

Patterns of Productivity and Survivorship from the MAPS Program

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ABSTRACT—The Monitoring Avian Productivity and Survivorship (MAPS) Program is a cooperative, continentwide program of constant-effort mist netting and banding designed to provide: (1) annual indices and long-term trends in adult population size and post-fledging productivity for target landbird species from capture rates of young and adult birds; and (2) annual estimates and long-term trends in adult population size, adult survivorship, and recruitment into the adult population from modified Cormack-Jolly-Seber analyses of mark-recapture data. Here I investigate patterns in productivity indices and survival-rate estimates obtained at two spatial scales (a large sub-continental region-eastern North America; and a single physiographic province-the Sierra Nevada) from data from the four-year (1992-1995) pilot MAPS program. Productivity indices for species groups from eastern North America varied as a function of nest location (in descending order: cavity, ground, open-cup tree, and open-cup shrub nesters) and migration strategy (in descending order: permanent residents, temperate-wintering migrants, and Neotropical-wintering migrants). These patterns agree with those found by direct nest-monitoring and those predicted from theoretical considerations, and were robust with respect to both time and space (being similar in each of the four years and similar whether data were included from only the 61 stations operated during each of the four years or from all stations operated each year, which increased from 81 stations in 1992 to 203 stations in 1995). The same general patterns of productivity as a function of nest location and migratory strategy also were found at the smaller spatial scale of the Sierra Nevada physiographic province. In addition, survival-rate estimates for Neotropical migrants tended to be higher than those for temperate migrants and permanent residents at both spatial scales, again in agreement with current life-history theory. These results suggest that patterns of productivity and survivorship generated by MAPS data reflect real population processes at large and varying geographic scales.

INTRODUCTION

Recent analyses of data from the North American Breeding Bird Survey (BBS) and other large-scale, long-term monitoring programs suggest that many species of landbirds, including a number of Nearctic-Neotropical migratory species, have undergone pronounced population declines over the past three decades, and that these declines may be accelerating, at least in the eastern and central parts of the continent (Robbins et al. 1989, Terborgh 1989, Peterjohn et al. 1995, 1996). Indeed, these analyses have provided much of the impetus for the establishment and growth of the Neotropical Migratory Bird Conservation Initiative, "Partners in Flight."

Despite the general success of large-scale monitoring programs, such as the BBS, in describing geographic and temporal patterns of avian population trends and identifying potentially declining species, such monitoring programs provide little information as to factors responsible for population declines and even less direction as to appropriate management actions to reverse declines (Peterjohn et al. 1995, DeSante and Rosenberg 1998). This is because they provide no information about the stages of the life cycle that control the population changes (Temple and Wiens 1989), and thus fail to distinguish problems caused by productivity factors that operate on the breeding grounds from those caused by mortality factors that may operate primarily on the wintering grounds and migration routes (DeSante 1992, Sherry and Holmes 1995). Clearly, critical

data on primary demographic parameters (productivity and survivorship) are needed to determine the factors responsible for the population declines in Neotropical migratory birds and to identify conservation and management actions to reverse the declines (DeSante 1995).

The Monitoring Avian Productivity and Survivorship (MAPS) Program was established by The Institute for Bird Populations to provide these critical data (DeSante et al. 1993, 1995). MAPS uses standardized, constant-effort mist netting and banding during the breeding season at a continentwide network of stations, and was patterned after the British Constant Effort Sites Scheme (Baillie et al. 1986, Peach et al. 1996, Peach and Baillie in press) that has been in operation since 1981.

The specific objectives of MAPS are to provide, for a suite of target landbird species (including both Neotropical- and temperate-wintering species) and at multiple spatial scales: (1) annual indices of adult population size and post-fledging productivity from data on the numbers and proportions of young and adult birds captured; and (2) annual estimates of adult survivorship, adult population size, and recruitment into the adult population from mark-recapture data on the adult birds captured. These demographic indices and estimates are to be used to describe temporal and spatial patterns in the demographic parameters of the target species, and to model interrelationships between demographic parameters and environmental variables including weather and landscape-level habitat characteristics (particularly those resulting from management actions).

The major long-term goal of MAPS is to use the demographic information generated on target species to aid in: (1) identifying proximate demographic causes of population changes in these species; (2) identifying conservation strategies and management actions to reverse population declines; and (3) evaluating the effectiveness of the conservation strategies and management actions implemented. Indeed, monitoring primary demographic parameters may be the most judicious way to determine whether management actions are working effectively (DeSante and Rosenberg 1998). This is because management actions affect primary demographic parameters directly, and these effects can potentially be observed over a short time period (Temple and Wiens 1989). Because of buffering effects of floater individuals and density-dependent responses of populations, substantial time lags may occur between changes in primary parameters and resulting changes in population size or density (DeSante and George 1999). Moreover, because of the vagility of most bird species, local variations in population size may be masked by recruitment from a wider area (George et al. 1992) or accentuated by lack of recruitment from a larger area (DeSante 1990).

Additional long-term goals of MAPS are to: (1) forge cooperative partnerships among federal and state agencies, non-governmental organizations, researchers, and independent banders to use public lands for long-term avian monitoring efforts; and (2) provide a means for direct public participation in landbird conservation efforts by encouraging banders to collect rigorous mark-recapture data. These two objectives are addressed elsewhere in this volume (see [Burton and DeSante](#) this volume). Whether MAPS can achieve its major long-term goal depends upon whether temporal and spatial patterns in demographic parameters of target species generated from MAPS data reflect actual population processes at the scale of interest. Criticism of MAPS has primarily been twofold: (1) because of constraints on locations where long-term mist netting is practical and permissible, stations are not sited by a probability-based sampling strategy—thus, inferences regarding productivity indices and survival-rate estimates cannot be made beyond the sample of stations; and (2) with regard to productivity indices, the populations sampled at MAPS stations are not clearly identified due to limitations on our knowledge of bird dispersal patterns—thus, the adequacy of productivity indices based on the proportion of young captured is not well known.

This paper documents the growth of the MAPS Program from 1989 through 1996, and describes, at two geographic scales (a large semi-continental scale--North America east of the Rocky Mountains and north of Mexico; and a smaller regional scale--the Sierra Nevada physiographic province as defined by the BBS), patterns of productivity with respect to nest location and migration strategy and patterns of survivorship with respect to migration strategy. I show that patterns generated by these data are temporally and spatially consistent both with patterns expected from ecological theory and with patterns generated from other empirical data.

METHODS

MAPS PROGRAM

The overall design of the MAPS Program and the methods used to collect data were outlined in DeSante et al. (1993, 1995) and were described in detail in DeSante and Burton (1999). Briefly, MAPS stations were established in 20 ha study areas where long-term mist netting was practical and permissible. Typically, about 10 permanent net sites were distributed opportunistically (at locations where birds can be captured efficiently) but rather uniformly throughout the central 8 ha of the study area, and one 12 m, 30 mm-mesh mist net was erected at each net site.

Stations were operated in a standardized manner, typically for six hours per day, beginning at sunrise, for one day per 10-day period, and for 8-12 consecutive 10-day periods, depending on latitude, from May 1 to August 28 (MAPS protocol was changed in 1999 to minimize captures of fall migrant individuals: the last two 10-day periods, August 9-28, were eliminated). To minimize captures of spring migrant individuals and subsequent net avoidance by permanent resident and early arriving summer resident individuals, starting dates for MAPS stations were delayed until the time when most spring migrant individuals of the target species have moved through the study area; thus, starting dates were later at more northern latitudes.

Each bird captured was marked with a uniquely numbered aluminum leg band and all birds captured (including recaptures) were identified to species, age, and (if possible) sex. The times of opening and closing each net and beginning each net run were recorded each day so that effort could be calculated for each 10-day period and standardized between years. A separate record was kept of all species seen or heard within the boundaries of each station on each day of operation, to determine, for each year, whether the species was a summer resident and probable breeder at the station.

DATA ANALYSIS

Methods of data analysis were described in detail in DeSante et al. (1993) and DeSante and Burton (1999). Briefly, after computer entry and proofing, capture data were run through verification programs that: (1) checked the validity and ranges of all coded data; (2) compared the species, age, and sex determinations against the aging and sexing criteria used, and flagged discrepancies or suspicious data; (3) screened data for unusual band numbers or band sizes; and (4) screened all records of each band number for inconsistent species, age, or sex determinations. All inconsistencies, discrepancies, or suspicious data were examined in detail and corrected if necessary.

Following procedures pioneered by the British Trust for Ornithology in its CS Scheme (Baillie et al. 1986, Peach et al. 1996), I used the proportion of young (hatching-year) birds in the catch of young (young/adults) during the entire MAPS season (May 1 to August 28) each year as the annual index of post-fledging productivity. For productivity (or survivorship) analyses in any given year, I included only stations that were operated for at least five periods, at least three of which occurred during the earlier portion of the season (when adults predominate in the catch) and at

least two of which occurred during the later portion of the season (when young birds predominate in the catch).

I investigated patterns of productivity from eastern North America over the four years, 1992-1995, by two approaches: (A) the constant-stations approach, in which I pooled data from the 61 stations east of the Rocky Mountains that lay within the breeding range of the species and that fulfilled the above criteria during every one of the four years; and (B) the variable-stations approach, in which I pooled data from all stations east of the Rocky Mountains that lay within the breeding range of the species and that fulfilled the above criteria in any of the four years. The numbers of stations from which data were pooled using this latter approach were 81 in 1992, 109 in 1993, 169 in 1994, and 203 in 1995.

I included species in productivity analyses from eastern North America for which at least 50 aged individuals were captured during each of the four years at all stations that were pooled each year. I classified each species by nest location (cavity nester, open-cup tree nester, open-cup shrub nester, ground nester) using information from Hrlach et al. (1988), and by migration strategy (permanent resident, temperate-wintering migrant, Neotropical-wintering migrant) using information from AOU (1983) and DeSante and Pyle (1986). I excluded Brown-headed Cowbird (*Molothrus ater*) from these analyses because it is a brood parasite, and an appropriate nest location classification could not be assigned. I also excluded Cedar Waxwing (*Bombycilla cedrorum*) and American Oldfinch (*Carduelis tristis*), because adults of these species begin nesting in eastern North America substantially later than other species and, unlike all species that were included, pre-breeding adults often were captured in sizeable flocks during the MAPS data-collection period. For this reason, productivity indices for these two species likely would be biased low compared to all other species.

For the Sierra Nevada analyses, I used the variable stations approach; that is, I pooled data for each species each year from all stations within the Sierra Nevada physiographic province that lay within the breeding range of the species. I included species in this analysis for which a total of at least 100 aged individuals were captured during the four years at all stations that were pooled each year. I classified species by nest location and migration strategy as described above. I excluded House Wren (*Troglodytes aedon*), Orange-crowned (*Vermivora celata*) and Nashville (*V. ruficapilla*) warblers, and Lesser Oldfinch (*Carduelis psaltria*) from these analyses because large numbers of individuals of these species, especially juveniles, undergo up-mountain drift after the breeding season. Therefore, productivity indices for these species likely would be biased high compared to all other species.

I calculated maximum-likelihood estimates of annual adult survival rates from four years (1992-1995) of mark-recapture data pooled from stations that were operated in every one of the four years. I used a modified time-constant Cormack-Jolly-Seber analysis (Pollock et al. 1990) that incorporated the transient model described by Pradel et al. (1999) into the computer program SURGE (White 1983). The transient model allows estimation of the time-constant proportion of resident birds among newly captured individuals, as well as estimation of the time-constant recapture probability. In order for the estimate of proportion of residents to be biologically meaningful, I pooled only data from stations where the species was known to be a regular breeder, that is, where evidence existed that the species was a summer resident in at least three of the four years, 1992-1995. In order to make meaningful comparisons of productivity and survivorship, I recalculated productivity indices for both eastern North America and the Sierra Nevada using the same stations from which survival rates were estimated, that is, stations that were operated during each of the four years 1992-1995 and at which the species was a regular breeder. For analyses from eastern North America, I included species for which a total of at least 200 aged individuals were captured over the four years; for the Sierra Nevada analyses, I included species for which a

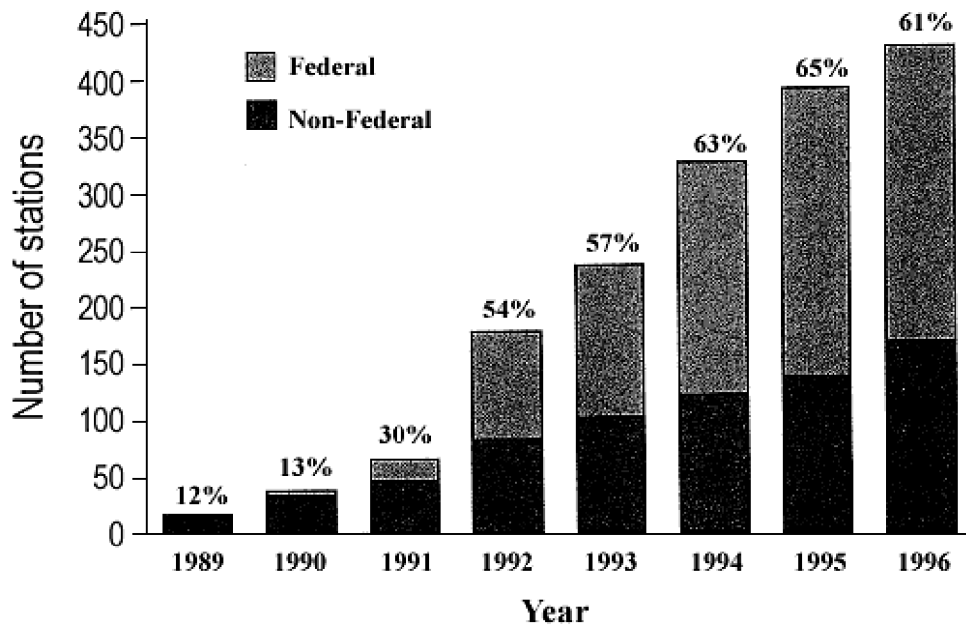
total of at least 60 aged individuals were captured over the four years. I inferred the statistical significance of differences in productivity indices or survival-rate estimates between groups of species having different migration strategies from non-overlapping 95 confidence intervals.

RESULTS

MAPS

MAPS grew from 1 stations in 1989 to 38 in 1990, 66 in 1991, 18 in 1992, 236 in 1993, 326 in 1994, 391 in 1995, and 13 stations in 1996 (Figure 1). The substantial growth of the program in and subsequent to 1992 and the increase in the percentage of stations supported at least partially by federal funds was caused by the increased involvement of various federal agencies in PIF, particularly the USDA Forest Service; the USDI Fish and Wildlife Service, National Park Service, and National Biological Service (now Biological Resources Division of USFWS); and the US DoD Departments of the Navy and Army. The distribution of the 13 stations operated in 1996 is shown in Figure 2.

Figure 1. Number of MAPS stations supported by federal and non-federal funds from 1989 to 1996. The percentage of stations supported by federal funds is indicated above each bar.



Productivity and Migration Status

Annual (1992-1995) productivity indices (proportion of young in the catch) and nest-location and migratory-status classifications are presented for each of the 3 species included in this analysis in [Appendix 1](#). In terms of nest type, they included 8 cavity nesters, 12 open-cup tree nesters (hereafter, tree nesters), 1 open-cup shrub nesters (hereafter, shrub nesters), and 9 ground nesters. In terms of migratory status they included permanent residents, 13 temperate-wintering migrants (hereafter, temperate migrants), and 23 Neotropical-wintering migrants (hereafter, Neotropical migrants). For 36 of these 3 species, a total of 50 or more aged individuals were captured each year at the 61 stations that were operated during each of the four years.

Figure 2. Map of North America showing the distribution of the 413 MAPS stations operated in 1996 (as determined by the 10-minute block in which the station was located).



Figure 3. Productivity indices for 1992 through 1995 for species in eastern North America (all stations pooled east of the Rocky Mountains lying within the breeding range of the species) as a function of nest location from: (A) constant-stations and (B) variable-stations analyses (see text).

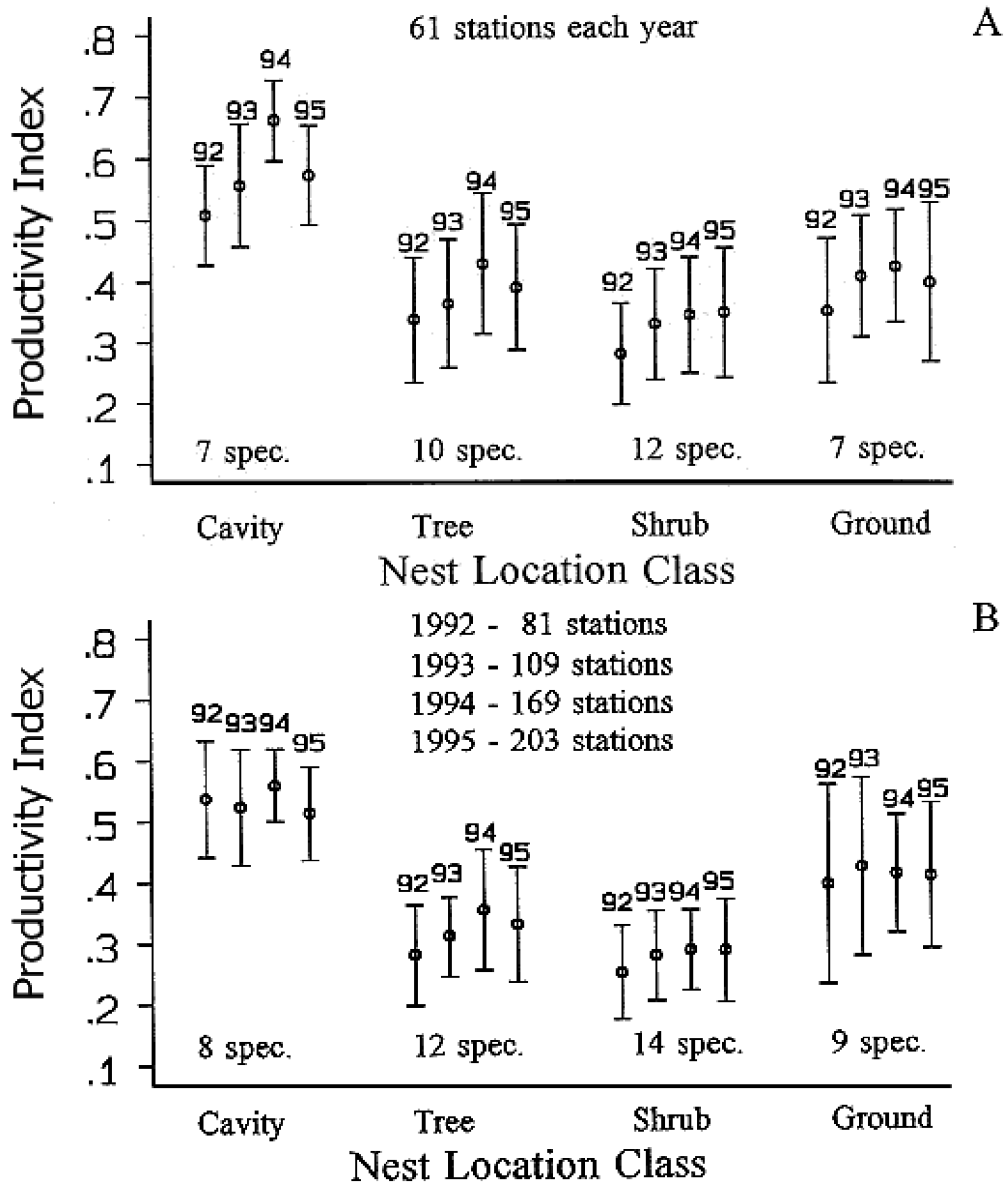
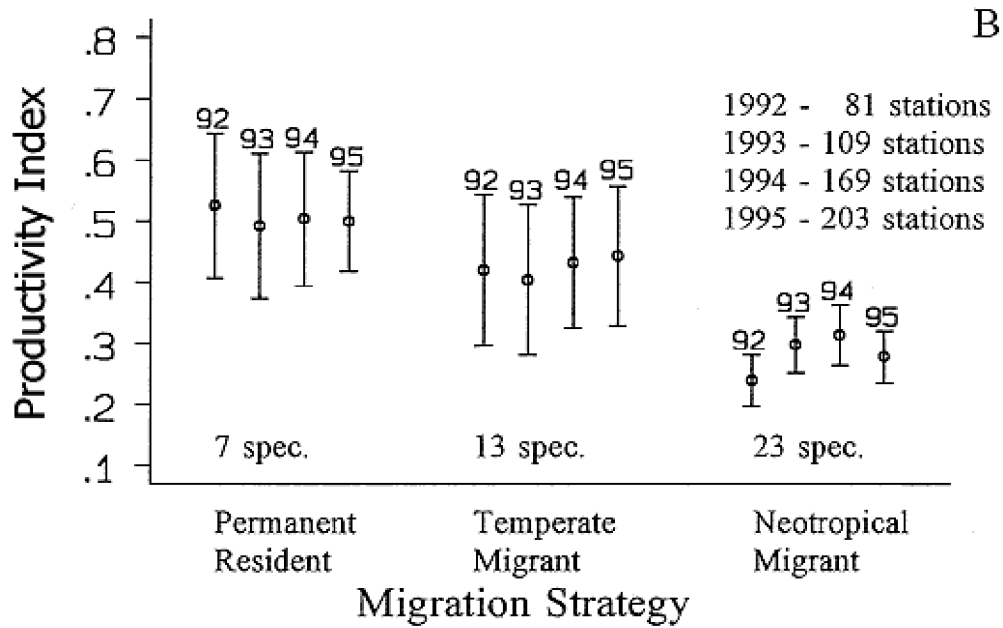
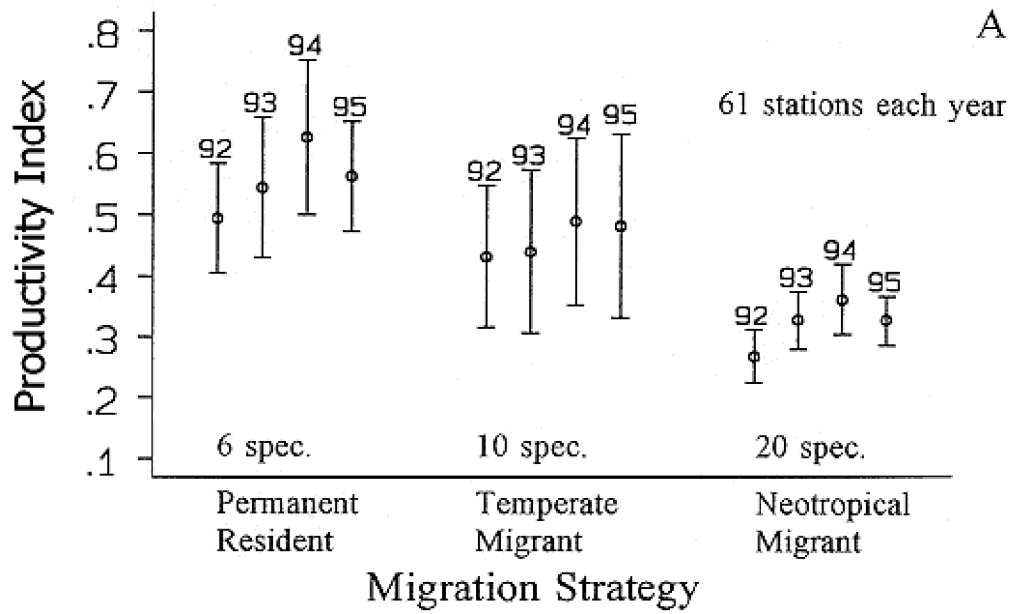
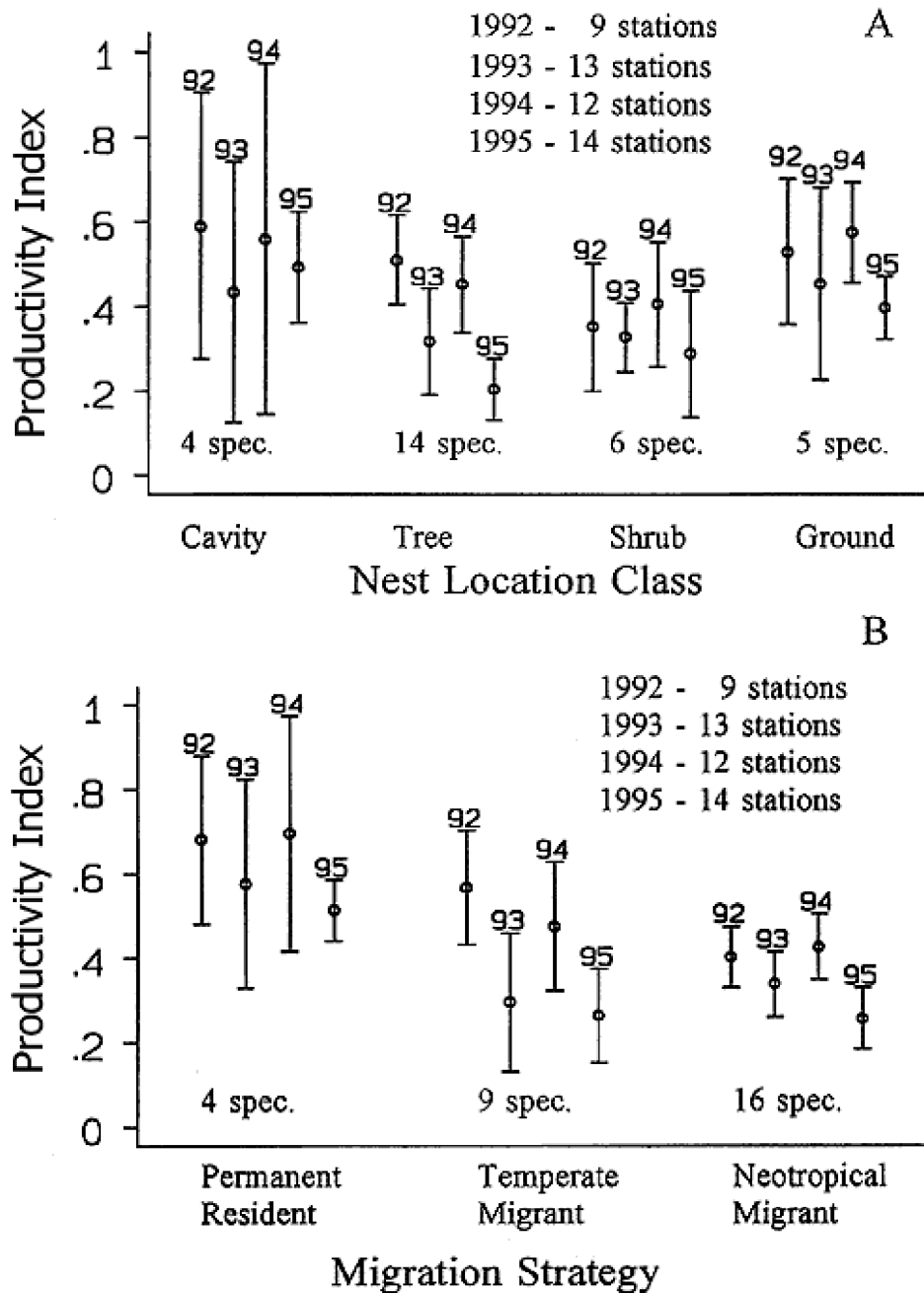


Figure 4. Productivity indices for 1992 through 1995 for species in eastern North America (all stations pooled east of the Rocky Mountains lying within the breeding range of the species) as a function of migration strategy from: (A) constant-stations and (B) variable-stations analyses (see text).



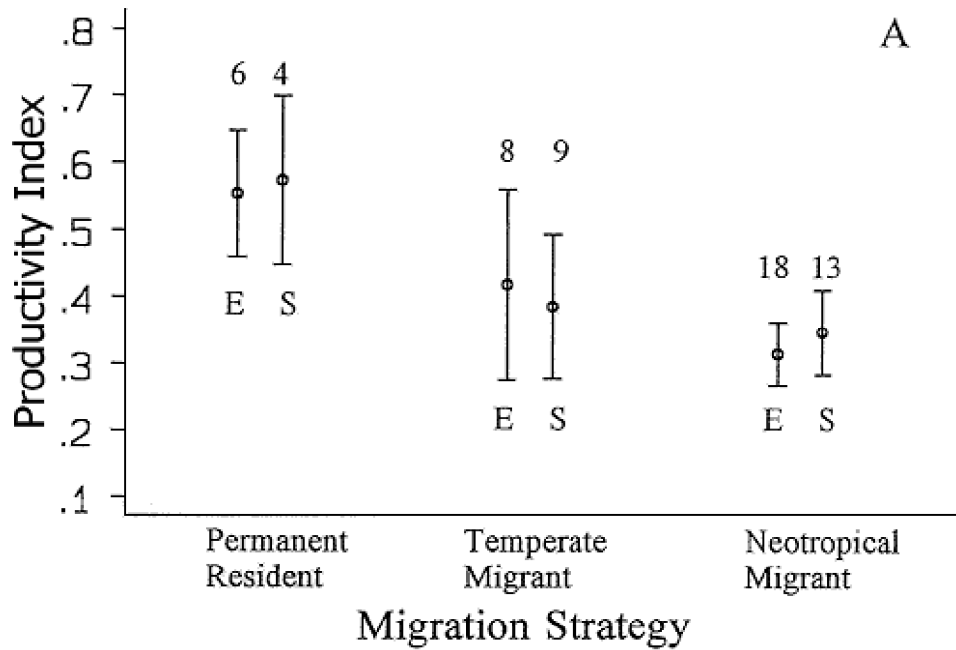
Patterns of Productivity from the Sierra Nevada

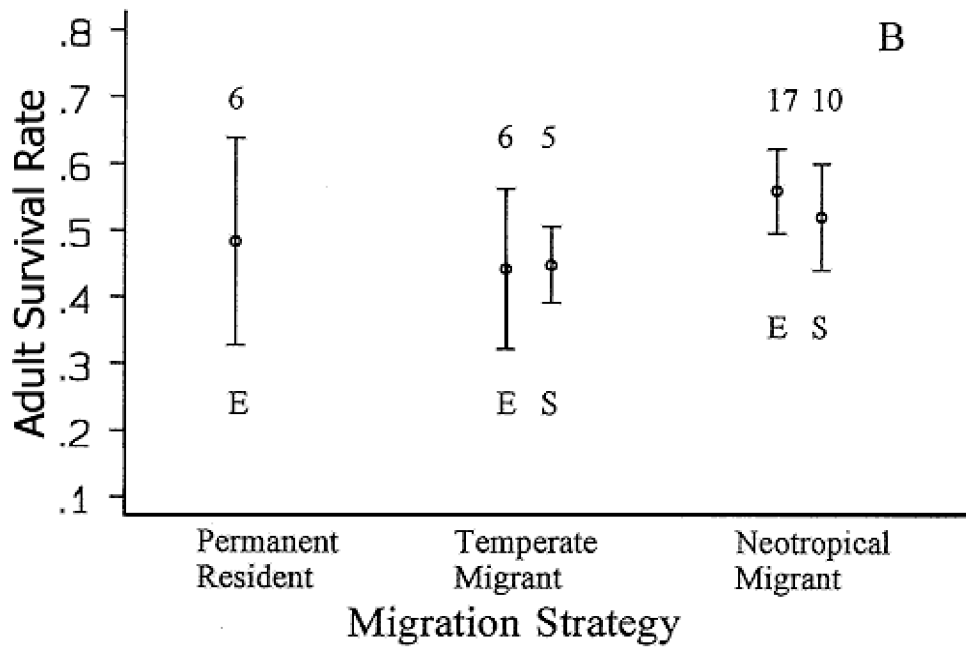
Figure 5. Productivity indices for 1992 through 1995 for species in the Sierra Nevada (all stations pooled in the Sierra Nevada physiographic province lying within the breeding range of the species) using the variable stations approach as a function of (A) nest location and (B) migration strategy.



The Relationship between Patterns of Productivity and Survivorship

Figure 6. (A) mean (1992-1995) productivity indices and (B) time-constant (1992-1995) annual adult survival-rate estimates from MAPS for species in eastern North America (E) from data pooled from 61 stations operated during each of the four years and the Sierra Nevada physiographic province (S) from data pooled from 13 stations operated during each of the four years as a function of migration strategy.





[Appendix 1](#)

[Appendix 2](#)

[Appendix 3](#)
