

Monitoring, Modeling, and Management: Why Base Avian Management on Vital Rates and How Should it Be Done?¹

David F. DeSante,^{2,3} M. Philip Nott,² and Danielle R. Kaschube²

Abstract

In this paper we argue that effective management of landbirds should be based on assessing and monitoring their vital rates (primary demographic parameters) as well as population trends. This is because environmental stressors and management actions affect vital rates directly and usually without time lags, and because monitoring vital rates provides a) information on the stage of the life cycle where population change is being effected, b) a good measure of the health and viability of populations, and c) a clear index of habitat quality. We suggest that modeling lambda (λ , the rate of change in population size) as a function of vital rates provides useful information on potential responses of populations to management actions, but because of covariation among vital rates and density dependence, the predicted responses may not occur. We suggest that modeling spatial variation in vital rates as a function of spatial variation in lambda provides added insight into the proximate demographic “cause(s)” of population change and permits identification of “deficient” vital rates. We illustrate this at two spatial scales with analyses of BBS and MAPS data on Gray Catbird and MAPS data on five other species. We then suggest that the formulation of effective avian management actions should be based on modeling vital rates as functions of habitat characteristics and, because of substantial amounts of annual variation in vital rates, as functions of weather and climate variables. We illustrate these concepts with threshold relationships between productivity and mean forest/woodland patch size in four forest-inhabiting species; relationships between precipitation and annual productivity indices for two landbird species in Texas; and relationships between reproductive indices in Pacific Northwest landbirds and both the El Niño/Southern Oscillation and the North Atlantic Oscillation. These latter results indicate that annual variation in the productivity of Neotropical-wintering birds may be driven more by events and conditions on their wintering grounds and migration

routes than on their breeding grounds. Finally, we suggest that, because avian management should be based on vital rates as well as population trends, effectiveness monitoring must include the monitoring of the targeted vital rates along with monitoring the appropriate population trends.

Introduction

Goals for the management of Neotropical migratory birds and other landbird species typically include efforts to reverse population declines, to increase the populations of rare species even if they are not declining, and to expand the ranges of localized species. With the creation in 1990 of the Neotropical Migratory Bird Conservation Initiative (“Partners in Flight;” Finch and Stangel 1993) and the firm establishment of the concept of “keeping common birds common,” an additional management goal for landbird species was articulated, to maintain stable or increasing populations. In the process of attempting to achieve these goals, management efforts must sometimes be directed to avian nest predators and brood parasites with the goal of decreasing populations of “problem” species. All of these management efforts thus aim to create or maintain changes in population sizes of some target species. Why then, we might ask, is it appropriate and important to base management on goals related to vital rates or, as they are also known, primary demographic parameters? Why not simply base management on goals related to population size or population trends?

The reason is straightforward: environmental stressors and management actions do not affect population size directly. Rather, they directly affect the vital rates of the population and, through the vital rates, affect the population size and population trend (DeSante and Rosenberg 1998). Moreover, the vital rates are usually affected without substantial time lags, whereas substantial time lags can exist between the time when the vital rate is affected and when that effect is translated into a change in population size or trend (Temple and Wiens 1989).

Other important benefits also accrue when management is based on vital rates. First, assessing and mon-

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²The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956-1346.

³Corresponding author. E-mail: ddesante@birdpop.org

itoring vital rates provides crucial information about the stage(s) of the life cycle at which population change is being controlled (DeSante 1992). This is very important when dealing with Neotropical migratory birds because birth rates and death rates can be driven by processes acting at different times of the year and at locations many thousands of kilometers away from each other. Second, without information on vital rates, the “health” or viability of populations cannot be ascertained (Noon and Sauer 1992). Third, information on vital rates provides a clear index of habitat quality. Because of confounding effects of population sources and sinks, information on presence/absence or even relative abundance or population size can provide misleading indicators of habitat quality (Van Horne 1983, Pulliam 1988). And finally, spatially explicit information on vital rates can provide insights into source-sink dynamics.

Key Vital Rates upon Which Avian Management Can be Based

For landbird species that reach breeding maturity when one year old, we follow DeSante (1995) and identify six key vital rates or demographic events that drive population change. We suggest that these six vital rates should be assessed and monitored, and should be the vital rates upon which management should be based. They include: (1) productivity—the number of young per adult that reach independence from their parents; (2) survival of young—the probability of surviving from independence to the beginning of the first breeding season; (3) recruitment of young—the probability of a surviving young recruiting into the breeding population (this includes the spatial component of natal dispersal); (4) annual survival of adults—the probability of an adult bird surviving from the beginning of one breeding season to the beginning of the next; (5) site fidelity—the probability of a surviving adult returning to the same site and again recruiting into the breeding population; and (6) immigration—the probability of a surviving adult from a different site immigrating to a new site and becoming a breeder there. Note that mortality is the complement of survival and emigration is the complement of site fidelity.

We further identify six components of productivity, using the definition given above, that could be included in demographic modeling: number of breeding attempts per season (which may depend upon whether or not the attempts were successful); clutch size; survival of eggs to hatching; hatching success; survival of nestlings to fledging; and survival of fledglings to independence from their parents. For effective demographic modeling, a complete measure of productivity must include the product of all six components. Nest

monitoring efforts typically include only four of these components and neglect both the number of breeding attempts per season (unless all adults are individually color marked and all breeding attempts are monitored) and the survival of fledglings to independence (unless all nestlings are individually color marked and followed after fledging). Monitoring programs that use constant-effort mist netting (e.g., MAPS — Monitoring Avian Productivity and Survivorship) provide a complete index of productivity, because they capture dispersing young that have reached independence from their parents (DeSante et al. 1995). Such programs do not, however, provide any information on the six components of productivity discussed above.

Survival also has a number of temporal components. For annual survival of adults, these include survival during the breeding season, during the post-breeding dispersal period, during fall migration, during the overwintering period, and during spring migration. Survival of young, as defined here, lacks the breeding season component, but includes the remaining four temporal components. It should also be noted that most measures of survival generated by mark-recapture protocols, whether in standardized mist-netting programs such as MAPS (DeSante et al. 1995) or in intensive single species resighting studies with study areas of limited size, are actually measures of apparent survival, in which true survival, the complement of mortality, is confounded with site fidelity, the complement of emigration (Cilimburg et al. 2002).

Strategies for Basing Management on Vital Rates

Given, then, that we should base management on vital rates, exactly how can this be accomplished? For example, if our goal is to reverse the population decline of a particular target species, how do we use information on vital rates to accomplish this? Clearly, if we are trying to reverse a population decline, our ultimate goal is to increase λ , the rate of change in population size, from a negative to a positive value. The proximate goal must be to affect one or more vital rates in such a way that λ will increase. Recall that the key vital rates include productivity, survival of young, recruitment of young, survival of adults, site fidelity of adults, and immigration of adults. Theoretically, we could design our management efforts to increase any of these vital rates, because enhancing any of them should lead to an increase in λ . The question then becomes, toward which vital rate should we direct our efforts?

This question was addressed by Nichols and Hines (2002) who discussed three important strategies regarding vital rates and λ that should be con-

sidered when attempting to formulate effective avian management plans. The first is to enhance the vital rate for which the smallest change would produce the largest increase in lambda. The approach here is to estimate gamma, the relative contribution to lambda of a given proportional change in the vital rate. This approach in many ways is analogous to elasticity analyses (Caswell 2001, Heppel et al. 2000), although there are important distinctions (Nichols et al., this volume). The second strategy is to enhance the vital rate that is most sensitive to management action. This strategy examines the proportion change in vital rates associated with an incremental change in some continuous management action. The third strategy is to enhance the vital rate that is most cost-effective to manipulate. The idea here is to evaluate the cost of implementing a particular incremental change in a given management action.

The Nichols and Hines (2002) approach makes the important point that management decisions should be based not only on elasticity and related issues, but also on the existence and knowledge of management actions that influence the various vital rates and upon the true cost of these management actions. Nevertheless, as they point out, their model is still oversimplified and ignores potential real-world complications such as covariance among vital rates and density dependence. Thus, situations may exist in which a vital rate can be enhanced, but its enhancement will not enhance lambda because another vital rate will be decreased. For example, if survival of young through their first winter is density dependent, management actions that increase productivity might not increase lambda because survival of those young will be decreased proportionally. Moreover, situations may exist in which a vital rate simply cannot be increased any further because it already is at its maximum, has not historically declined, and thus is not “deficient.”

Identifying “Deficient” Vital Rates— the Proximate Demographic Cause of Population Declines

This kind of situation suggests that an additional strategy for effective avian management, at least for reversing population declines, is to attempt to identify the deficient vital rate, that is, the vital rate that has “caused” the population decline (the decrease in lambda), and to formulate management actions to increase that deficient vital rate. This approach is not really new; identification of the deficient vital rate has long been the goal of key-factor analysis and, to some extent, provides a guiding principle behind retrospective elasticity analysis. Such efforts attempt to model temporal variation in vital rates as a function of temporal variation in population trends or lambda. The idea here

is to focus on *historical* patterns of temporal covariation between vital rates and lambda. Nichols et al. (this volume) demonstrate this approach by focusing on actual temporal covariation between a vital rate (or appropriate component of a vital rate, in this case, the proportion of females that produced two broods) and lambda.

It is important to note, however, that efforts to apply this approach to declining populations will typically require long-term historical monitoring data on both lambda and the various vital rates, data that often do not exist. Moreover, a vital rate does not necessarily need to be currently declining to be deficient and, thus, to be causing a population to decline. All that is necessary is for the deficient vital rate (e.g., productivity) to be too low to balance “normal” mortality of adults or young. In this respect, even an increasing vital rate can be deficient, at least for some period of time.

Modeling Spatial Variation in Vital Rates as a Function of Spatial Variation in Population Trends

An alternative approach for identifying the deficient vital rate is to model spatial variation in vital rates as a function of spatial variation in population trends. The idea is to focus on *current* patterns of spatial covariation between vital rates and lambda, essentially substituting space for time. DeSante et al. (2001) used such an approach at two spatial scales to identify the deficient vital rate(s) for various target species. For the larger spatial scale, mean annual productivity indices and time-constant annual adult survival estimates during 1992-1998 for Gray Catbird (*Dumetella carolinensis*) were modeled from MAPS data from stations located in two areas comprised of physiographic strata where 1992-1998 population trends from the Breeding Bird Survey (BBS) were significantly ($P < 0.01$) positive or negative (*table 1a*). Annual estimates of adult survival probabilities were best modeled as area-dependent, with the survival probability in the area with positive BBS population trends (0.555; 0.033 SE) being substantially greater than in the area with negative BBS population trends (0.443; 0.048 SE). In contrast, mean annual productivity indices (proportion of young in the catch) were best modeled as independent of area (0.295). The difference between the two areas in population changes modeled from MAPS productivity indices and adult survival estimates (0.147) agreed well with the difference between the two areas in BBS population trends (0.157), although the modeled population trends for both areas were substantially more negative than BBS trends, presumably because MAPS productivity indices tend to be biased low. The fact that

Table 1— Vital rates (SE when available) from selected models (those with lowest AIC), modeled population changes (from those vital rates), and observed population trends (SE) for: (A) Gray Catbird from continent-wide MAPS (vital rates) and BBS (population trends) data; and (B) five selected target species from MAPS (vital rates and population trends) data from stations on military installations in the western (Kansas and Missouri) and eastern (Indiana and Kentucky) Midwest. (From DeSante et al. 2001)

		Productivity ^a	Survival rate ^b	Modeled population change ^c	Population trend ^c
A. Continent-wide scale, 1992-1998					
Gray Catbird	Positive strata ^d	0.295	0.555 (0.033)	-0.271	0.102 (0.026)***
	Negative strata ^e	0.295	0.443 (0.048)	-0.418	-0.055 (0.013)***
B. Regional (Midwest) scale, 1994-1999					
Carolina Chickadee	Eastern	0.494 (0.161)	0.476 (0.127)	-0.176	0.553 (0.196)**
	Western	0.250	0.476 (0.127)	-0.405	-0.114 (0.052)*
Gray Catbird	Western	0.270	0.634 (0.051)	-0.190	0.055 (0.063)
	Eastern	0.160 (0.026)	0.283 (0.041)	-0.677	-0.123 (0.063)***
Ovenbird	Eastern	0.344 (0.134)	0.489 (0.073)	-0.319	0.004 (0.039)
	Western	0.170	0.489 (0.073)	-0.436	-0.125 (0.039)**
Yellow-breasted Chat	Western	0.164	0.610 (0.067)	-0.300	0.027 (0.084)
	Eastern	0.034 (0.017)	0.329 (0.062)	-0.662	-0.133 (0.025)***
Field Sparrow	Western	0.179	0.453 (0.063)	-0.473	0.033 (0.051)
	Eastern	0.119 (0.031)	0.453 (0.063)	-0.501	-0.100 (0.022)**

^aProportion of young in the catch, modeled using logistic regression

^bModeled using Cormack-Jolly-Seber mark-recapture analysis (Pollock et al. 1990) with a between- and within-year transient model (Pradel et al. 1997, Nott and DeSante 2002)

^cAnnual proportional change

^dIncludes all BBS physiographic strata for which the 1992-1998 population trend for Gray Catbird was significantly (P < 0.01) positive.

^eIncludes all BBS physiographic strata for which the 1992-1998 population trend for Gray Catbird was significantly (P < 0.01) negative.

* 0.05 < P < 0.10; ** 0.01 < P < 0.05; *** P < 0.01.

some degree of spatial variation in survival and productivity should be expected does not negate these results. The important result here is the existence of spatial covariation between survival rates and population trends and the lack of such covariation between productivity and population trends. These results suggest that, at the spatial scale of the entire species' range, annual adult survival in physiographic strata where the species was declining was deficient, and this low survival was the proximate demographic cause of the population decline. These results also suggest that successful management strategies to reverse population declines in Gray Catbirds at the continental scale must address this deficient survival.

At the smaller scale, productivity and adult survival were modeled during 1994-1999 for Carolina Chickadee (*Poecile carolinensis*), Gray Catbird, Ovenbird (*Seiurus aurocapillus*), Yellow-breasted Chat (*Icteria virens*), and Field Sparrow (*Spizella pusilla*) from MAPS stations on military installations in the western (Kansas and Missouri) and eastern (Indiana and Kentucky) Midwest (table 1b). Species were selected because their trend in adult captures from the six years of MAPS data was significantly (P < 0.05) positive or negative on the installations in either the eastern or western Midwest, and of the opposite sign (but not necessarily significant) on the installations in the other area. We were able to identify the deficient vital rate(s)

causing the population declines for all five species. Deficient productivity was identified as a proximate demographic cause of population decline for all five species, while deficient adult survival was identified as an additional cause for Gray Catbird (again) and Yellow-breasted Chat. Moreover, the regression of modeled population changes on trends in adult captures for the five species in the two areas showed a significant positive relationship (*fig.1*) which suggests that, although the y-intercept of the regression was negative again suggesting that MAPS productivity indices are biased low, the biases are relatively constant between areas and among species.

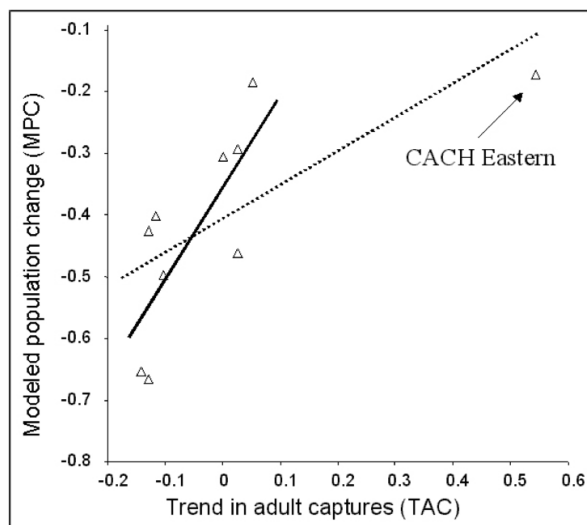


Figure 1— Regression of modeled population changes on trend in adult captures for five selected target species (Carolina Chickadee, Gray Catbird, Ovenbird, Yellow-breasted Chat, Field Sparrow) from 1994-1999 MAPS data from 18 stations on military installations in each of two areas (the western Midwest – Kansas and Missouri; and the eastern Midwest – Indiana and Kentucky). The dashed line is the regression for all ten points: slope = 0.580, y-intercept = -0.418, $r = 0.688$, $P = 0.028$; the solid line is the regression for nine points (eliminating Carolina Chickadee eastern Midwest: slope = 1.507, y-intercept = -0.361, $r = 0.747$, $P = 0.021$). (From DeSante et al. 2001).

Modeling Vital Rates as a Function of Habitat Characteristics

These results, at both spatial scales, suggest that this approach is useful for identifying the deficient vital rates that need to be addressed to reverse population declines. Once these proximate demographic causes of population change have been identified, how should we proceed to formulate management strategies to reverse the declines? We suggest that one effective approach is by modeling the appropriate vital rates as functions of the major environmental factors that affect them—

habitat and weather.

Habitat affects vital rates primarily by affecting access to food resources and exposure to predation (including nest predation) pressure. Weather also affects vital rates by affecting access to food resources and exposure to predation pressure, but additionally affects the birds and their behavior (and thus their vital rates) directly through exposure to heat, cold, wind, and precipitation. It is possible that the strongest effects of habitat and weather occur through their interactions with each other. Thus, the most illuminating models of the effects of habitat and weather on vital rates might involve multivariate analyses of both factors.

Substantial progress has been achieved on efforts to model vital rates derived from MAPS data as functions of habitat and weather (Nott 2000, Nott 2002, Nott et al. 2002, 2003). One of the most promising approaches is to model MAPS productivity indices as a function of remote-sensed, landscape-level habitat characteristics (such as Shannon’s diversity index of cover types, total amount of forest cover, mean forest patch size, mean forest interpatch distance, total amount of forest edge, total amount of water, etc.) within 2- to 5-km radius areas surrounding the MAPS station (Nott 2000, Nott et al. 2003).

Utilization of an area of this size is appropriate for modeling productivity indices, because the young birds captured by the MAPS protocol do not all originate from within the boundaries of the MAPS station, but include substantial numbers of dispersing young from the surrounding landscape (DeSante et al. 1995). Hard data on the dispersal characteristics of juvenile landbirds are notoriously few, but now include an excellent radio-transmitter study of juvenile Wood Thrushes (*Hylocichla mustelina*) (Anders et al. 1997) that suggests that virtually all of the young Wood Thrushes captured at a MAPS station before August 8 likely originate from nests within a 4-km radius area surrounding the station. It seems likely that many other forest-inhabiting passerine species might have similar juvenile dispersal distances. (Note that juvenile dispersal should not be confused with natal dispersal, which is defined as the vector between where a bird was hatched and where it first attempts to breed, and which could involve much larger distances.)

Nott (2000) provides an example of this approach utilizing data from six MAPS stations on Big Oak National Wildlife Refuge (formerly Jefferson Proving Ground) for four forest-inhabiting species (Acadian Flycatcher [*Empidonax vireescens*], Wood Thrush, Ovenbird, and Kentucky Warbler [*Oporornis formosus*]). We plot numbers of adult and young birds captured at each of the six stations as a function of mean forest/woodland patch size at the stations in the four

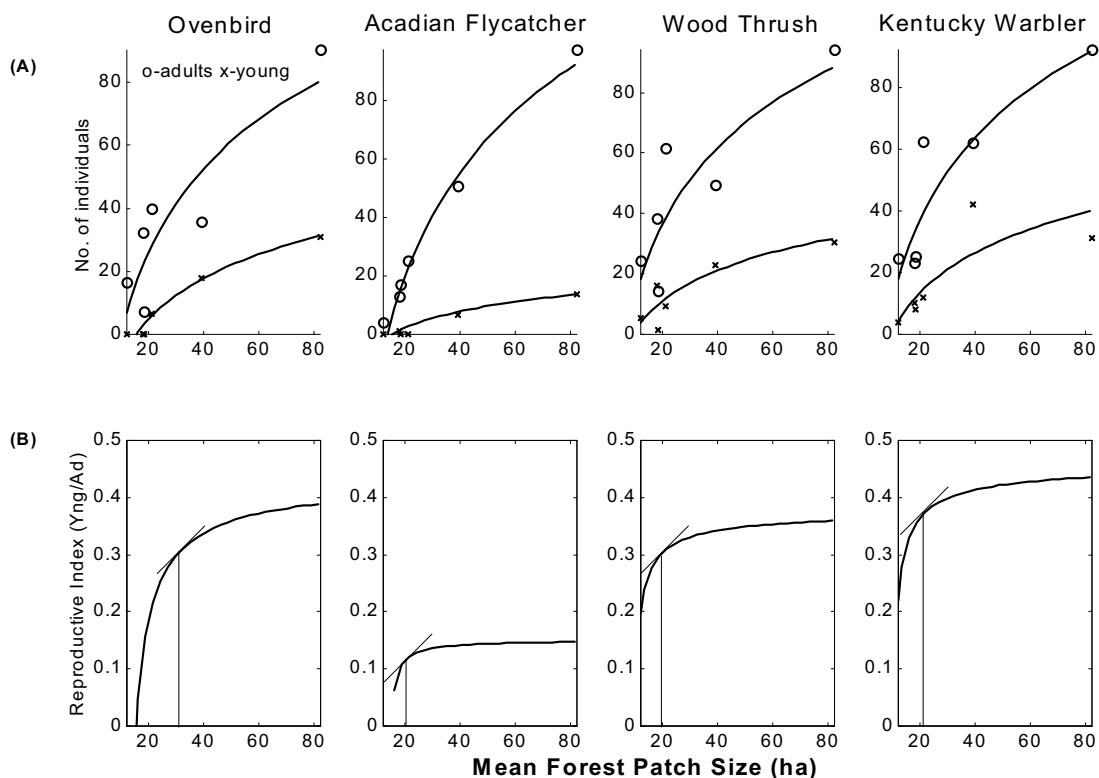


Figure 2— (A) Numbers of individual adult (o) and young (x) birds of four forest interior species captured per 3600 net-hours at six MAPS stations operated during 1994-1999 on Jefferson Proving Ground, Indiana, as a function of mean forest patch size in the 4-kilometer radius area surrounding each station. (B) Relationship between reproductive index (young/adult) and mean forest patch size at Jefferson Proving Ground for these four species (obtained from the linear-log regressions shown in A).

upper panels (*fig.2A*). For each of the four species, mean forest/woodland patch size was the landscape metric having the highest correlation coefficient with (i.e., that explained the greatest variation in) numbers of captures of adults. This metric also provided the most powerful determinant for the number of captures of young for each species except Kentucky Warbler (for which the most powerful determinant was a negative relationship with the percentage of cropland/grassland). All of these relationships with mean forest/woodland patch size, however, for both numbers of adults and young, were significant. The log-linear regression models fitted to each of these relations are shown in *Figure 2A* for both adults and young.

Finally, for each species, we calculated the reproductive index (the ratio of young to adults) at regular intervals along the fitted curves shown in *Figure 2A*, and thereby found threshold relationships between reproductive index and mean forest/woodland patch size, as shown in *Figure 2B*. Thus, below a threshold patch size for each of the four species (determined by the patch size at which a 45° line is tangent to the curve), productivity decreased dramatically, while above that threshold patch size, productivity increased slowly.

The existence of such patch-size thresholds can provide powerful and straightforward management guidelines that can be formulated into specific avian management actions or that can be included in other more generalized land management plans.

We suggest that similar types of relationships can also be developed between adult survival estimates and habitat characteristics. For permanent resident species, such relationships could be developed using habitat characteristics on the breeding grounds. However, since it is likely that annual survival rates for migratory species are affected by events and conditions that occur on the wintering grounds or migration routes (Sillert and Holmes 2002), we will need to model survival as a function of habitat characteristics on the wintering grounds. The newly created Monitoreo de Sobrevivencia Interval (MoSI—monitoring overwintering survival, see DeSante et al., this volume) Program aims to do exactly that for Neotropical migratory landbirds, that is, to provide habitat-, age-, and sex-specific estimates of overwintering survival rates and indices of physical condition (body mass/wing chord ratio). The ultimate goal of MoSI is to model these estimates of overwintering survival and indices of physical con-

dition as a function of habitat characteristics, and to use these models to formulate management strategies for reversing population declines in species for which deficient survival is driving the decline.

Modeling Vital Rates as a Function of Weather

One of the important results of the MAPS Program is the demonstration of a high level of annual variability in vital rates, especially productivity, presumably caused by annual variability in weather (DeSante and O'Grady 2000). Because of the pronounced effects of weather on vital rates, especially over the short term, vital rates must be modeled as a function of weather, as well as habitat, variables. We have recently begun such modeling of productivity and weather variables. Nott (2002), for example, found that annual productivity indices over the eight years 1994-2001 correlated positively with precipitation in Texas for six species of Texas landbirds, including Bewick's Wren (*Thryomanes bewickii*) and Painted Bunting (*Passerina ciris*) (fig.3). Interestingly, for five of the six species, the three months immediately prior to breeding (December-February) was the season for which the strongest correlation was found between precipitation and productivity (March-May for the sixth species). It is not clear from these results whether the increased winter rainfall enhanced productivity the following summer by increasing the winter food supply and enhancing the birds' physical condition at the start of the breeding season, or by increasing the spring and summer food supply available for nesting birds, or both.

Strong evidence that both of these effects can occur has

been obtained from MAPS data from 36 stations on national forests in the Pacific Northwest (Nott et al. 2002). There we showed that MAPS reproductive indices (young/adult) for 29 of 33 species tended to correlate positively with both the El Niño/Southern Oscillation (as measured by the El Niño/Southern Oscillation Precipitation Index, ESPI) and the North Atlantic Oscillation (as measured by the North Atlantic Oscillation Index, NAOI). Reproductive indices of Neotropical-wintering species, however, both individually and as a group, correlated much more strongly with ESPI than with NAOI (fig.4A), while reproductive indices of temperate-wintering species, again both individually and as a group, correlated much more strongly with NAOI than with ESPI (fig.4B). For both groups of species and for both global climate cycles, the season for which the strongest correlations were found between reproductive indices and climate cycle was March-May. This was, again, just prior to their breeding season.

Only weak correlations exist between the March-May ESPI and weather variables in the Pacific Northwest. Very strong correlations exist, however, between the March-May ESPI and both precipitation (positive) and temperature (negative) in western Mexico, both in highlands along the crest of the Sierra Madre Occidental (fig.4C) and in lowlands along the Pacific coast. These weather variables result in substantial increases in surface soil moisture during El Niño years (years with a positive ESPI) throughout western Mexico (the wintering grounds for most Neotropical-wintering species breeding in the Pacific Northwest). There is also a tendency during March-May for following winds out of the Southeast during El Niño years, as opposed to headwinds out of the Northwest during La Niña years (years with a negative ESPI), throughout

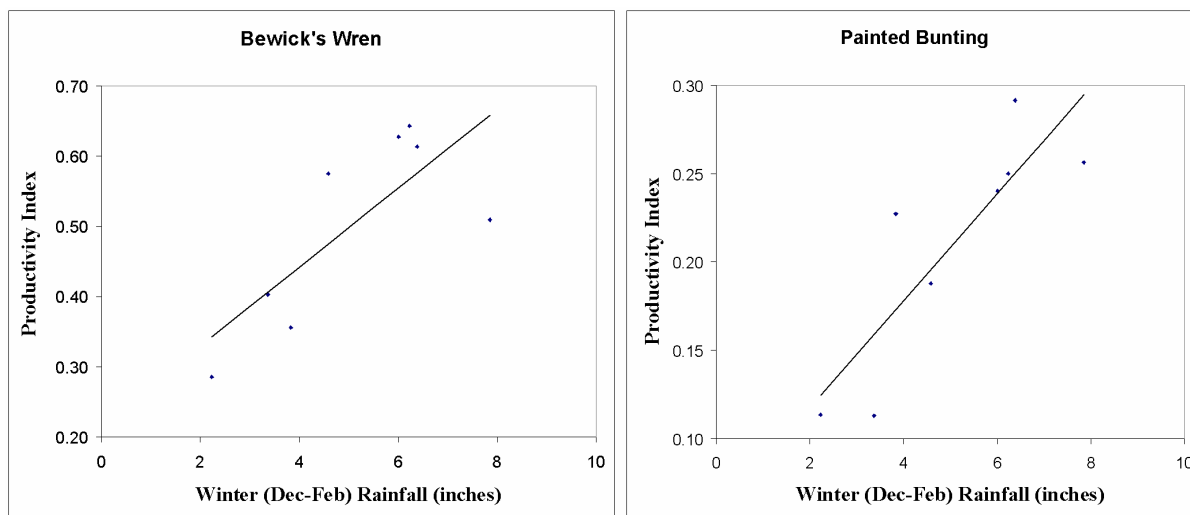


Figure 3— Regressions of annual productivity indices (proportion of young in the catch, 1994-2001) on winter (Dec-Feb) precipitation for Bewick's Wren ($R^2 = 0.59$, $P < 0.05$) and Painted Bunting ($R^2 = 0.73$, $P < 0.01$) from MAPS data from 18 stations in southeastern Texas. (From Nott 2002)

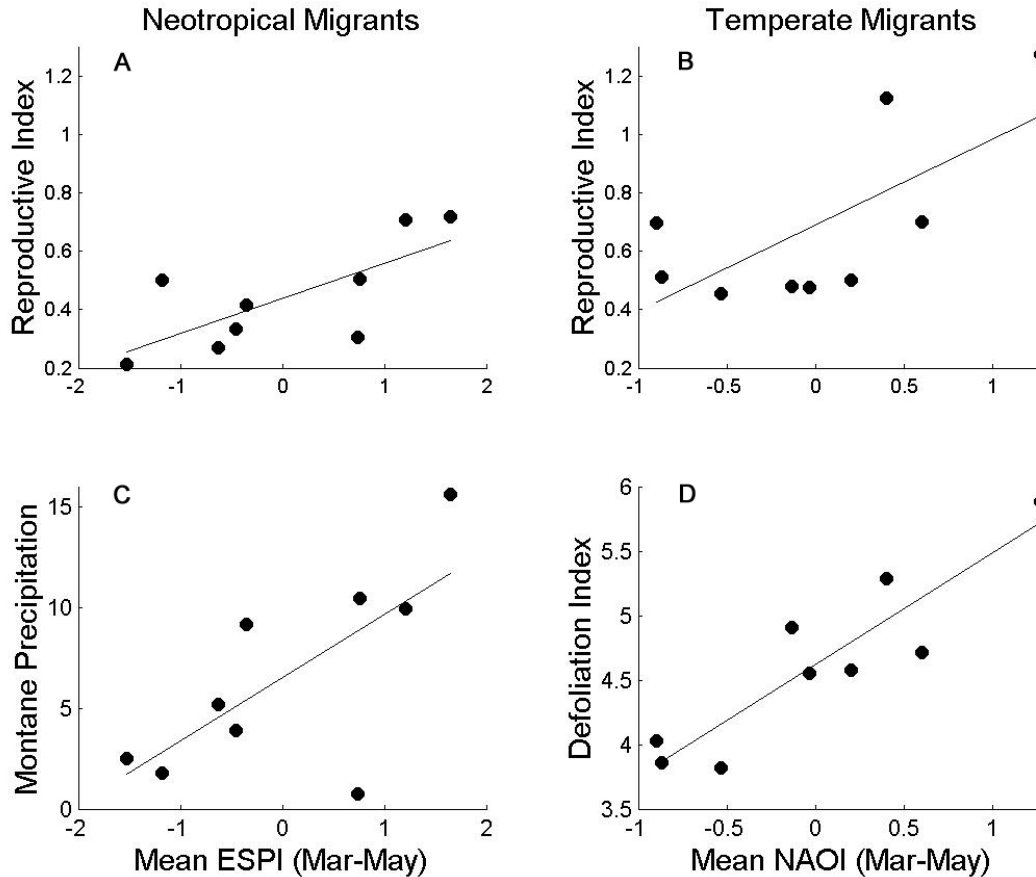


Figure 4— Regressions of annual reproductive index (young/adult, 1992-2001) from 36 MAPS stations on six national forests in Oregon and Washington for (A) all Neotropical-wintering species pooled on mean Mar-May El Niño/Southern Oscillation Precipitation Index (ESPI) ($R^2 = 0.528$, $P = 0.027$); and (B) all temperate-wintering species pooled on mean Mar-May North Atlantic Oscillation Index (NAOI) ($R^2 = 0.472$, $P = 0.041$). Regressions of (C) Feb-Apr precipitation at montane weather stations along the crest of the Sierra Madre Occidental in western Mexico on mean Mar-May ESPI ($R^2 = 0.488$, $P = 0.036$); and (D) annual defoliation index by irruptive insects on the six national forests in the Pacific Northwest on mean Mar-May NAOI ($R^2 = 0.817$, $P = 0.001$). (From Nott et al. 2002)

northwestern Mexico and California. We suggest that these weather effects during El Niño years, operating prior to the breeding season and on the wintering grounds or spring migration routes of these Neotropical-wintering species, likely result in their being in better physical condition at the start of the breeding season and/or arriving earlier on their Pacific Northwest breeding grounds, and thus result in their raising more young during El Niño than La Niña years. It has been assumed for some time that annual survival of Neotropical-wintering landbirds might well be driven by events or conditions on their wintering grounds and/or migration routes, but this is one of the first demonstrations that the breeding productivity of these species can also be driven by conditions on their wintering grounds and/or migration routes. Such dynamics likely exist between productivity and winter habitat conditions, as well as winter weather, and must be considered when developing overall management strategies for migratory birds.

In contrast to the situation with ESPI, strong correlations exist between the March-May NAOI and weather in the Pacific Northwest, where less precipitation and warmer temperatures occur during March-May in years with a positive, rather than negative, NAOI. One result of these weather variables is a greatly increased amount of forest defoliation by the western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir tussock moth (*Orygia pseudotsugata*) during positive NAOI years. Indeed, the index of forest defoliation from these species was highly correlated with the March-May NAOI and with reproductive indices of temperate-wintering birds (fig. 4D). We suggest that these weather effects during years of positive NAOI result in more food available for permanent resident Pacific Northwest species just prior to their breeding season, and for temperate-wintering migrants as soon as they arrive on their Pacific Northwest breeding grounds (which typically occurs earlier than for Neotropical wintering migrants), and thus result in their producing more young than in negative NAOI years.

Again, the weather effects on productivity appear to occur just prior to the breeding season but, in this case, occur on the breeding grounds rather than on the wintering grounds or migration route.

Evaluating the Effectiveness of Management Actions

We have argued that, because management actions affect bird populations (including population size and trends) by affecting vital rates, appropriate management strategies, including generalized guidelines that can be applied whenever land management is done and management actions designed specifically for avian conservation, should be based on targeted vital rates as well as population trends. As a result, a well-designed effectiveness-monitoring program must also monitor the targeted vital rates as well as the resulting population trends. Put simply, if your management goal is to reverse the population decline of a given species by increasing its productivity, you must monitor its productivity as well as population size or trend. Monitoring only its population size or trend is not sufficient, because other vital rates besides productivity could have changed, and your management actions might have contributed nothing to the observed change in population size or trend.

In summary, we suggest that an effective conservation program for landbirds should be built around integrated monitoring, research, and management goals. The monitoring goals should aim to provide annual indices and estimates of critical vital rates as well as population sizes and trends. The research goals should aim to identify temporal and spatial patterns in those indices and estimates, and relationships among those temporal and spatial patterns and ecological characteristics of the target species, landscape-level and station-specific habitat characteristics, and spatially explicit weather variables. The management goals should aim to identify the proximate demographic cause(s) of population change, to formulate management guidelines and actions to reverse population declines and maintain stable or increasing populations, and to evaluate the effectiveness of the management actions implemented. These, in fact, are the objectives upon which the establishment of the MAPS program was based (DeSante, this volume).

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