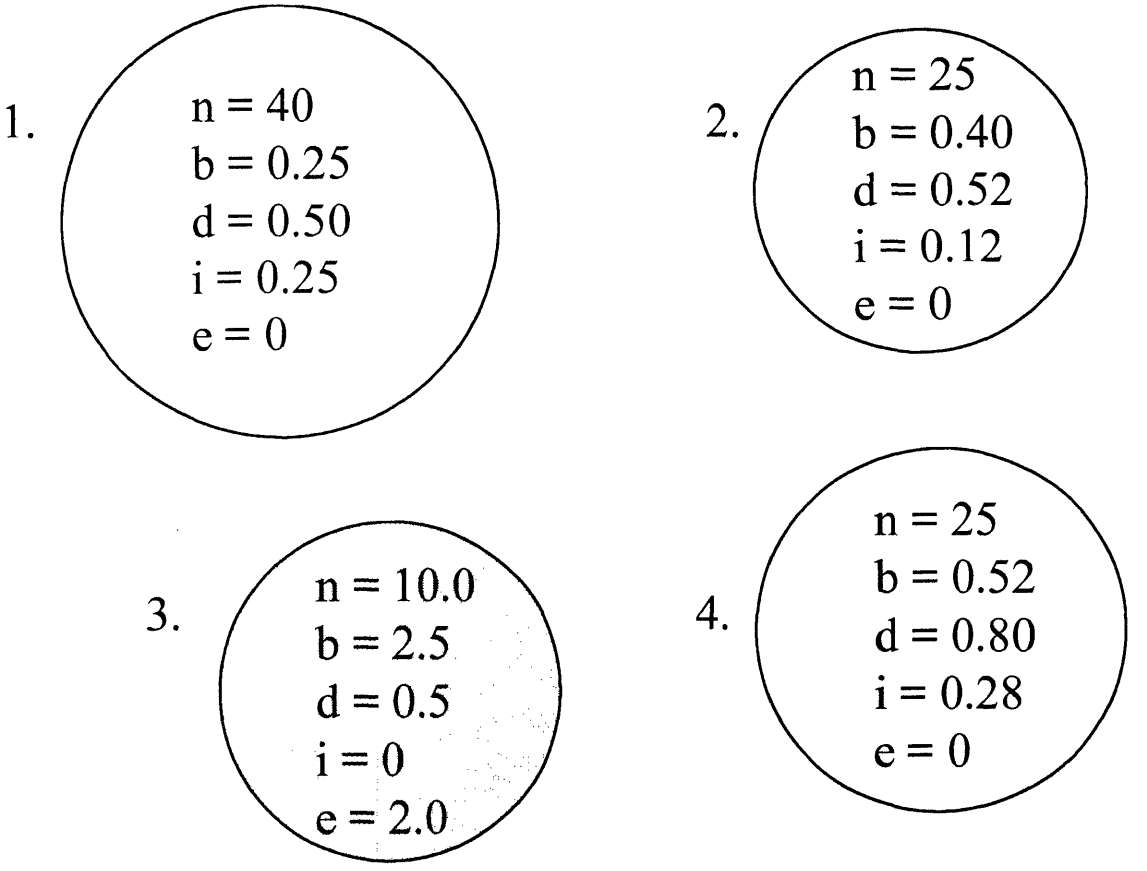

Figure 3.—*Hypothetical example of a source-sink model with four demographically independent subpopulations, three sinks and one source. The number of individuals (n), birth rate (b), death rate (d), immigration rate (i), and emigration rate (e) are given for each subpopulation. Each subpopulation is at equilibrium (growth = 0), and the overall population is not changing. Source: 2.5+0-(2+.5) = 0; Sink 1: .25+.25-(.5+0)=0; Sink 2: .4+.12-(.52+0)=0; Sink 3: .52+.28-(.80+0)=0.*

(although if subpopulations are assumed to be of equal size, then the number of individuals at equilibrium in a metapopulation will remain unchanged, but the distribution of individuals is constantly shifting); (2) within-subpopulation dynamics are important in determining the overall equilibrium population size, since the numbers of individuals on each patch and their growth rates are implicit in the model. Source and sink subpopulations can be characterized by their "strength," depending on their intrinsic rate of growth and the number of individuals present; (3) the source-sink status of a subpopulation has nothing to do with the size (number of individuals) within the subpopulation. Sinks can support a vast number of individuals and sources can be numerically very small. Nonetheless, sources must have enough individuals with a high enough per capita production to support sink populations.

A variation in Pulliam's source-sink model was introduced by Howe *et al.* (1991) and Davis and Howe (1992), who added a density-independent dispersal term to the source-sink system. In their model, emigrants (e.g., juveniles) leave a subpopulation even when unoccupied territories might be available. Population simulations show that changes in the conditions of local subpopulations (e.g., as a result of logging) can have significant impacts on other subpopulations, even if the affected subpopulations are not demographic sources (see also Donovan *et al.* 1995b).

Empirical Evidence of Source-Sink Dynamics

Many field studies show that reproductive success of neotropical migrant birds varies across a species' range (e.g., Probst and Hayes 1987, Robinson *et al.* 1995), but few examine the interaction of subpopulations from a source-sink viewpoint. To evaluate source-sink dynamics, one must know the BIDE parameters of each subpopulation. To identify source or sink habitat, the fecundity and death rates of adults in the subpopulation must be measured. Annual censuses, therefore, are not capable of establishing source-sink status unless local abundance is strictly correlated with productivity (Brawn and Robinson 1996).

Most empirical studies that document sink populations use nesting and mortality data from the subpopulation and model population persistence over time in the absence of immigration or emigration (e.g., Ricklefs 1970, Stacey and Taper 1992, Pulliam and Danielson 1991, Donovan *et al.* 1995a). Without immigration, sink populations decline over time and will eventually go extinct. Returning to our forest bird examples, many forest bird populations in Illinois woodlots suffer high rates of predation by mammals/birds and parasitism by brown-headed cowbirds and, thus, do not produce enough young to balance adult mortality (Robinson 1992, Brawn and Robinson 1996). Similarly, demographic models of three forest species on forest fragments in Wisconsin and Missouri show that, in the absence of immigration, populations would decline over time to extinction (Temple and Cary 1988, Donovan *et al.* 1995a).

The same demographic characteristics (fecundity and mortality rates) are used to identify source habitats. Sources, by definition, have more births than deaths, but equilibrium is maintained because emigration is greater than immigration. Most empirical studies document "potential" sources, and use nesting data and mortality data from the subpopulation to show that populations would either stay the same or grow over time in the absence of immigration (Ricklefs 1970, Sherry and Holmes 1992, Donovan *et al.* 1995a). If it is shown that reproductive success is very high relative to mortality, and yet population size remains nearly constant over time, then source status can be inferred because emigration is necessary for the population to be stable in size.

Management Implications of Source-Sink Demography

Source-sink demography provides additional implications for population management. Like metapopulation dynamics, independent breeding subpopulations are linked by dispersal and the scale at which sources and sinks interact is unknown (Brawn and Robinson 1996). In the absence of dispersal data, regional-scale management is preferred over local-scale management (Robinson *et al.* 1995). Furthermore, local-scale management almost certainly will have regional-scale impacts. Since dispersal in birds probably does not follow political boundaries, we suggest a physiographic or regional approach until more information is obtained.

Source-sink dynamics might operate at many scales, and demographic units might vary in size over time and space. Sinks depend on sources for persistence. A single source patch may well be able to support several sink patches, which may be larger numerically than the source itself. If that source is extinguished through habitat destruction, a catastrophic event, or a change in management policy, all the sinks that it supports (assuming one source supplies many sinks) inevitably will become extinct as well. Thus, the complete or even partial loss of a source subpopulation directly affects the long-term viability of a spatially subdivided population or population mosaic. Sources that produce a large number of young per unit area should be identified because they contribute a relatively large number of individuals to the larger population. Sources that produce a small number of young per unit area may be of less management concern, but nevertheless they may be important in maintaining regional populations. For example, they may serve as stepping stones that promote dispersal to other patches. They are also potential refuges from local catastrophes that may befall other patches. As in metapopulation systems, managers should realize that actions taken at one location can influence population dynamics in another location (Temple and Cary 1988, Howe *et al.* 1991, Donovan *et al.* 1995b).

Additionally, the habitat associated with source or sink status varies with species. Since managers often must manage for multiple species that may have conflicting habitat needs, increasing source habitat for one species may mean decreasing source habitat for another. Thus, managers need to assess the source-sink status of species of interest and determine how actions taken on a local scale can affect their local population as well as distant subpopulations that may depend on them.

It may be tempting for managers to eliminate a patch of sink habitat since it cannot support demographically viable populations. However, because bird populations are linked, maintenance of sink habitats can be very important. First, the bulk of a population may reside in a sink at any point in time (Pulliam 1988, Van Horne 1983, Howe *et al.* 1991, Donovan *et al.* 1995b). Sources, although demographically viable, may be subject to stochastic extinction risks, and sink habitat can bridge source populations that periodically go extinct. Furthermore, sinks may be the genetic storehouse of unique or rare genes or may facilitate gene flow between sources. Individuals in sinks may contribute significantly to the genetic diversity of the larger population if individuals in the sink can successfully reproduce (Allendorf 1983). However, if sinks act as ecological traps that draw birds away from higher quality source habitats (Gates and Gysel 1978, Pulliam and Danielson 1991) or act as a conduit to spread risk or disease, maintenance of sink habitats may not be desirable. These factors should be weighed in any management action.

SUMMARY OF MANAGEMENT IMPLICATIONS

The practical implications of traditional metapopulation models and source-sink models are similar. In both cases, dispersal between local areas plays a central role in population dynamics. Field studies of neotropical migrant birds provide evidence (albeit indirect) that isolated breeding populations are linked by dispersal. The scale at which populations interact by dispersal is largely unknown; understanding this scale should be a primary research objective in the future. In the absence of dispersal data, regional-scale management (of physiographic regions or greater) is preferred over traditional, local-scale management.

Both metapopulation models and source sink models emphasize the need to set management goals at the regional scale. Because of dispersal from one location to another, setting management goals directed solely at the local scale may have limited success because populations may be regulated by events occurring at scales beyond the local scale. For example, management actions directed at decreasing the abundance of a species (such as cowbirds) at the local scale may be futile if ample cowbird habitat is available beyond the local scale and allows cowbirds to infiltrate the local habitat of concern. Similarly, management actions directed at increasing a priority species at the local scale may be offset by management actions elsewhere that impact the number of birds available to disperse to their patch. Thus, management goals should be targeted at the regional scale, and local managers should realize that their actions may impact dynamics at the local scale and beyond.

We conclude by providing some general management considerations that pertain to both metapopulation and source-sink structure in birds.

Metapopulation considerations:

(1) In a metapopulation context, managers should realize that presence or absence of a priority species in their locations may be part of a larger process that involves subpopulations beyond their managed areas.

(2) Since local extinction and local recolonization rates are key parts of the metapopulation paradigm, managers should promote conditions that decrease local extinction or increase the number of colonists (typically young birds) that can disperse to other areas.

(3) Local extinction is a natural part of metapopulation processes, but decreasing habitat availability for a priority species changes the total number of habitat patches available for the priority species; loss of suitable habitat patches potentially decreases the population size. Therefore, habitat should be maintained for priority species.

Source-sink considerations:

(1) Each priority species should be evaluated separately to determine habitats associated with high and low productivity. Because priority species often have conflicting habitat needs, increasing the amount of source habitat for one species may decrease source habitat for a second species.

(2) Identifying and maintaining source populations for priority species is vital for the persistence of regional populations. Annual variation in quality can change the source-sink status of a particular habitat patch. Density and local population trends are not useful in establishing source-sink status; sinks can be numerically large and show no sign of population decline, and sources can be numerically small and show population decline due to emigration.

(3) Not all sources are equal; a source that produces a high number of young per unit area may be of more value to the larger population than a source that produces a low number of young per unit area; thus assessment of priority species should include evaluation of where each management area is in relation to the center of distribution of high priority species.

(4) Sink habitat may house many individuals. Even if reproductive success is low in a sink, a large number of young can still be produced there depending on the number of adults. However, if birds readily disperse away from high-quality source habitats to low-quality habitats, then sinks may be 'traps' that change the number of individuals in sources and sinks and thus can impact how many young are produced in a given year.

So far we have not considered how subpopulations are configured with respect to one another. An extension of the metapopulation/source-sink concept examines the specific distribution of individuals in space. These so called "spatially explicit" models can define populations as collections of individuals or collections of local subpopulations (Conroy *et al.* 1995, Dunning *et al.* 1995). Analysis of spatially explicit models inevitably involve computer simulations, and they require empirical information about the distribution of individuals in a given region. Although a detailed analysis of spatially explicit models is beyond the scope of this review, managers should be aware that such models provide tools for examining specific populations in appropriately large management units.

We have much to learn about the dynamics of heterogeneous landscapes and their influence on bird populations. Metapopulation and source-sink theories and their extensions provide a theoretical framework for understanding population dynamics at large and realistic scales. The critical need today is for a combination of improved theories and empirical information about specific neotropical migratory bird populations in specific management landscapes.

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