

Demographic Modeling of Migratory Bird Populations: The Importance of Parameter Estimation Using Marked Individuals

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Abstract—We argue that monitoring of population abundance, or even of general demographic features such as nesting success, is not sufficient to understand what factors cause migratory bird population declines or changes in abundance. Instead, a demographic approach is needed, based on data from marked individuals and coupled with population modeling. The dynamics of a population can be modeled most simply using only one parameter, the population growth rate, which is given by the per capita birth rate minus the per capita death rate. Simple model refinements, including habitat- and season-specific vital rates, can add considerable realism and model utility. Empirical estimation of vital parameters requires monitoring the activities and fates of uniquely marked individuals. With such models and parameter estimates one can (1) assess whether particular populations have sufficient production of offspring (e.g., by habitat) to offset annual mortality; (2) investigate ecological influences on population dynamics, including effects of winter versus summer circumstances, population size, and actual or hypothetical environmental changes; and (3) identify where new empirical data are most critical (e.g., dispersal, age effect). We illustrate these points with emphasis on long-term data on color-banded Black-throated Blue Warblers (*Dendroica caerulescens*) and American Redstarts (*Setophaga ruticilla*) in the Hubbard Brook Experimental Forest, NH, and in Jamaica, and we discuss practical aspects of parameter estimation and demographic modeling for migratory species.

Many populations of birds and other organisms are threatened or endangered now, or will likely become threatened soon, as a result of human-induced global change. Aspects of global change include altered ecosystems, climate, land-use patterns, and species distributions (Terborgh 1989; Wilson 1992; Vitousek 1994; Vitousek and others 1996). Improvements in scientists' ability to document species loss and decline have motivated a variety of programs to monitor the health and status of populations, and to investigate the causes of population changes. The Audubon Christmas Bird Count, for example, arose early in the present century out of the need to monitor populations of colonial wading birds threatened by the plume trade. More recently, the Breeding

Bird Survey was initiated to monitor all species of birds detectable along roadside transects throughout North America (Robbins and others 1986). The data so collected are being used to assess the extent and location of diverse population changes throughout the continent (e.g., Robbins and others 1989b; Fleury and Sherry 1995; Sauer and others 1996b), including the declines of many Neotropical-Nearctic migrant songbird species (Hagan and Johnston 1992; Martin and Finch 1995; James and others 1996).

Although much has been deduced or inferred about the nature and scope of population problems using abundance surveys, efforts are under way to identify the specific localities and causes of population declines by studying birth and death processes (demography) and the possible ecological bases for changes in those demographic parameters (Sherry and Holmes 1995, 1996). For example, two North American programs were begun recently to monitor avian demographic parameters at a continental scale: Monitoring Avian Productivity and Survival (MAPS) of the Institute for Bird Populations, and Breeding Biology Research & Monitoring Database (BBIRD) of the Biological Resources Division of the U.S. Geological Survey. Both of these programs are increasing in number of participatory sites, and thus in the size of databases with which to detect regional or temporal patterns. Even with large databases of demographic information, however, pinpointing the ultimate ecological factors causing the population changes or declines observed will be difficult. The problem results from the myriad potential factors that can separately or jointly influence population birth and death rates, including food abundance at different times of year, predators, parasites, direct and indirect effects of climate (Sherry and Holmes 1995), and presence or abundance of various chemicals in the environment. Disentangling the effects of these various factors is difficult without intensive studies designed to address specific ecological factors, and such studies generally require intensive effort focused on one or a few species. Intensive demographic or experimental studies must often be restricted, for practical reasons, to relatively local geographic scales. Neotropical-Nearctic migrants pose a special challenge to understanding present or future population risks because of the diversity of habitats they occupy, their often large geographic ranges, and the different political and geographic regions they typically encounter over an annual cycle.

In this paper we define and describe a demographic approach to the study of migrant bird populations using a series of heuristic mathematical and graphical models. We focus attention on what we have learned already from these models, and what kinds of information and model development are still needed to take full advantage of a demographic

In: Bonney, Rick; Pashley, David N.; Cooper, Robert J.; Niles, Larry, eds. 2000. Strategies for bird conservation: The Partners in Flight planning process; Proceedings of the 3rd Partners in Flight Workshop; 1995 October 1-5; Cape May, NJ. Proceedings RMRS-P-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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approach to population studies of migratory birds. We discuss conservation implications of our findings, as well as the advantages and disadvantages of intensive demographic studies in comparison to broader surveys such as BBIRD and MAPS.

A Simple Model of Birth and Death Rates

The very simplest population models project some initial number of individuals into the future based on one parameter—in this case the Malthusian parameter, or population growth rate. In practice the population growth rate per individual is simply the difference between the per capita birth rate and the per capita death rate. Here we turn the problem around by asking what birth rate is needed to offset the annual mortality rate (the complement of annual survival) so that the population does not decline (see also Sherry and Holmes 1995). Asking this question allows us to consider real demographic variables in a context that is immediately valuable to resource managers. We assume first that inputs (number of juveniles entering population) equal outputs (number of losses due to death or emigration), and define N_J = number of juvenile offspring produced annually per pair of sexually reproducing adults; J = the probability that a juvenile offspring survives its first year; NA = the number of adults lost from the population annually per pair of adults; and A = the probability that an adult survives one year. Based on these assumptions and definitions, $N_J * J = NA = 2 * (1 - A)$. Thus, $N_J = 2 * (1 - A) / J$. If we assume, further, that juveniles survive about half as well as adults (see references in Sherry and Holmes 1995, p. 102), on average (i.e., $J = A / 2$), then $N_J = 2 * (1 - A) / (A / 2) = 4 * (1 - A) / A$. This model tells us what range of juvenile production rates is adequate to offset typical annual mortality rates for a migratory bird population (fig. 1). An annual adult sur-

vival rate or probability of 0.5 (and juvenile survival of 0.25) necessitates production on average of 4 juveniles per adult for replacement; and adult survival of 0.6 necessitates production of 2.7 juveniles. Any birth rates greater than these threshold values, depending on what the actual death rate is, will at least sustain the population, and greater birth rates will allow a population to grow.

To illustrate the use of this model, demographic studies of individually marked Black-throated Blue Warblers in the Hubbard Brook Experimental Forest, NH, indicate that a pair of adults produces, on average, 3.7 to 5.1 fledglings per summer (table 1). This number of fledglings is sufficient in most years to replace the annual losses due to mortality (probably about 0.5; Holmes 1994 and unpublished data), and thus this population breeding in an old growth, non-fragmented northern hardwoods forest is probably in no imminent danger of decline (Holmes and others 1986, 1996; Holmes and Sherry 1988; Holmes 1994). This model can be modified easily with different parameter estimates or with other species. Other demographic models have focused on genetic and stochastic aspects of populations (e.g., Lande 1988; Lebreton and Clobert 1991; Lebreton and others 1992), and habitat fragmentation effects (e.g., Donovan and others 1995b). The most important point to be made from this simple population model is that accurate demographic parameter estimates are vital for accurate empirical modeling.

Generalization in Space: Source-Sink and Site-Specific Models

The foregoing model assumed that demographic rates are constant, both in space and time. This assumption is probably rarely, if ever, true in real populations. For example, many animals can be found living in habitats in which reproduction is not sufficient to maintain the population, but the population persists because of continuous immigration from other habitats. This notion has led to the development of source-sink models (e.g., Pulliam 1988, 1996; Pulliam and Danielson 1991). A source habitat is one in which reproduction exceeds annual survival; a sink is one in which reproduction is not sufficient to maintain the population.

Table 1—Total seasonal reproductive effort by female Black-throated Blue Warblers, Hubbard Brook Experimental Forest, NH, 1986-1989 (Data from Holmes and others 1992).

Parameter:	Year			
	1986	1987	1988	1989
No. females in sample	15	19	14	20
No. eggs laid	95	152	117	113
No. young hatched	83	116	84	92
No. young fledged	69	91	72	74
Proportion of females double-brooding	40.0%	57.9%	71.0%	35.0%
Mean no. fledglings per female $\pm$ 1 s.d.	4.6 $\pm$ 2.2	4.8 $\pm$ 2.0	5.1 $\pm$ 3.0	3.7 $\pm$ 1.7

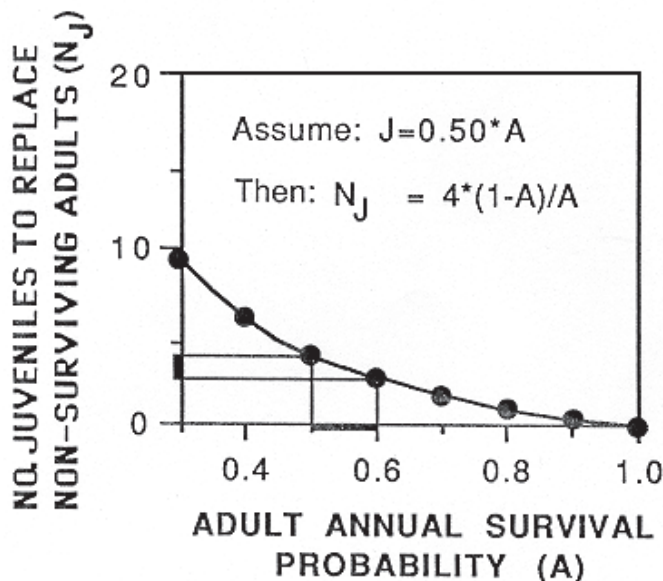


Figure 1—Number of fledglings needed on average to offset adult mortality (see text; modified from Sherry and Holmes 1995).

Animals tend to move asymmetrically from sources to sinks. Pulliam (1988) used his model to make several nonintuitive deductions highly relevant to conservation: (1) Sink populations can support large populations despite the fact that the entire population would disappear without the source, (2) loss of a small proportion of occupied (but source) habitat can cause extinction, (3) numbers of individuals in a habitat can sometimes be a very misleading indicator of habitat suitability or quality, and (4) in general, managers must be aware of habitat suitability (as reflected in demographic success) to manage populations wisely in complex landscapes with multiple habitat types.

Research on Black-throated Blue Warblers illustrates the idea that demographic success depends on habitat (table 2), and that only some habitats act as sources. In this example, habitats with greater density of shrubs, which are preferred by the species as inferred from relatively high bird density, were found in fact to support greater annual productivity of fledglings (3.6 fledglings on average per female or pair) than habitats with fewer shrubs (2.5 fledglings). Reproductive success in the shrubby habitat was probably sufficient to offset annual mortality, making it a source habitat, whereas the low-shrub-density habitat was probably a sink. Thus, even at a very local scale, habitats can differ in the demographic success of occupants, and careful reproductive studies are necessary to understand population dynamics (see below).

Data on Neotropical-Nearctic migrant populations breeding in Midwestern United States woodlots indicate that reproduction there is often insufficient to maintain the populations, leading to the conclusion that some of these woodlots are habitat sinks maintained by distant source populations (Robinson 1992; Robinson and others 1995b; Donovan and others 1995a,b). In the winter nonbreeding season we have found that survival of birds also can differ among habitats (reviewed by Sherry and Holmes 1996). For example, American Redstarts persist significantly less successfully over the winter in Caribbean dry limestone forest in Jamaica than in other habitats studied, and also lose body mass during the dry season in the dry limestone forest (Sherry and Holmes 1996). Redstarts also experience different ecological conditions by sex in winter, in ways that can

influence subsequent survival and even carry over into the reproductive season (Marra and Holberton 1998; Marra and others, in press). Long-distance migratory birds in particular tend to have broad geographic ranges, facilitated by their high mobility, and they often occupy a correspondingly wide range of habitats facilitated by ecological opportunism (Sherry 1990; Sherry and Holmes 1995). We infer that habitats for many, perhaps most, migratory songbirds are heterogeneous, some acting as population sources and others as sinks.

Neotropical-Nearctic migrants tend to compete with members of their own species for mutually preferred habitat, at least during some seasons (Sherry and Holmes 1995, 1996; Rodenhouse and others, in press). When the first individuals arrive in a region to begin a phase of the life cycle, such as breeding or establishment of winter survival territories, individuals tend to settle first in the most preferred habitat, and eventually constrain or force subsequent arrivals to settle in less-preferred habitats. Such constrained habitat selection is often termed despotic or preemptive (Fretwell and Lucas 1970; Pulliam and Danielson 1991). One important consequence of such habitat-settlement dynamics, which are widespread in Neotropical-Nearctic migrants both in summer and winter (Sherry and Holmes 1995, 1996), is that individuals in some habitats experience better demographic success than those in other habitats (e.g., table 2).

Another important consequence of preemptive habitat dynamics is that populations tend to be *regulated*. A regulated population is one that tends to remain within some bounds, i.e., it stays relatively constant because of the tendency for individuals to experience relatively poor demographic success when the population is large versus relatively good success when the population is small. Thus regulation involves demographic success that decreases with population size, or in some cases with population density. Preemptive habitat selection tends to stabilize a population because as the population size increases, and thus as individuals are forced to expand into poorer habitats, the average per-individual demographic success tends to decline (Sherry and Holmes 1995; Rodenhouse and others 1997; fig. 2). Regulation is a special case of limitation, which is the restriction of a population by *any* kind of ecological conditions, regardless of whether the population is regulated.

Rodenhouse and others (1997) generalized this result further to the effect of specific sites or territories on demography (a habitat is a collection of sites with similar demographic success, and often found in similar vegetation structures or types). Rodenhouse and others characterized a mechanism of population regulation which they termed "Site-Dependent Regulation" (SDR), and they parameterized a simulation model with demographic characteristics of Hubbard Brook Black-throated Blue Warblers. This model showed that the SDR mechanism is powerful, potentially widely applicable to animal populations, and operational over a variety of spatial scales—often independently of local population density, but not independently of population size (fig. 3). Rodenhouse and others also conjectured that the suitability of a site is largely extrinsic to characteristics of the organisms rather than intrinsic to the population itself. Intrinsic characteristics include population density and

Table 2—Habitat-specific demography of female Black-throated Blue Warblers in Hubbard Brook Experimental Forest, NH, 1990-1992 (from Holmes and others 1996).

Parameter:	Habitat	
	Low shrub density	High shrub density
Bird density (no./10 ha)	6.6 ± 0.4	15.1 ± 1.1
Percent older males	35% (N = 71)	68% (N = 100)
Percent older females	36% (N = 44)	71% (N = 86)
Percent unmated males	12.7% (N = 63)	1.3% (N = 76)
Percent females double-brooding	5.6%	24.6%
Mean no. fledglings produced per female (± 1 S.E.)	2.5 ± 0.3	3.6 ± 0.3

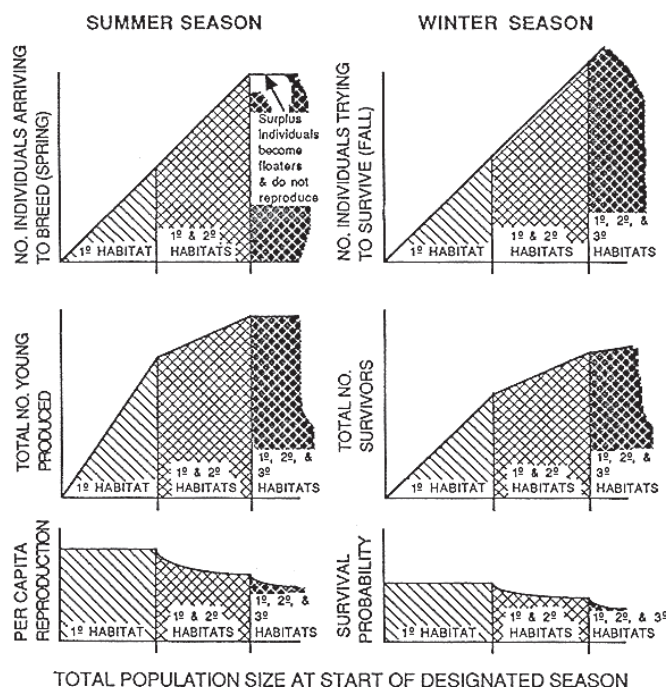


Figure 2—Density-dependent total and per capita productivity in a summer (breeding) season and a winter (nonbreeding) season for organisms occupying multiple-habitat landscapes. As a population increases, it expands from occupying just primary to occupying primary plus secondary habitats, and so forth. The total productivity and survival tends to reach an asymptote as suitable habitats become saturated, and per capita fitness declines, indicative of population regulation (from Sherry and Holmes 1995).

proximity to neighbors. Extrinsic characteristics, which could set limits to local abundance, include food resources, predators, and parasites.

The importance of both preemptive habitat selection and of regulation, from the perspective of population management, is that the number of individuals in the population depends on both the quality of the habitat and its quantity, and so populations can be managed in principle by manipulating either the quality or quantity of available habitat (as well as its configuration and connectivity of patches—see Discussion). However, preemptive use of space in many species tends to set an upper limit to local population density, above which boosting the population is very difficult, in which case it will generally be far easier to maintain populations of such animals by maintaining the amount of habitat than by improving its quality. In this context, the task of wildlife management is ultimately to help guarantee a sufficient amount of high quality habitat for the individuals to maintain their own populations via high reproduction and survival (Sherry and Holmes 1993, 1995; Donovan and others 1995b).

Generalization in Time: Seasonal Migration

Another level of complexity in population models is added when organisms migrate between geographic regions. Each

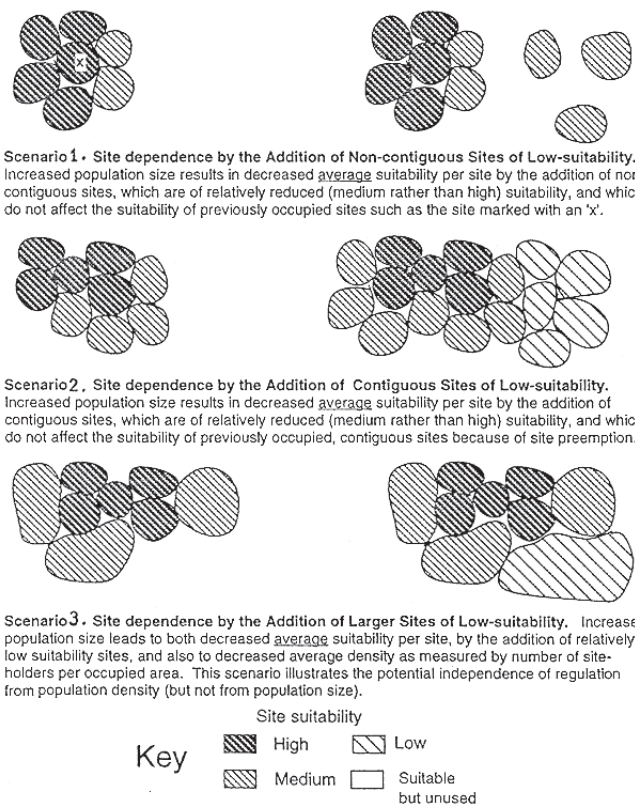


Figure 3—Three scenarios of site-dependent population regulation, in which an increase in population size (number of territories or sites occupied), going from left to right panel, results in decreased average per-capita site suitability as determined by demographic success (from Rodenhouse and others 1997).

region has its own array of habitats (or sources and sinks) in which organisms can reproduce and die, and between which they can disperse. Pulliam (1987) devised a graphical way to study preemptive populations regulated by the interaction of both summer and winter ecological circumstances, and Sherry and Holmes (1995) extended Pulliam's approach to deduce consequences of migratory bird habitat-selection mechanisms. Again, demographic success is assumed to vary by habitat in both seasons, and individuals shuttle between a reproductive season (in North America, for example) that boosts the population through reproduction, and a nonreproductive season (in tropical America, for the bulk of most Neotropical-Nearctic migrant populations) characterized by just mortality (mortality also may occur, of course, during the reproductive season and during migration, as discussed below). The graphical model is constructed from per capita success across a range of habitats within a season, and then by putting effects of multiple seasons together on the same set of axes.

Specifically, the number of individuals in fall is assumed to increase asymptotically with the total population starting the reproductive season in spring (fig. 4A); and, similarly, numbers in spring increase asymptotically as a function of those starting the fall non-breeding period (fig. 4B). Both of these curves are assumed to be asymptotic simply because as the population beginning a season increases, more and

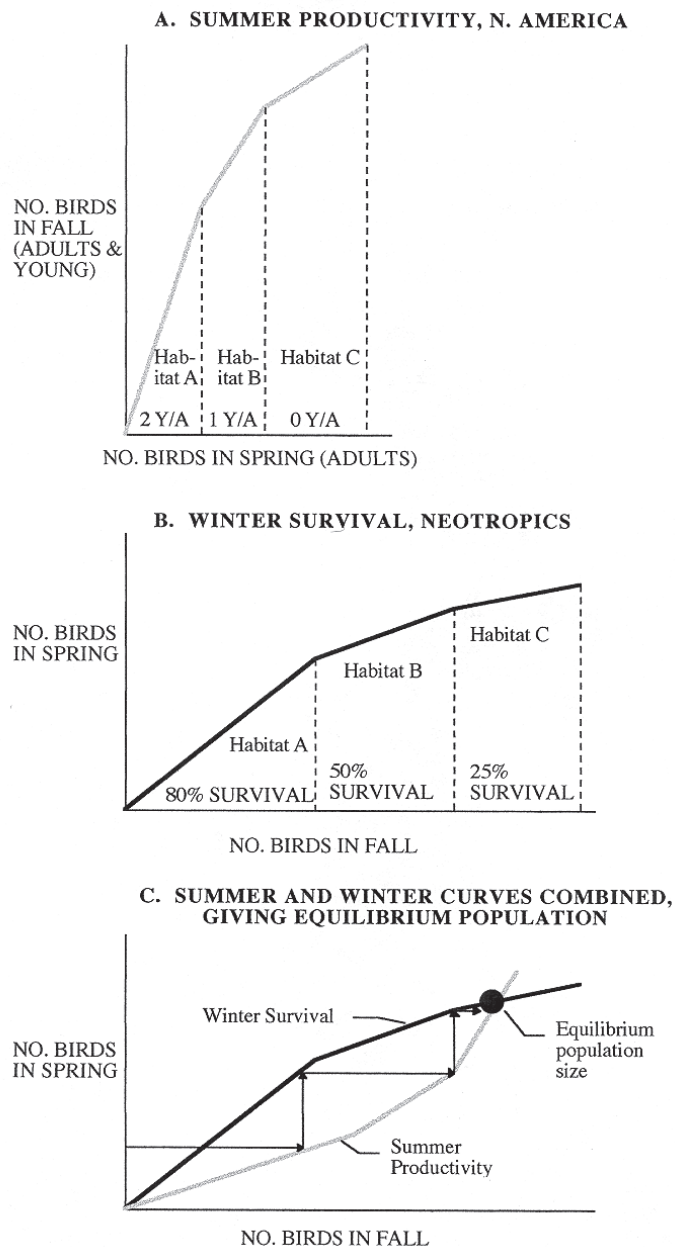


Figure 4—Regulation of migratory population as a result of ecological circumstances in both summer and winter seasons. A. Numbers of individuals in the fall population increases asymptotically as a function of numbers beginning the spring season on breeding grounds, because proportionately more and more individuals are constrained to reproduce in less productive habitats as the population size increases. B. Numbers of individuals in the spring population increases asymptotically as a function of numbers beginning fall (nonbreeding) season on wintering grounds, again because of poorer average demographic success (survival) in larger population. C. A combination of curves from parts A and B onto one set of axes (the axes from part B), and a hypothetical population trajectory, shown by arrows, indicates the tendency of any population to move toward an equilibrium point, indicative of population regulation by a combination of both summer and winter circumstances (see fig. 2 and text; modified from Sherry and Holmes 1995).

more individuals are constrained by despotic behavior to occupy poorer and poorer habitats, resulting in poorer per capita reproductive (or survival) success (as in figs. 2 and 3). One may then combine the curves in figures 4A and 4B on the same set of axes by transposing the axes of figure 4B (fig. 4C). The population size is then determined by starting with an arbitrary initial population size, and rising (or dropping) to the relevant curve in one season, then rotating perpendicularly and moving (increasing in population size) to the other curve in the other season, and so on, alternating between seasons (fig. 4C). The result of this exercise is that any nonzero population eventually will converge on the globally stable equilibrium point at the intersection of the two curves, assuming such an intersection exists. Thus, any population behaving according to this model is regulated, i.e., kept within bounds, and the set point or carrying capacity for the system is determined by *both* the summer and winter demographic circumstances.

We can make several useful deductions from this model. First, because regulation of the population size is determined by both breeding and non-breeding season circumstances, it makes no sense to think of the population as being regulated in either season alone. To the extent that this graphical model captures essential aspects of migratory birds, then by analogy, it makes no sense to say that a population is in general regulated either in summer or in winter. On the other hand, a migratory population is sensitive to limiting conditions in both summer and winter (and other times of year, such as during migration, as considered below), and is thus vulnerable to the worst set of conditions, as a chain is as weak as its weakest link. Specifically, deterioration of habitat either in winter or summer can cause the population to decline to extinction.

Second, the shape of the curves for a particular season depends on both habitat quality and quantity. Habitat quality determines the *slope* of a segment of the curve (e.g., fig. 2) and is identical to the per capita demographic success. Habitat quantity determines the *length* of the segment of the curve having a particular slope. Thus, the number of individuals experiencing a particular per capita demographic success is proportional to the size of a particular habitat, and is given by the length of that segment of the curve (of particular slope) projected perpendicularly onto the axis for the appropriate season. For example, in figure 2, the number of individuals in 1° summer habitat is equal to the length of the abscissa under the habitat labeled 1° habitat. The curves in figure 4 are idealized (smoothed) versions of the curves in figure 2. Thus the overall curve reflects the relative proportions of each potentially occupied habitat type available. Therefore, this heuristic model clarifies how accurate modeling of a real population depends on knowledge about both the habitat-specific demographic rates and the extent of the relevant habitats available to a population.

Third, this model clarifies the fact that population size is determined by alternating (thus additive) effects of different seasons (breeding season, wintering season, migration), each with its own ecological circumstances. The advantage of decomposing annual cycles into components representative of different life-history stages is that this allows one to investigate the separate effects of different seasons, which correspond to different geographic locations in the case of migrants.

Fourth, this graphical approach to seasonal population processes is flexible, and can be modified easily to accommodate a variety of different assumptions and situations. We illustrate this flexibility by incorporating explicitly the effects of mortality during migration, which can be accomplished by decomposing the spring population curve into components attributable to mortality during migrations and during winter, the latter occurring after individuals reach their non-breeding geographic range following the fall migration (i.e., in the Neotropics, in the case of Neotropical-Nearctic migrants). For simplicity we assumed that the mortality rate during migration is independent of the size of the population, and thus is a constant fraction of the population; and that the effects of mortality from fall migration, spring migration, and winter are additive (fig. 5). We also assumed that winter mortality is dependent on population size, which is indicated here by reduced demographic success (winter survival) at larger population sizes occupying increasingly poor habitats.

Discussion and Conclusions

We have presented several heuristic mathematical and graphical models, incorporating increasing levels of complexity, to illustrate how demographic parameters can be used to investigate population regulation and limitation in migratory species and to help identify the particular ecological circumstances that determine their population sizes. In the discussion that follows, we summarize general lessons of the models, indicate the most important weaknesses in our present ability to model migratory bird populations,

emphasize the complementary relationship of modeling to population monitoring, and indicate the challenges of obtaining accurate demographic parameter estimates for migratory birds in the field.

Lessons of the Models

In the context of seasonal migrants, these models lead us to deduce that populations are regulated by circumstances in both summer and winter, because the population depends on both high enough birth rates in summer and low enough death rates, primarily outside of summer, for birth rate to exceed death rate, which is necessary for a population to persist. We deduce that deterioration of demographic circumstances (habitats) in either season can cause a population to decline, and thus migratory animals are vulnerable to the weakest ecological link in their annual cycle. These models illustrate how the availability of high-quality habitat (indicated by sufficiently high birth and survival rates) is required for healthy populations, and the models indicate how preservation of a sufficient amount of high-quality habitat in both summer and winter is the single most important conservation need.

We cannot emphasize enough the value of preserving large quantities of high-quality habitat as a conservation tool. In the case of endangered species populations, intensive management efforts are warranted to accomplish this goal. For example, the endangered Kirtland's Warbler (*Dendroica kirtlandii*) requires large areas of young jack pine (*Pinus banksiana*) stands, which regenerate following fires, and the largest remaining stands occur on the sandy soils of

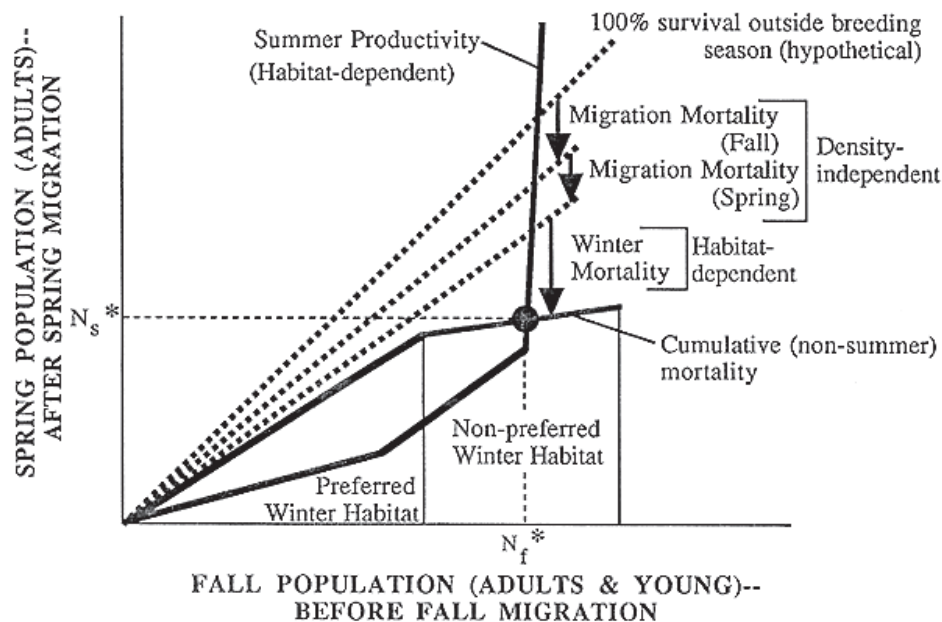


Figure 5—Nonbreeding season mortality components partitioned into density-independent migration components and habitat-dependent (i.e., population size-dependent) winter component, to indicate flexibility of modeling approach introduced in figure 4. N_s^* and N_f^* are equilibrium spring and fall population sizes, respectively, given by the intersection of the summer productivity and nonbreeding season mortality curves.

Michigan (Mayfield 1993; Sherry and Holmes 1995). Fire is used as a management tool to maintain young jack pine stands, although the most dramatic population increases resulted from out-of-control burns, due to their relatively large size (Mayfield 1993). Similarly, game birds are managed intensively by such measures as increasing ground cover, creating openings within forest, creating second-growth habitats preferred by some game species, and creating conditions favorable to regeneration of food plants. With over a hundred species of Neotropical-Nearctic migrant songbird populations, many of which are declining at present (Terborgh 1989; Finch 1991; Peterjohn and others 1995), prudence would dictate that we manage the quantity of native habitats rather than try to maintain habitat quality intensively for each of the declining species' populations. We suggest that the single best means to protect the future of the diverse migratory birds in the western hemisphere is to preserve large, representative landscapes including each of the distinctive habitat types on which these migrants depend, so as to include sufficient quantities of high-quality habitat for migrant species to persist. The abundance of individual species would need to be monitored, of course, to be sure that such habitat preservation and management was successful.

Migration habitats have been largely ignored in the present review, but figure 5 illustrates how migration habitat quality can influence population abundance. Recent work indicates that not all habitats available to birds during critical stages of migration are equally suitable, and thus the relative abundance of different habitats during migration can influence populations (Moore and others 1995).

An important consequence of thinking about populations using demographic parameters is that it helps link population trends to the ecological conditions causing the trends. For example, birth rates are increased when reproductive success is greatest, and reproduction is influenced in turn by factors such as food abundance, availability of safe nesting sites, predator population sizes, and nest parasite abundance. Similarly, during migration and in winter the biology of survival involves habitats that provide sufficient food throughout the winter period, protection from predators, and havens from disease or other hazardous conditions. The value of knowing these ecological factors is that management efforts can sometimes alter them so as to improve habitat quality.

What We Need to Know to Improve Models

All the models that we have discussed in this paper are heuristic. Thus their value is to inform us about general population processes in migratory animals, rather than how to manage a particular species. To accomplish the latter goal, we would need a more detailed model parameterized for a particular species, and to our knowledge, no such year-round population model exists for any Neotropical-Nearctic migrant bird. Moreover, if models are to be developed that allow prediction of how changing ecological conditions (e.g., land-use patterns, global warming) will affect populations, then the relevant ecological variables must be coupled to demographic parameters within the models. What the

foregoing models and discussion can accomplish is to help us focus on the kinds of information needed to structure more useful models.

Because of the importance of habitats, ages, and sexes on demographic rates in general, representative measurements of demographic parameters are needed for each of these strata of data that is important for a particular species (in each of multiple seasons including summer, winter, and spring and fall migrations). Considering habitat, for example, we need some estimate of the relative abundance of the major habitat types used by the population of concern, and we need accurate demographic rates for the population occupying each of those habitat types. This is a daunting task that will require an efficient sampling strategy, and careful attention to statistical treatments of appropriately stratified data. Remote sensing of vegetation and land-use types, coupled with on-the-ground demographic monitoring, almost certainly will be required to accomplish these tasks (e.g., Powell and others 1992). This approach can be applied in principle both locally, e.g., within a national forest or geographic region, and at more global spatial scales.

Survival rate estimates of many long-distance migratory birds are available, but these probably remain highly biased, particularly for females, due to the difficulty of distinguishing those losses of birds that are attributable to disappearance (dispersal) versus actual mortality (Marshall and others, this proceedings; Robinson and Morse, this proceedings). Juvenile survival, i.e., survival from the time a bird hatches until the time it attempts breeding for the first time as a sexually mature adult, is particularly difficult to measure empirically because of the large distances that juveniles often disperse. Thus, few reliable juvenile survival data exist.

Dispersal distances are in general poorly known in birds. Migratory birds are efficient fliers, which permits them to disperse great distances between breeding (or wintering) areas. In populations occupying large geographic areas, knowing how the populations are structured is helpful, e.g., whether subpopulations exist that function largely independently of each other, or whether birds that breed together in summer disperse throughout the winter range (and vice versa—e.g., Chamberlain and others 1997), so that one can effectively treat the population as a single entity. Dispersal distances influence the distances that animals can travel from source habitats to sinks, and thus indicate the potential sources for a particular habitat sink. Dispersal distances also indicate the extent to which habitat configurations (e.g., lack of corridors connecting habitat patches) impede movements, thereby reducing demographic rates by preventing animals from reaching suitable habitats. We recommend that scientists and managers place top priority on developing new methodologies for estimating dispersal rates and distances.

For most species, we lack knowledge about the levels of annual and seasonal variability of demographic parameters. For example, avian nesting (reproductive) success at Hubbard Brook varies annually and seasonally, primarily in relation to mammalian nest predator populations and behavior (Reitsma and others 1990; Sloan and others 1998; Sherry and Holmes 1992; Holmes and others 1992, 1996; TWS and RTH, unpublished data). Similarly, migration-related mortality must

vary annually with changing weather patterns, and anecdotal accounts of mass-mortality of birds during inclement weather are abundant, but we know of no quantitative data on how such mortality affects annual survival rates for any Neotropical-Nearctic migrant bird. Stochastic variation can be incorporated into models of migrant populations (e.g., Rodenhouse and others, in press), but we need better data before such stochasticity improves model accuracy.

To summarize, due to the lack of sufficiently accurate or representative demographic parameter estimates, models remain to be constructed that can project the population size of any Neotropical-Nearctic migrant bird realistically. We also lack the data for most species to incorporate genetic aspects of populations. Sufficient data do exist, however, to construct at least approximate demographic models for a few species, and this should be a major focus of avian population ecologists in the next few years.

Demography and Hypothesis Testing

Intensive demographic data have another important function, besides model development, which is to test hypotheses about the cause(s) of population change. Demographic measurements can indicate, for example, whether a population is locally a source or sink (Pulliam 1996), and can provide the link between population changes and ecological conditions that could be causing the change. Thus demographic data are necessary to follow up on population declines that are of concern to conservationists. In the case of migratory birds, national surveys have identified species whose populations are declining steadily, such as Cerulean Warbler (*Dendroica cerulea*), Wood Thrush (*Hylocichla mustelina*), and Olive-Sided Flycatcher (*Contopus borealis*) (e.g., Peterjohn and others 1995). These species are thus good candidates for more intensive demographic studies. Similarly, population abundance surveys such as the Breeding Bird Survey can identify problem areas ("hot spots for decline" such as the Adirondack Mountains and Blue Ridge Mountains in the eastern U.S.; James and others 1996), where further demographic work would help to focus scientists on the cause of the problem.

Broad-scale, multi-species demographic monitoring programs (e.g., BBIRD, MAPS) already are being conducted within North America and elsewhere. We do not see these programs as a substitute for the kind of intensive demographic studies that we have conducted using Black-throated Blue Warblers and American Redstarts. Instead, different kinds of demographic monitoring are complementary, because they have different strengths and weaknesses. The key advantages of intensive, localized demographic studies is the ability to measure demographic parameters accurately and to link these with specific ecological conditions. For example, BBIRD protocols involve monitoring of nest success, but not necessarily following individually marked animals, which precludes gathering information about annual survival or multiple brooding frequencies, either of which could be key to the maintenance of a particular population. The advantages of programs such as BBIRD and MAPS, compared with intensive single-species monitoring, is the geographic scale and number of species that can be monitored, at least to some extent. Such large-scale

monitoring programs also have the statistical power, due to their often large sample sizes, to detect subtle changes in population parameters, but usually not at just one site (Rosenberg and others, this proceedings).

Practical Aspects of Demographic Modeling

The value of obtaining demographic data for migratory birds should be clear from the foregoing discussions. The data can be used in particular to assess the consequences of alternative land management practices. Such practices can include various kinds of agriculture and aquaculture, forestry, landscape management, and other impacts such as suburban and rural residential land-use. For example, Greater Antillean shade-coffee plantations contribute to excellent winter-long persistence of migrants, probably due to abundant food resources late in the dry season (Wunderle and Latta 1998, in review; M. Johnson, unpublished data). In the breeding season as well, human land-use practices and habitat structure demonstrably alter reproductive success of migratory birds (e.g., Robinson and others 1995b; Holmes and others 1996). However, we still lack the kinds of demographic data needed to understand land-use effects, let alone develop management models, for most migrant bird species under most circumstances.

Despite the potential theoretical and practical benefit of population modeling, the empirical estimation of population parameter values is challenging, and thus requires the commitment of time and resources. To illustrate the challenges, Black-throated Blue Warblers breed on 1-2 ha territories spread out patchily throughout northern hardwoods forest (Holmes 1994); finding enough nests and banding sufficient individuals to obtain reliable demographic information requires working in large woodlands (often hundreds of hectares). The fact that this warbler is double-brooded (table 2), i.e., particular females and their mates may fledge two or more successful broods in a season, necessitates capturing and uniquely marking individual birds to obtain the entire season's reproductive productivity per individual bird (Holmes and others 1992). Studies of wintering migrants' demographic success (Holmes and others 1989; Sherry and Holmes 1996) is also time-intensive, because of effort needed to find, capture, and mark individual animals. Survival of redstarts in winter can vary by habitat (Sherry and Holmes 1996), age of bird (R. T. Holmes; T. W. Sherry; T. E. Martin, in preparation), and probably sex (Marra and others 1993), necessitating adequate sample size for each relevant category of individuals, and several biases make data analyses challenging (Marshall and others, this proceedings). Our experience indicates that capturing and marking sufficient animals to accomplish these tasks is most efficient when working with just one or two species, because methods often need to be tailored to particular species (Hejl and Holmes, this proceedings). General methods to capture, mark, and study birds in the field are well known, and training is widely available (Ralph and others 1993). In summary, we need demographic field and modeling studies of migratory birds, and a variety of tools are available to conduct these studies. The field is thus ready to advance rapidly.

Acknowledgments

This synthesis was completed while TWS was on sabbatical leave from Tulane University at Dartmouth College, and was supported financially by NSF grants to Tulane University

and Dartmouth College. We acknowledge the logistic support of the Northeast Forest Experiment Station, U.S. Forest Service, for our research at Hubbard Brook, and the many research associates and field assistants who have made our field research possible.