TEN-YEAR (1992-2001) REPORT OF THE MONITORING AVIAN PRODUCTIVITY AND SURVIVORSHIP (MAPS) PROGRAM IN DENALI NATIONAL PARK

FINAL REPORT

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EXECUTIVE SUMMARY

Since 1989, The Institute for Bird Populations has been coordinating the Monitoring Avian Productivity and Survivorship (MAPS) Program, a cooperative effort among public and private agencies and individual bird banders in North America, to operate a continent-wide network of constant-effort mist-netting and banding stations. The purpose of the MAPS program is to provide annual indices of adult population size and post-fledging productivity, as well as estimates of adult survivorship and recruitment into the adult population, for various landbird species. Broad-scale data on productivity and survivorship are not obtained from any other avian monitoring program in North America and are needed to provide critical information upon which to initiate research and management actions to reverse the recently-documented declines in North American landbird populations. A second objective of the MAPS program is to provide standardized population and demographic data for the landbirds found on federally managed public lands, such as national parks, national forests, and military installations. In this light, the MAPS program has been evaluated and is being operated in Denali National Park as part of the Long-Term Ecological Monitoring (LTEM) program for the Park. It is expected that information from MAPS will be capable of aiding research and management efforts within the park to protect and enhance the park's avifauna and ecological integrity.

We operated six MAPS stations in 2001 in Denali National Park. Four of these (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) were in the same locations along the eastern portion of the park road where they were operated from 1992 to 2000; the other two (Strangler Hill and Buhach Creek) were in the same locations along the western portion of the park road where they were operated from 1997 to 2000. With few exceptions, the ten net-sites per station were operated for six morning hours per day on one day per 10-day period for six consecutive ten-day periods between June 10 and August 8. A total of 957 birds of 29 species were banded at the six stations during the summer of 2001, various individuals were recaptured a total of 344 times, and 25 birds were captured and released unbanded. Thus, a total of 1325 captures of 30 species was recorded. Analyses of constant-effort data indicated that the numbers of both adult and young birds captured increased from 2000 to 2001. For all species pooled, the number of adults captured increased by a non-significant 18.0% while the proportion of young in the catch (an index of productivity) increased significantly by 0.177 from 0.405 in 2000 to 0.583 in 2001.

Despite the increased population sizes in 2001, populations of all species pooled showed a relatively small but nearly significant ten-year (1992-2001) decline of -2.1% per year when data from all six stations were combined. Moreover, population trends were negative for seven of eleven study species. Several species showed pronounced ten-year increases or decreases in their breeding populations. These included significant and highly significant increases, respectively, for Boreal Chickadee and Yellow-rumped Warbler, significant declines for Arctic Warbler and Swainson’s Thrush, a nearly significant decline for Wilson’s Warbler when data from all six stations were pooled, and a significant decline for American Tree Sparrow over the four eastern stations. Trends in the populations of the other six species appeared rather stable, although generally with slightly decreasing tendencies.

Five-year (1997-2001) population trends were quite similar between the two western and four eastern stations for five of seven species and all species pooled. Meaningful differences for the remaining two species, Wilson's Warbler and American Tree Sparrow, could be explained by differences in the annual population changes for just one or two (of the five) years of data. Population trends at the four eastern stations were more negative (or less positive) during the second five-year period (1997-2001) than during the first five-year period (1992-1996) for seven of eleven species as well as for all species pooled. This could be cause for concern although, interestingly, a comparison of five-year and ten-year mean values indicate a greater reproductive output during the latter half of the study period.

Productivity trends over the ten years (1992-2001) were fairly stable for seven of eleven species as well as all species pooled, although productivity fluctuated widely for Fox Sparrow. Significantly increased productivity in 2001 (the highest recorded to date) caused several species and all species pooled to show positive ten-year (1992-2001) productivity trends as compared with negative nine-year (1992-2000) trends. Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed significant increases, a third species (Orange-crowned Warbler) showed a substantial but non-significant increase (at least when data from all six stations were pooled), and a fourth species (Boreal Chickadee) showed a substantial but non-significant decline. Five year (1997-2001) productivity trend were very similar between the two western and four eastern stations for four of six species and all species pooled. Meaningful differences were found only for Wilson's Warbler and American Tree Sparrow. Productivity trends at the four eastern stations were more positive during the second five-year period (1997-2001) than during the first five-year period (1992-1996) for nine of eleven species and all species pooled. Most of this difference, however, was caused by the very high productivity in 2001.

Nine of eleven study species (all but Fox Sparrow and Common Redpoll), as well as all species pooled, showed positive "productivity/population correlations," indicating that a change in productivity one year resulted in a corresponding change in population size the following year. These positive relationships were significant or nearly significant for three species and for all species pooled. From 1992 through 1998, this positive productivity/population correlation was manifest at Denali by an alternating cycle of declines and increases, with productivity decreasing in even-numbered years and increasing in odd-numbered years, followed by the same pattern of decreases and increases in numbers of adults captured the following year. We suggest that this pattern was caused by a density-dependent effect on productivity along with low productivity of first-time breeders. This dynamic was disrupted during the 1999-2001 seasons, when both productivity and population size showed changes in the same direction (negative during the 1998-1999 and 1999-2000 comparisons, and positive during the 2000-2001 comparison).

To examine the possibility that global climate patterns are affecting productivity at Denali, we regressed annual productivity indices on mean monthly Southern Oscillation Index (SOI) values and found an overall negative relationship between productivity at Denali and SOI, with productivity being higher in El Niño years than La Niña years. Thus it is likely that the severe La Niña event of 1999-2000, resulting in the highest SOI values during the ten-year period, caused productivity to be lower than expected and disrupted the density-dependent effect. Accounting for the significant positive increase in SOI with year during the ten-year study period, the predicted trend in productivity for all species pooled based on these correlations was -0.006 per year, compared with the observed productivity trend for all species pooled at Denali of +0.004 per year. Similar analyses were performed for two individual species showing significant but opposite relationships between productivity and SOI, Swainson's Thrush (positive) and Wilson's Warbler (negative). In each case the predicted trends (+0.021 and -0.021, respectively) were similar to the actual trends (+0.046 and -0.020), with the actual productivity trend for Swainson's Thrush, like that for all species pooled, being somewhat higher than the predicted trend. The discrepancy between the predicted and actual productivity trends likely resulted from the very high productivity observed at Denali in 2001.

We have recently completed analyses showing how global climate patterns affect landbird productivity in Pacific Northwest national forests (Nott et al. in press) using other global climate indices, such as the El Niño/Southern Oscillation Precipitation Index (ESPI, another measure of La Niña and El Niño events) and the North Atlantic Oscillation (NAO). These analyses showed that El Niño conditions greatly enhanced productivity of species that breed in Pacific Northwest forests and winter in or migrate through western Mexican (apparently by producing favorable weather conditions on their wintering grounds and migration routes), but had a much smaller effect on the productivity of temperate-wintering species breeding in the Pacific Northwest. Other researchers (Sillett et al. 2000) have documented the opposite effect along the Atlantic Coast, that is, higher productivity during La Niña conditions in Black-throated Blue Warblers breeding in New Hampshire and wintering in the West Indies. These results nicely explain differences among Denali's Wilson's Warblers (that winter in or migrate through Mexico), Swainson's Thrushes (that are trans-Gulf migrants that winters in South America), and temperate-wintering species in the responses of their productivity to the El Niño/Southern Oscillation. These results beg for additional data from Denali National Park on other species, such as Gray-cheeked Thrush and Blackpoll Warbler, that also winter in South America.

It is also likely that the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO, which measures a Pacific global climate cycle that shifts every 25 years), could also affect productivity of Denali's birds. This latter cycle underwent a major shift between 1999 and 2001, which might explain the higher-than expected productivity observed in 2001. We suggest that after 2006, when 15 years of data will be available (that will include ten years of data from the two eastern stations that capture substantial numbers of Alder Flycatchers and Gray-cheeked Thrushes), we model both annual productivity indices and annual survival-rate estimates as a function of SOI, ESPI, NAO, PDO, and other global climate cycles to more fully understand how climate affects productivity of the study species at Denali National Park.

Reasonably precise estimates of annual adult survival and recapture probabilities and proportion of young among newly captured adults are now being obtained from modified Cormack-Jolly-Seber mark-recapture analyses (using the program SURVIV and a between- and within-year transient model) from ten years (1992-2001) of MAPS data for eleven breeding species at Denali National Park. The precision of the estimates increased from 2000 to 2001 and should continue to increase for several more years as additional years of data accumulate. This will allow improved analyses of the effect of adult survivorship in influencing population trends. With more years of data, temporal effects on survival may also become more evident, although it is likely that as many as twenty years of data will be necessary to determine actual temporal trends in adult survivorship.

In order to investigate possible causes of population trends for individual study species at Denali National Park, we examined trends in productivity, relationships between changes in productivity and changes in population size the following year (“productivity/population correlation”), annual variability in survival, and comparisons of mean adult survival rates and mean productivity indices with those expected based on relationships of these parameters with body mass both at Denali and across North America. Five of ten species showed relatively stable population dynamics at Denali, having non-significant population trends, expected adult survival rates, and expected or higher-than-expected productivity given their body mass. For each of the remaining five species, our data suggest explanations for the observed population trends, with high adult survival causing observed increases in Boreal Chickadee and Yellow-rumped Warbler, low (and time-dependent) adult survival and low productivity causing declines in Arctic Warbler, low adult survival causing declines in Wilson’s Warbler, and low productivity (or possibly low first-year survival) causing declines in Swainson’s Thrush.

Thus it appears that, at Denali National Park, mean annual survivorship, which is probably affected primarily on the wintering grounds or migration routes, is a greater factor in driving landbird population trends (both increasing and decreasing) than is mean annual productivity. This might be expected considering the near pristine nature of the breeding habitat at Denali. In contrast, however, annual changes in population size appear to be driven by annual changes in productivity more than by annual changes in adult survival rates. Evidence for this includes the positive productivity/population correlations for nine of eleven species, which were significant for two species and all species pooled, and the relatively small amount of time-dependence observed in adult survival rates. Climatological events may, in turn, be driving these annual variations in productivity at Denali.

One important population parameter that we have not been able to measure adequately is first-year survival, that is, the survival of young birds between fledging and breeding the following year. In future analyses we will attempt to index first-year survival through a combination of two methods: (1) by using data that distinguish captures of one-year-old adults (second year birds, SYs) from older adults (after-second-year birds, ASYs), and (2) by modeling temporal symmetry in mark-recapture data (that is, by running survival analyses in the reverse direction) to estimate annual recruitment (and thus to make inferences regarding survival) of one-year-old birds.

Ten years of MAPS data from Denali National Park have consistently shown higher breeding bird densities in willow and scrub habitats than in spruce forest habitats, but slightly higher productivity in forested habitats. This suggests that the best way to optimize both productivity and population sizes of birds in Denali National Park may be to maintain the high quality of a mosaic of habitats. It must be stressed, however, that the six currently operated MAPS stations sample a small portion of the Park that lies entirely on north side of the Alaska Range. It is likely that the population dynamics of landbirds could vary dramatically in other portions of the park. In particular, the population dynamics of landbirds south of the Alaska Range could be strikingly different, because they would be influenced more by maritime conditions than would birds north of the Range. We would welcome opportunities to establish pilot MAPS in other areas of the Park, if the logistical difficulties could be overcome.

In this report we demonstrate how MAPS data can be used to measure and assess the effects of productivity and survivorship as driving forces of population trends at Denali. In future analyses we will add estimates of recruitment of young and indices of first-year survival in order to fully understand which parameters are most affecting population changes in each study species. As a result, the indices and estimates of primary demographic parameters produced by MAPS will be extremely useful for the management and conservation of landbirds at Denali National Park and Preserve and, in combination with similar data from other areas, across all of North America. We conclude that the MAPS protocol is extremely well-suited as a component of Denali's Long-term Ecological Monitoring Program.

We have initiated two additional types of broad-scale analyses of MAPS data to help us further understand the population dynamics of landbirds and potential management actions to reverse population declines. First, by modeling spatial variation in vital rates as a function of spatial variation in population trends, we are able to identify the proximate demographic causes of population decline for species at multiple spatial scales (DeSante et al. 2001a). Second, we have found that patterns of landscape structure detected within two- to four-kilometers of each station are good predictors not only of the numbers of birds of each species captured but, more importantly, of their productivity levels as well. Based on these analyses, threshold values of various landscape-level habitat characteristics, such as woodland/forest patch size, can be determined that will maximize productivity, thereby providing an extremely powerful tool to aid in formulating management actions aimed at reversing landbird population declines (Nott 2000b). With appropriate funding, we hope to be able to undertake such analyses of Denali data in conjunction with data from other more heavily managed landscapes in Alaska and elsewhere when 15 years of data have been obtained, that is, after the 2006 field season.

Based on the above information, we recommend that the MAPS Program continue to be included as an integral part of Denali's Long-term Ecological Monitoring Program, and that operation at the six currently active stations be sustained indefinitely into the future. We recommend that, if possible, additional stations be established in other areas of the park in order to gain a more comprehensive picture of landbird population dynamics at Denali National Park. We also recommend, if possible, siting these additional stations at locations where increased numbers of individuals of species targeted by Boreal Partners in Flight, such as Gray-cheeked Thrush, Blackpoll Warbler, and Golden-crowned Sparrow, could be captured.

Finally, we recommend greatly reducing the extent and thoroughness of the MAPS annual reports submitted each year to the LTEM Program, and recommend providing comprehensive reports with additional analyses as described above at approximately five-year intervals. This would help defer the cost operating additional stations in the Park.

INTRODUCTION

The National Park Service (NPS) has been charged with the responsibility of managing natural resources on lands under its jurisdiction in a manner that conserves them unimpaired for future generations. In order to carry out this charge, the NPS is implementing integrated long-term programs for inventorying and monitoring the natural resources in national parks and other NPS units. A pilot study to develop and evaluate field and analytical techniques to accomplish these objectives was first implemented in four national parks across the United States; Denali National Park and Preserve was selected as one of the four. The goals of the pilot program in Denali National Park and Preserve were to develop: (1) quantitative sampling and analytical methods that can provide relatively complete inventories and long-term trends for many components of biological diversity; and (2) effective means of monitoring the ecological processes driving the trends (Van Horn et al. 1992). An additional goal was that the methods evaluated at Denali be useful in other national parks in Alaska and, if possible, across the United States. These programs, including the one in Denali National Park and Preserve, are referred to as Long-term Ecological Monitoring (LTEM) Programs.

The development of an effective long-term ecological monitoring program in the national parks can be of even wider importance than aiding the NPS in managing its resources. Because lands managed by the NPS provide large areas of relatively pristine ecosystems that promise to be maintained in a relatively undisturbed manner indefinitely into the future, studies conducted in national parks can provide invaluable information for monitoring natural ecological processes and for evaluating the effects of large-scale, even global, environmental changes. The national parks and other NPS units can also serve as critical control areas for monitoring the effects of relatively local land-use practices. Thus, long-term monitoring data from the national parks can provide information that is crucial for efforts to preserve natural resources and biodiversity on multiple spatial scales, ranging from the local scale to the continental or even global scale.

Landbirds

Landbirds, because of their high body temperature, rapid metabolism, and high ecological position on most food webs, may be excellent indicators of the effects of local, regional, and global environmental change in terrestrial ecosystems. Furthermore, their abundance and diversity in virtually all terrestrial habitats, diurnal nature, discrete reproductive seasonality, and intermediate longevity facilitate the monitoring of their population and demographic parameters. It is not surprising, therefore, that landbirds have been selected by the NPS to receive high priority for monitoring. Nor is it surprising that several large-scale monitoring programs that provide annual population estimates and long-term population trends for landbirds are already in place on this continent. They include the North American Breeding Bird Survey (BBS), the Breeding Bird Census, the Winter Bird Population Study, and the Christmas Bird Count.

Recent analyses of data from several of these programs, particularly the BBS, suggest that populations of many landbirds, including forest-, scrubland-, and grassland-inhabiting species, appear to be in serious decline (Peterjohn et al. 1995). Indeed, populations of most landbird species appear to be declining on a global basis. Nearctic-Neotropical migratory landbirds (species that breed in North America and winter in Central and South America and the West

Indies; hereafter, Neotropical migratory birds) constitute one group for which pronounced population declines have been documented (Robbins et al. 1989, Terborgh 1989). In response to these declines, the Neotropical Migratory Bird Conservation Program, "Partners in Flight - Aves de las Americas," was initiated in 1991 (Finch and Stangel 1993). The major goal of Partners in Flight (PIF) is to reverse the declines in Neotropical migratory birds through a coordinated program of monitoring, research, management, education, and international cooperation. As one of the major cooperating agencies in PIF, the NPS has defined its role in the program to include the establishment of long-term monitoring programs at NPS units using protocols developed by the Monitoring Working Group of PIF. Clearly, the long-term ecological monitoring goals of the NPS and the monitoring and research goals of PIF share many common elements.

The goals of these programs differ, however, in at least one important respect. A major goal of PIF is to reverse population declines, especially in rare or uncommon (although not threatened or endangered) “priority” species, while a major objective of the NPS’ LTEM program is to understand the ecological processes driving population changes. This latter goal often necessitates concentrating on relatively common or even abundant species that are undergoing population changes, rather than rare or uncommon ones. Thus, appropriate study species might be expected to differ somewhat between PIF and LTEM efforts.

Primary Demographic Parameters

Existing population-trend data on Neotropical migrants, while suggesting severe and sometimes accelerating declines, provide no information on primary demographic parameters (productivity and survivorship) of these birds. Thus, population-trend data alone provide no means for determining at what point(s) in the life cycles problems are occurring, or to what extent the observed population trends are being driven by causal factors that affect birth rates, death rates, or both (DeSante 1995). In particular, large-scale North American avian monitoring programs that provide only population-trend data have been unable to determine to what extent forest fragmentation and deforestation on the temperate breeding grounds, versus that on the tropical wintering grounds, are causes for declining populations of Neotropical migrants. Without critical data on productivity and survivorship, it will be extremely difficult to identify effective management and conservation actions to reverse current population declines (DeSante 1992).

The ability to monitor primary demographic parameters of study species must also be an important component of any successful long-term inventory and monitoring program that aims to monitor the ecological processes leading from environmental stressors to population responses (DeSante and Rosenberg 1998). This is because environmental factors and management actions generally affect primary demographic parameters directly and these effects usually can be observed over a short time period (Temple and Wiens 1989). Because of the buffering effects of floater individuals and density-dependent responses of populations, there may be substantial timelags between changes in primary parameters and resulting changes in population size or density as measured by census or survey methods (DeSante and George 1994). Thus, a population could be in trouble long before this becomes evident from survey data. Moreover, because of the vagility of many animal species, especially birds, local variations in secondary parameters (e.g., population size or density) may be masked by recruitment from a wider region

(George et al. 1992) or accentuated by lack of recruitment from a wider area (DeSante 1990). A successful monitoring program should be able to account for these factors.

Finally, a successful monitoring program should be able to detect significant differences in productivity as a function of such local variables as landscape-level habitat characteristics or degree of habitat disturbance. The detection of such differences can lead to immediate management implementation within a national park, especially for species for which long-term demographic monitoring suggests that declines are related to local (e.g., productivity) rather than remote (e.g., overwinter survival in Neotropical migrants) factors.

MAPS

In 1989, The Institute for Bird Populations (IBP) established the Monitoring Avian Productivity and Survivorship (MAPS) program, a cooperative effort among public agencies, private organizations, and individual bird banders in North America to operate a continent-wide network of constant-effort mist-netting and banding stations to provide long-term demographic data on landbirds (DeSante et al. 1995). The design of the MAPS program was patterned after the very successful British Constant Effort Sites (CES) Scheme that has been operated by the British Trust for Ornithology since 1981 (Peach et al. 1996). The MAPS program was endorsed in 1991 by the Monitoring Working Group of PIF and the USDI Bird Banding Laboratory, and a four-year pilot project (1992-1995) was approved by the USDI Fish and Wildlife Service and National Biological Service (now the Biological Resources Division [BRD] of the U.S. Geological Survey [USGS]) to evaluate its utility and effectiveness for monitoring demographic parameters of landbirds. A peer review of the program and of the evaluation of the pilot project was completed by a panel assembled by USGS/BRD (Geissler 1996). The review concluded that: (1) MAPS is technically sound and is based on the best available biological and statistical methods; and (2) it complements other landbird monitoring programs such as the BBS by providing useful information on landbird demographics that is not available elsewhere.

Now in its thirteenth year (tenth year of standardized protocol and extensive distribution of stations), the MAPS program has expanded greatly from 178 stations in 1992 to over 500 stations in 2001. The substantial growth of the Program since 1992 was caused by its endorsement by PIF and the subsequent involvement of various federal agencies in PIF, including the NPS, USDA Forest Service, US Fish and Wildlife Service, Department of Defense, Department of the Navy, and Texas Army National Guard. Within the past ten years, for example, IBP has been contracted to operate up to six MAPS stations in Denali, five in Yosemite, six in Shenandoah, and two in Kings Canyon national parks, and six on Cape Cod National Seashore. MAPS stations were established in these NPS units in order to evaluate the usefulness of MAPS methodology as a major component of the NPS's Long-Term Ecological Monitoring Program and, subsequently, to implement its use as part of that program.

Goals and Objectives of MAPS

MAPS is organized to fulfill three tiers of goals and objectives: monitoring, research, and management.

! The specific monitoring goals of MAPS are to provide, for over 100 study species, including Neotropical-wintering migrants, temperate-wintering migrants, and permanent residents:

(A) annual indices of adult population size and post-fledging productivity from data on the numbers and proportions of young and adult birds captured; and

(B) annual estimates of adult population size, adult survival rates, proportions of residents among newly captured adults, recruitment rates into the adult population, and population growth rates from modified Cormack- Jolly-Seber analyses of mark-recapture data on adult birds.

! The specific research goals of MAPS are to identify and describe:

(1) temporal and spatial patterns in these demographic indices and estimates at a variety of spatial scales ranging from the local landscape to the entire continent; and

(2) relationships between these patterns and ecological characteristics of the study species, population trends of the study species, station-specific and landscape-level habitat characteristics, and spatially-explicit weather variables.

! The specific management goals of MAPS are to use these patterns and relationships, at the appropriate spatial scales, to:

(a) identify thresholds and trigger points to notify appropriate agencies and organizations of the need for further research and/or management actions;

(b) determine the proximate demographic cause(s) of population change;

(c) suggest management actions and conservation strategies to reverse population declines and maintain stable or increasing populations; and

(d) evaluate the effectiveness of the management actions and conservation strategies actually implemented through an adaptive management framework.

The overall objectives of MAPS are to achieve the above-outlined goals by means of long-term monitoring at two major spatial scales. The first is a very large scale — effectively the entire North American continent divided into eight geographical regions. It is envisioned that the national parks, along with national forests, military installations, and other publically owned lands, will provide a major subset of sites for this large-scale objective.

The second, smaller-scale but still long-term objective is to fulfill the above-outlined goals for specific geographical areas (perhaps based on BBS physiographic strata, such as the Open Boreal Forest, Southern Alaska Coast, or Tundra, or the newly created Bird Conservation Regions) or specific locations (such as individual national parks, national forests, or military installations).

The objective for MAPS at these smaller spatial scales is to aid research and management efforts within the parks, forests, or installations to protect and enhance their avifauna and ecological integrity. The sampling strategy utilized at these smaller scales should be hypothesis-driven and should be integrated with other research and monitoring efforts.

Both long-term objectives are in agreement with objectives laid out for the NPS's Long-Term Ecological Monitoring Program. Accordingly, the MAPS program was established in Denali National Park and Preserve as part of the development of Denali's LTEM Program. It is expected that information from the MAPS program will be capable of aiding research and management efforts within the park to protect and enhance the park's avifauna and ecological integrity.

SPECIFICS OF THE DENALI MAPS PROGRAM

Goals

The specific goals for the initial operation of the MAPS Program in Denali National Park were to:

(1) evaluate the ability and effectiveness of MAPS to provide a useful component of the Long-term Ecological Monitoring Program in Denali National Park;

(2) determine the effectiveness of various MAPS stations in Denali National Park to provide reliable demographic information on selected landbird study species of the Alaskan montane environment; and

(3) develop detailed written protocols for the long-term monitoring of these landbird species' population and demographic parameters, to be used in Denali's Long-term Ecological Monitoring Program, by refining and altering the MAPS protocol to fit the specific needs of Denali National Park.

With the submission and acceptance by the Denali LTEM Program of "Monitoring Avian Productivity and Survivorship (MAPS) in Denali National Park", a handbook of field and analytical techniques for monitoring primary demographic parameters in Denali and other national parks (IBP 1997), the specific goals for the initial operation of MAPS in Denali have been achieved.

The current goal for the Denali MAPS program is to continue to monitor the primary demographic parameters of selected landbird species as part of Denali's LTEM Program in order to provide critical information that can be used to aid our understanding of the ecological processes leading from environmental stressors to population responses. To achieve this goal, we will first need to analyze spatial patterns in productivity indices and survival rate estimates as a function of spatial patterns in population trends for study species, in order to determine the proximate demographic factor (i.e., productivity or survivorship) causing the observed population trends (DeSante et al. 2001a). We will then need to link MAPS data with landscape-level habitat data and spatially explicit weather data in a geographical information system (GIS) to identify relationships between landscape-level habitat and/or weather characteristics and the primary demographic responses (productivity and survival rates) of the study species. This will allow hypotheses to be generated regarding the ultimate environmental causes of the population trends. Successful completion of this approach will necessitate analyses of MAPS data from stations located other areas in addition to the stations in Denali National Park and Preserve.

In this respect, it is appropriate to point out the importance of primary demographic data on study species from Denali National Park, as these data provide the controls against which data from more heavily managed or disturbed areas in Alaska can be compared. Thus, the approach championed here is to include data from Denali National Park in larger-scale analyses. Denali data, for example, will need to be compared to data from relatively pristine ecosystems (e.g., other national parks) at lower latitudes, and to data from more heavily managed ecosystems elsewhere in Alaska. It should be noted that funding for such analyses does not currently exist and sources of future funding have not yet been identified. We suggest that such analyses should be implemented after 15 consecutive years of data have been collected, that is, after the 2006 breeding season.

Establishment and Operation of Stations

Four of the six MAPS stations in operation in Denali National Park in 2001 (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) were established in 1992. In 1997, two new stations, Strangler Hill and Buhach Creek, were added to the four continuing stations, and these continued to be operated through 2001. The six current stations do not represent a cross-section of the major habitats encompassed by the park, nor even a truly representative sample of habitats along the roaded corridor. Rather, they provide a stratified sample of two major types of montane habitat -- willow or dwarf birch scrub (Strangler Hill, Buhach Creek, and Igloo Creek) and spruce forest with varying patch sizes (Mile Seven, Permafrost, and Rock Creek) -- along the main road corridor in the northeastern portion of Denali National Park. Following consideration of habitat type, logistical constraints, and requirements of the LTEM program design, each station was selected at random from a small group of potential stations. The six stations, ordered geographically from west to east, are: (1) the Strangler Hill station, representing alder-birch scrub, located along the McKinley River south of the Denali Park road at milepost 83.7; (2) the Buhach Creek station, representing a mix of alder and willow scrub, also located along the McKinley River south of the Denali Park road at milepost 69.8; (3) the Igloo Creek station, representing riparian willow scrub, located on the east (north) side of the main park road along Igloo Creek about five km north (west) of the Igloo Creek campground; (4) the Mile Seven station, representing patchy spruce forest, spruce-birch scrub, and wet willow scrub, located just north of the main park road at milepost seven; (5) the Permafrost station, representing mature spruce forest, riparian alder, and wet willow scrub, located just south of the main park road at the former "Permafrost" interpretive sign; and (6) the Rock Creek station, representing a mature open spruce forest and riparian alder woodland, located in the Rock Creek watershed about 0.4 km north of the main park road. Two other MAPS stations were operated temporarily in Denali National Park: the Hogan Creek station, operated in 1992, which represented small-patch-size spruce forest (somewhat similar to Mile Seven) and was located just north of the main park road where it crosses Hogan Creek; and the Lost Forest Station, operated in 1993-1996, which represented mature spruce forest (somewhat similar to Rock Creek) and was located in the upper Rock Creek drainage. These two stations were discontinued due to logistical reasons.

The 2001 Denali MAPS Program

The 2001 Denali field biologist interns were Traci and Brad Clemens. Both had previously served as a MAPS interns for the Institute for Bird Populations in Shenandoah National Park. They received a comprehensive training course in mist-netting techniques from IBP biologists Pilar Velez and Neil Chartier at the Red Bluff Conservation Area, California, during the first two weeks of May, and further instruction in banding Alaskan bird species from staff biologists at the Alaska Bird Observatory (ABO) during the final third of May. Traci and Brad were responsible for all of the MAPS data collected in Denali National Park during 2001.

All ten net-sites at each of the six stations were re-established in the exact same locations as in previous years. One 12-m, 30-mm-mesh, 4-tier, nylon mist net was erected at each of the sites on each day of operation. Each station was operated for six morning hours per day (beginning at 0530 or local sunrise, whichever was later) on one day in each of six consecutive 10-day periods between Period 5 (beginning June 10) and Period 10 (beginning July 30). The operation of all stations occurred on schedule during each of the six 10-day periods. A summary of the operation of the 2001 Denali MAPS Program is presented in Table 1 along with the latitude-longitude, elevation, and major habitats present at each of the six stations. Further details on MAPS procedures at Denali are provided below and in the Denali MAPS Handbook (IBP 1997).

METHODS

The operation of each of the six stations during 2001 and of all stations in operation during the previous seven years followed MAPS protocol, which is described in detail in DeSante and Burton (1997), which comprises Part II of "Monitoring Avian Productivity and Survivorship (MAPS) in Denali National Park," a handbook of field and analytical techniques for monitoring primary demographic parameters of landbirds in Denali National Park (IBP 1997). The final, revised, peer-reviewed draft of this handbook was submitted to USGS/BRD personnel at the Alaska Science Center on December 29, 1997, and since then has been accepted as standardized LTEM protocol. A brief overview of both the field and analytical techniques applied in 2001 is presented here.

Data Collection

With few exceptions, all birds captured during the course of the study were identified to species, age, and sex and, if unbanded, were banded with USGS/BRD numbered aluminum bands. Birds were released immediately upon capture and before being banded if situations arose where bird safety would be comprised. Such situations involved exceptionally large numbers of birds being captured at once, or the sudden onset of adverse weather conditions such as high winds or sudden rainfall. The following data were taken on all birds captured, including recaptures, according to MAPS guidelines using standardized codes and forms:

(1) capture code (newly banded, recaptured, band changed, unbanded);
(2) band number;
(3) species;
(4) age and how aged;
(5) sex (if possible) and how sexed (if applicable);
(6) extent of skull pneumaticization;
(7) breeding condition of adults (i.e., presence or absence of a cloacal protuberance or brood patch);
(8) extent of juvenal plumage in young birds;
(9) extent of body and flight-feather molt;
(10) extent of primary-feather wear;
(11) fat class;
(12) wing chord and weight;
(13) date and time of capture (net-run time); and
(14) station and net site where captured.

Effort data, i.e., the number and timing of net-hours on each day (period) of operation, were also collected in a standardized manner. In order to allow constant-effort comparisons of data to be made, the times of opening and closing the array of mist nets and of beginning each net check were recorded to the nearest ten minutes. The breeding status (confirmed breeder, likely breeder, non-breeder) of each species seen, heard, or captured at each MAPS station on each day of operation was recorded using techniques similar to those employed for breeding bird atlas projects.

For each of the six stations operated, simple habitat maps were prepared on which up to four major habitat types, as well as the locations of all structures, roads, trails, and streams, were identified and delineated; when suitable maps from previous years were available, these were used. The pattern and extent of cover of each major habitat type identified at each station, as well as the pattern and extent of cover of each of four major vertical layers of vegetation (upperstory, midstory, understory, and ground cover) in each major habitat type were classified into one of twelve pattern types and eleven cover categories according to guidelines spelled out in the MAPS Habitat Structure Assessment Protocol, developed by IBP Landscape Ecologist, Philip Nott (Nott 2000a).

Computer Data Entry and Verification

The computer entry of all banding data was completed by John W. Shipman of Zoological Data Processing, Socorro, NM. The critical data for each banding record (capture code, band number, species, age, sex, date, capture time, station, and net number) were proofed by hand against the raw data and any computer-entry errors were corrected. Computer entry of effort and vegetation data was completed by IBP biologists using specially designed data entry programs. All banding data were then run through a series of verification programs as follows:

(1) Clean-up programs to check the validity of all codes entered and the ranges of all numerical data;
(2) Cross-check programs to compare station, date, and net fields from the banding data with those from the summary of mist netting effort data;
(3) Cross-check programs to compare species, age, and sex determinations against degree of skull pneumaticization, breeding condition (extent of cloacal protuberance and brood patch), and extent of body and flight-feather molt, primary-feather wear, and juvenal plumage;
(4) Screening programs which allow identification of unusual or duplicate band numbers or unusual band sizes for each species; and
(5) Verification programs to screen banding and recapture data from all years of operation for inconsistent species, age, or sex determinations for each band number.

Any discrepancies or suspicious data identified by any of these programs were examined manually and corrected if necessary. Wing chord, weight, station of capture, date, and any pertinent notes were used as supplementary information for the correct determination of species, age, and sex in all of these verification processes.

Data Analysis
To facilitate analyses, we first classified the landbird species captured in mist nets into five groups based upon their breeding or summer residency status. Each species was classified as one of the following: a regular breeder (B) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station *during all years* that the station was operated; a usual breeder (U) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station *during more than half but not all of the years* that the station was operated; an occasional breeder (O) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station *during half or fewer of the years* that the station was operated; a transient (T) if the species was *never* a breeder or summer resident at the station, but the station was within the overall breeding range of the species; and a migrant (M) if the station was not located within the overall breeding range of the species. Data for a given species from a given station were included in productivity analyses if the station was within the breeding range of the species; that is, data were included from stations where the species was a breeder (B, U, or O) or transient (T), but not where the species was a migrant (M). Data for a given species from a given station were included in survivorship analyses only if the species was classified as a regular (B) or usual (U) breeder at the station.

A. Population-size and productivity analyses — The proofed, verified, and corrected banding data from 2001 were run through a series of analysis programs that calculated for each species and for all species combined at each station and for all stations pooled:

(1) the numbers of newly banded birds, recaptured birds, and birds released unbanded;
(2) the numbers and capture rates (per 600 net-hours) of first captures (in 2001) of individual adult and young birds; and
(3) the proportion of young in the catch.

Following the procedures pioneered by the British Trust for Ornithology (BTO) in their CES Scheme (Peach et al. 1996), the number of adult birds captured was used as an index of adult population size, and the proportion of young in the catch was used as an index of post-fledging productivity.

For all six stations we calculated changes between 2000 and 2001 in the indices of adult population size and post-fledging productivity and determined the statistical significance of any changes that occurred according to methods developed by the BTO in their CES scheme (Peach et al. 1996). These year-to-year comparisons were made in a "constant-effort" manner by means of a specially designed analysis program that used actual net-run (capture) times and net-opening and -closing times on a net-by-net and period-by-period basis to exclude captures that occurred in a given net in a given period in one year during the time when that net was not operated in that period in the other year. For species captured at several stations in Denali National Park, the significance of park-wide annual changes in the indices of adult population size and post-fledging productivity was inferred statistically using confidence intervals derived from the standard errors of the mean percentage changes. The statistical significance of the overall change at a given station was inferred from a one-sided binomial test on the proportion of species at that station that increased (or decreased). Throughout this report, we use an alpha level of 0.05 for statistical significance and we use the term “near-significant” or “nearly significant” for differences for which $0.05 \leq P < 0.10$.

B. Analyses of trends in adult population size and productivity — We examined five-year and ten-year trends in indices of adult population size and productivity for study species for which an average of at least six individual adult birds were captured per year at all stations combined during the five-year periods 1992-1997 and 1997-2001, and during the ten-year period 1992-2001. For trends in adult population size, we first calculated adult population indices for each species for each of the ten years based on an arbitrary starting index of 1.0 in 1992 or 1997. Constant-effort changes (as defined above) were used to calculate these “chain” indices in each subsequent year by multiplying the proportional change (percent change divided by 100) between the two years times the index of the previous year and adding that figure to the index of the previous year, or simply:

$$PSI_{i+1} = PSI_i + PSI_i * (d_i/100)$$

where PSI_i is the population size index for year i and d_i is the percentage change in constant-effort numbers from year i to year i+1. A regression analysis was then run to determine the slope (*PT*) of these indices over the five-year or ten-year periods. Because the indices for adult population size are based on percentage changes, we further calculated the annual percent change (*APC*), defined as the average change per year over the five-year or ten-year period, to provide an estimate of the population trend for the species; *APC* was calculated as:

(actual 1992 value of *PT* / predicted 1992 value of *PT* based on the regression) * *PT*.

We present the *APC*, the standard error of the slope (*SE*), the correlation coefficient (*r*), and the significance of the correlation (*P*) to describe each trend. Species for which $r > 0.5$ are considered to have a substantially increasing trend, those for which $r < -0.5$ are considered to have a substantially decreasing trend, those for which $-0.5 < r < 0.5$ and $SE < 0.035$ for ten-year trends or $SE < 0.140$ for five-year trends are considered to have a stable trend, and those for which $-0.5 < r < 0.5$ and $SE > 0.035$ for ten-year trends or $SE > 0.140$ for five-year trends are considered to have widely fluctuating values but no substantial trend.

Trends in productivity, *PrT*, were calculated in an analogous manner by starting with actual productivity values in 1992 and calculating each successive year's value based on the actual constant-effort changes in productivity between each pair of consecutive years. For trends in productivity, the slope (*PrT*) and its standard error (*SE*) are presented, along with the correlation coefficient (*r),* and the significance of the correlation (*P*). Productivity trends are characterized in a manner analogous to that for population trends, except that productivity trends are considered to be highly fluctuating if the SE of the slope > 0.020 for ten-year productivity trends or > 0.080 for five-year productivity trends.

To evaluate the extent to which productivity in one year has a direct effect on adult population size the following year, we regressed changes in adult population size during one between-year comparison on changes in productivity during the previous between-year comparison.

C. Comparisons of productivity with Southern Oscillation Index — To assess the degree to which global climate patterns may be affecting landbird productivity, we compared annual productivity values (mean value for all species pooled from the four long-running stations) with the standardized Southern Oscillation Index (SOI), a measure of global climate based on the strength/weakness of El Niño and La Niña events in the tropical Pacific Ocean. SOI, calculated using pressure differentials between Tahiti and Darwin, Australia, has been used by climatologists as an index of relative global climate throughout the Pacific and North America; low negative SOI's indicate El Niño years and high positive SOI's indicate La Niña years. This SOI index has recently been correlated with productivity and survival in a migratory, eastern North American landbird (Sillett *et al.* 2001). For this report we use mean of the monthly SOI's for January-December of the year in question.

D. Survivorship analyses — Modified Cormack-Jolly-Seber mark-recapture analyses (Pollock et al. 1990, Lebreton et al. 1992) were conducted using the computer program SURVIV (White 1983) on datasets consisting of: (1) ten years (1992-2001) of banding data from the four stations operated during all ten years (Igloo Creek, Mile Seven, Permafrost, and Rock Creek); and (2) ten years (1992-2001) of banding data from those four stations plus five years (1997-2001) of banding data from two additional stations (Strangler Hill and Buhach Creek). Mark-recapture analyses were conducted on study species for which an average of at least six individual adults were captured per year at the four (or six) stations combined over the ten years, 1992-2001.

Using SURVIV, we estimated survivorship parameters for each of the study species using both a between- and within-year transient model which accounts for the presence of transient adults (migrant and floater individuals which are only captured once) in the sample of newly captured birds (Pradel et al. 1997, Nott and DeSante in press). The transient model permits calculation of maximum-likelihood estimates and standard errors (*SE*s) for adult survival probability (φ), adult recapture probability (p), and proportion of residents among newly-captured adults (τ). Recapture probability is defined as the conditional probability of recapturing a bird in a subsequent year that was banded in a previous year, given that it survived and returned to the place it was originally banded. These estimates were derived from the capture histories of all adult birds for each study species captured at all stations at which they were classified as regular (B) or usual (U) breeders (see above).

The ten years of data, 1992-2001, available for using the transient model allowed us to consider all possible combinations of both time-constant and time-dependent models for each of the three parameters estimated, for a total of eight models. We limited our consideration to models that produced estimates for both survival and recapture probability that were neither 0 nor 1. The goodness of fit of the models was tested by using a Pearson's goodness-of-fit test. Of those models that fit the data, the one that produced the lowest Akaike Information Criterion, correcting for dispersion of data and for use with smaller sample sizes relative to the number of parameters examined ($QAIC_C$), was chosen as the optimal model Burnham et al. 1995). Models showing $QAIC_C$'s within 2.0 $QAIC_C$ units of each other were considered effectively equivalent (Anderson and Burnham). The $QAIC_C$ was calculated by multiplying the log-likelihood for the given model by -2, adding two times the number of estimable parameters in the model, and providing corrections for overdispersed data and small sample sizes.

To assess the degree of annual variation in survival for each species, we calculated $\Delta QAIC_C$ as the difference between the completely time-constant model ($\varphi p \tau$) and the model with time-dependent survival but time-constant capture probability and proportion of residents ($\varphi_t p \tau$); thus, $\Delta QAIC_C$ was calculated as $QAIC_C(\varphi_t p \tau)$-$QAIC_C(\varphi p \tau)$, with lower (or more negative) $\Delta QAIC_C$ values indicating stronger interannual variation in survival.

E. Relationships of survival and productivity with body mass — In birds, both survival and productivity vary with body mass: on average, the larger the bird the higher the survival and the lower the productivity. Thus, in order to assess whether or not survival or productivity in a given species is higher or lower than expected, body mass needs to be accounted for. For analyses in this report, we have regressed both survival and productivity against body mass (log transformed to normalize the values), both for species throughout North America and for species at Denali, and compared individual survival and productivity rates with the regression lines produced by these fits. We used the log of mean body mass values given by Dunning (1993). In this way we could assess whether or not productivity or survival of a given species at Denali was as expected, lower than expected, or higher than expected based on body mass.

RESULTS

A total of 2,031.8 net-hours were accumulated at the six MAPS stations operated in Denali National Park in 2001 (Table 1). Data from 1,720.7 of these net-hours could be compared directly to 2000 data in a constant-effort manner.

Indices of Adult Population Size and Post-fledging Productivity

A. 2001 values — The 2001 capture summary of the numbers of newly-banded, unbanded, and recaptured birds is presented for each species and all species pooled at each of the six stations in Table 2. In 2001, Strangler Hill produced the greatest number of total captures (334), while Rock Creek produced the smallest (62). Mile Seven had the greatest species richness with 19 species, while species richness was poorest at Rock Creek, with 9 species.

In order to standardize the number of captures for the variability of mist-netting effort expended at the stations (due to unsuitable weather conditions and accidental net damage; see Table 1), we present the capture rates (per 600 net-hours) of individual adult and young birds as well as the proportion of young in the catch for each species and for all species pooled at each station in Table 3. These capture indices indicate that the total adult population size in 2001 was greatest at the Strangler Hill station, followed in descending order by Buhach Creek, Igloo Creek, Mile Seven, Permafrost, and Rock Creek, describing a pattern similar to that seen in previous years. The capture rate of young (Table 3) of all species pooled at each station in 2001 followed a somewhat different sequence than the capture rate of adults, being highest at Igloo Creek, followed by Strangler Hill, Permafrost, Mile Seven, Buhach Creek, and Rock Creek. Thus, the index of productivity at each station in 2001 (Table 3), as determined by the percentage of young in the catch, varied substantially at Denali, from 0.36 at Buhach Creek to 0.68 at Igloo Creek. The productivity index at Buhach Creek in 2001 was much lower than that at any other station.

Table 4 summarizes the banding results at all six 2001 Denali MAPS stations combined. Altogether, a total of 1,326 birds of 30 species were captured during the 2001 breeding season. Newly-banded birds comprised 72.2% of the total captures. Overall, Wilson's Warbler was the most frequently captured species, followed by White-crowned Sparrow, Orange-crowned Warbler, Common Redpoll, American Tree Sparrow, Dark-eyed Junco, Arctic Warbler, Fox Sparrow, Yellow-rumped Warbler, and Swainson's Thrush. The most abundant breeding species at the six Denali MAPS stations in 2001 (as determined by the number of adults captured per 600 net-hours), in decreasing order, were Wilson's Warbler, Common Redpoll, White-crowned Sparrow, Orange-crowned Warbler, Yellow-rumped Warbler, Arctic Warbler, Swainson's Thrush, Boreal Chickadee, Dark-eyed Junco, Alder Flycatcher, American Tree Sparrow, and Fox Sparrow. The following is a list of the common breeding species (captured at a rate of at least 6.0 adults per 600 net-hours), in decreasing order, at each station in 2001 (from Table 3):

Strangler Hill	**Buhach Creek**	**Igloo Creek**
Common Redpoll	Wilson's Warbler	Wilson's Warbler
Wilson's Warbler	Common Redpoll	Arctic Warbler
Orange-crowned Warbler	Orange-crowned Warbler	White-crowned Sparrow
Alder Flycatcher	American Tree Sparrow	Common Redpoll
Gray-cheeked Thrush	White-crowned Sparrow	Hermit Thrush
Fox Sparrow	Savannah Sparrow	Orange-crowned Warbler
White-crowned Sparrow		

Mile Seven	Permafrost	Rock Creek
Wilson's Warbler	White-crowned Sparrow	Swainson's Thrush
White-crowned Sparrow	Wilson's Warbler	Yellow-rumped Warbler
Yellow-rumped Warbler	Boreal Chickadee	Dark-eyed Junco
Dark-eyed Junco	Swainson's Thrush	
Boreal Chickadee	Yellow-rumped Warbler	
Orange-crowned Warbler		

The 2001 rankings were rather similar to those for 2000, suggesting that the composition of the breeding bird communities at Denali National Park tends to be relatively stable from year to year.

B. Comparisons between 2000 and 2001 — Constant-effort comparisons between 2000 and 2001 were undertaken at all six stations for numbers of adult birds captured (adult population size; Table 5), numbers of young birds captured (Table 6), and proportion of young in the catch (productivity; Table 7).

Adult population size for all species pooled for all stations combined increased by +18.0%, a substantial, but not statistically significant, increase (Table 5). Increases between 2000 and 2001 were recorded for 16 of 23 species, a proportion that was significantly greater than 0.50 (Table 5; $P = 0.047$). The overall adult population size for all species pooled increased at four of the six stations, by amounts ranging from +20.0% at Permafrost to +37.7% at Strangler Hill, but decreased at Buhach Creek (by -9.9%) and Rock Creek (by -4.3%). The proportion of increasing (or decreasing) species was not significantly greater than 0.50 at any station. A near-significant increase in the number of adults captured for all stations combined was recorded for Orange-crowned Warbler, while no significant or near-significant decreases were recorded for any species.

The number of young birds captured of all species pooled at all six stations combined also increased, by a significant +141.7% (Table 6). Increases were recorded for 20 of 25 species, a proportion highly significantly greater than 0.50. The number of young birds captured of all species pooled increased at all six stations, by amounts ranging from +10.3% at Buhach Creek to +369.7% at Igloo Creek. The proportion of increasing species was near-significantly or significantly greater than 0.50 at three of the six stations (Table 6). White-crowned Sparrow showed a highly significant increase in number of young captured across all stations, while Fox Sparrow showed a near-significant increase; no species showed a significant or near-significant decrease in number of young captured across stations.

Productivity (the proportion of young in the catch) showed a significant increase of +0.177 from 0.405 in 2000 to 0.583 in 2001 for all species pooled and all stations combined (Table 7). Increases were recorded for 16 of 25 species, a proportion not significantly greater than 0.50. Increases in productivity were observed at all six stations, ranging from an increase of +0.046 at Buhach Creek to +0.301 at Igloo Creek. Three species (Savannah, Fox, and White-crowned sparrows) showed near-significant or significant increases in productivity from 2000 to 2001 for all stations combined, whereas no species showed such decreases across stations.

Thus, both adult breeding populations and productivity showed increases in 2001 as compared with 2000 at Denali. For breeding populations, the non-significant increase in all species pooled, the significant proportion of increasing species overall, and the lack of significant increases among individual species indicates a moderate, species-wide but not station-wide increase through the area monitored by MAPS. Both number of young captured and productivity showed significant increases that appeared to be both species-wide and station-wide, although the increases at Mile Seven and, especially, Buhach Creek were relatively small. Overall, however, these increases in number of young and productivity were much more substantial than the increases in breeding populations.

C. Five- and ten-year trends in adult population size — "Chain" indices of adult population size are presented for study species (those with an average of at least six individual adults captured per year within the stations considered) and for all species pooled in Figures 1-3. For the sake of comparison we calculated chain indices in five ways: (1) five-year trend (1997-2001) at the four (long-running) eastern stations, Igloo Creek, Mile Seven, Permafrost, and Rock Creek (Fig. 1a); (2) the same five-year trend (1997-2001) at the two (short-running) western stations, Strangler Hill and Buhach Creek (Fig. 1b); (3) five-year trend (1992-1996) at the four eastern stations (Fig. 2; the two western stations were not operated in these years); (4) the full ten-year trend (1992-2001) at the four eastern stations (Fig. 3a); and (5) the same ten-year trend (1992-2001) using data from all six stations (Fig. 3b). Thus, we can compare five-year trends between eastern and western stations, the first five-year and second five-year trends at the eastern stations, and ten-year trends at the four long-running stations as compared to all six stations combined.

See Methods for an explanation of the calculations used to obtain the indices. We used the slope of the regression line for each species to calculate Annual Percentage Change (*APC*) of the population. *APC* along with the standard error of the slope (*SE*), the correlation coefficient (*r*), and the significance of the correlation (*P*) for each study species and all species pooled are included in Figures 1-3.

Adult population trends for 11 study species plus all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the five-year period 1997-2001 are shown in Figure 1a. Trends for three of the 11 species (Swainson's Thrush, Wilson's Warbler, and Dark-eyed Junco) were fairly stable (absolute $r < 0.5$ and *SE* of the slope ≤ 0.140 for a five-year population trend). The trend for Fox Sparrow was flat (absolute $r < 0.5$) but showed wide interannual fluctuation (*SE* of the slope > 0.140). Trends for two species (Boreal Chickadee and Yellow-rumped Warbler) showed substantial ($r > 0.5$) increases; that of the chickadee was highly significant. The remaining five species (Arctic Warbler, Orange-crowned Warbler, American Tree Sparrow, White-crowned Sparrow, and Common Redpoll), as well as all species pooled, showed substantial ($r < -0.5$) declines; the declines for Arctic Warbler and American Tree Sparrow were significant. Overall, as indicated by *APC* values, trends for eight species and all species pooled were negative whereas trends for only three species were positive.

Adult population trends for nine study species plus all species pooled at the two western stations (Strangler Hill and Buhach Creek) during the five-year period 1997-2001 are shown in Figure 1b.

Trends for six of the nine species (Alder Flycatcher, Arctic Warbler, Gray-cheeked Thrush, Orange-crowned Warbler, American Tree Sparrow, and Common Redpoll) were fairly stable (absolute $r < 0.5$ and SE of the slope ≤ 0.140 for a five-year population trend). No species showed wide fluctuations (absolute $r \leq 0.5$ and SE of the slope > 0.140). Trends for one species, Fox Sparrow, showed a substantial ($r \geq 0.5$) but non-significant increase. The remaining two species (Wilson's Warbler and White-crowned Sparrow), as well as all species pooled, showed substantial ($r < -0.5$) declines; the decline for Wilson's Warbler was significant and that for all species pooled was nearly significant. Overall, as indicated by *APC* values, trends for seven species and all species pooled were negative whereas trends for only two species were positive.

Among the seven species found at both the eastern and western stations, the five-year (1997-2001) adult population trends of all but two (Fox Sparrow and Common Redpoll) were in the same direction in both areas. The difference in Fox Sparrow reflects either a differing population dynamic between the two areas or the fact that data were minimal for this species at the eastern stations (and thus this trend may not be accurate), whereas that of Common Redpoll the difference is solely due to results of the 2001 season: numbers of adults decreased between 2000 and 2001 at the four eastern stations but increased between 2000 and 2001 at the two western stations, resulting in a substantial decrease at the former and a non-substantial increase at the latter. Among the remaining five species, the magnitude of the trends (declines in all five cases) varied for four species: the declines were substantial at the eastern stations but not the western stations for Arctic Warbler, Orange-crowned Warbler, and American Tree Sparrow, whereas the declines of Wilson's Warbler were substantial at the western stations but not the eastern stations. Of these, only those of Wilson's Warbler and American Tree Sparrow likely represent true biological differences, and both can be explained by variation in the values of just one or two (of the five) years of data. For Wilson's Warbler, the difference in trends is related to higher *vs* lower adult populations in 1998 as compared to 1997 at the four eastern *vs* the two western stations; all other constant effort changes were similar in the two areas. Likewise, for American Tree Sparrow, the difference in trends was related to higher *vs* lower adult populations in 2000 and 2001 at the western *vs* the eastern stations; again, all other constant effort changes were similar in the two areas.

Adult population trends for the 11 study species and all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the first five-year period (1992-1996) are shown in Figure 2. Trends for five of the 11 species (Arctic Warbler, Swainson's Thrush, American Tree Sparrow, White-crowned Sparrow, and Dark-eyed Junco), as well as all species pooled, were fairly stable (absolute $r \leq 0.5$ and SE of the slope ≤ 0.140 for a five-year population trend). Trends for four species (Boreal Chickadee, Orange-crowned, Yellow-rumped, and Wilson's warblers) showed substantial ($r > 0.5$) increases, with that of Wilson's Warbler being nearly significant. The remaining two species (Fox Sparrow and Common Redpoll) showed substantial ($r < -0.5$) and significant declines. Overall, as indicated by *APC* values, trends for six species and all species pooled were positive whereas trends for five species were negative.

Comparison of the first five-year period (1992-1996; Fig. 2) with the second five-year period (1997-2001; Fig. 1a) at the four eastern stations indicates that five species and all species pooled reversed the direction of their adult population trend during these two periods, whereas six species maintained the same trend direction. Four of the five species that reversed trends (Orange-crowned Warbler, Wilson's Warbler, American Tree Sparrow, and Dark-eyed Junco), as well as all species pooled, had positive trends in 1992-1996 and negative trends in 1997-2001. The only species that had a negative trend in 1992-1996 but a positive trend in 1997-2001 was Swainson's Thrush. Among the six species that maintained the same trend direction, two (Boreal Chickadee and Yellow-rumped Warbler) were positive and four (Arctic Warbler, Fox Sparrow, White-crowned Sparrow, and Common Redpoll) were negative. A comparison of r values indicates that trends were more negative (or less positive) during 1997-2001 than in 1992-1996 for seven of eleven species plus all species pooled, and less negative (or more positive) for four species (Boreal Chickadee, Swainson's Thrush, Fox Sparrow, and Common Redpoll).

Adult population trends for the 11 study species and for all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the entire ten-year period (1992-2001) are shown in Figure 3a. Trends for four of the 11 species (Fox Sparrow, White-crowned Sparrow, Dark-eyed Junco, and Common Redpoll), as well as all species pooled, were fairly stable (absolute $r \leq 0.5$ and *SE* of the slope ≤ 0.035 for a ten-year population trend). Trends for two species, Orange-crowned and Wilson's warblers, were flat (absolute $r \leq 0.5$) but showed wide annual fluctuation (*SE* of the slope > 0.035). Trends for two species (Boreal Chickadee and Yellow-rumped Warbler) showed substantial ($r > 0.5$) and significant or highly significant increases. The remaining three species (Arctic Warbler, Swainson's Thrush, and American Tree Sparrow) showed substantial ($r < -0.5$) and significant declines. Overall, as indicated by *APC* values, trends for seven species and all species pooled were negative whereas trends for four species were positive.

Finally, adult population trends for the same 11 study species and for all species pooled during the entire ten-year period (1992-2001) for all six stations (the four eastern stations during the entire period and the two western stations during 1997-2001 only) are shown in Figure 3b. A comparison of Figures 3a and 3b indicate that no differences in direction and few differences in magnitude or degree of fluctuation of trends resulted from adding the two eastern stations to the second half of the ten-year period. The only differences in magnitude noted involved the decline in Wilson's Warbler (which became substantial and nearly significant when the western stations were added, suggesting a greater decline in this species at the western stations than at the eastern stations, as indicated above), and the decline in American Tree Sparrow (which became non-substantial when the western stations were added, suggesting a greater decline of this species at the eastern stations than at the western stations, as also indicated above). The decline in all species pooled also became substantial and nearly significant when the western stations were added, indicating overall greater declines of landbirds at the western than at the eastern stations of Denali, although this was almost entirely caused by declines in Wilson's Warbler.

As noted in previous reports, between 1992 and 1999, adult population sizes of all species pooled showed an alternating pattern, decreasing in odd-numbered years and increasing in even-numbered years (Fig. 3). This pattern, however, was broken in 2000 when a second consecutive decrease was recorded. This decrease was likely related to the poor productivity in 1999, a year in which productivity was expected to be higher. That populations increased again in 2001 indicates the possible resumption of this two-year dynamic.

D. Five- and ten-year trends in productivity — "Chain" indices of productivity are presented for study species and for all species pooled in Figures 4-6. We calculated chain indices in the same five ways as were calculated for adult population sizes (see above), allowing comparison of five-year trends between eastern and western stations, the first and second five-year trends at the eastern stations, and the ten-year trends at the four long-running stations as compared to all six stations combined. The slope of the regression line for each species (an estimate of the productivity trend, *PrT)* along with the standard error (*SE*) of the slope (in parentheses), the correlation coefficient (*r)*, and the significance of the correlation(*P*) are presented for each study species and all species pooled in Figures 4-6.

Productivity trends for 11 species plus all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the five-year period 1997-2001 are shown in Figure 4a. Trends for five of the 11 species (Yellow-rumped Warbler, Wilson's Warbler, White-crowned Sparrow, Dark-eyed Junco, and Common Redpoll), as well as all species pooled, were fairly stable (absolute $r < 0.5$ and *SE* of the slope < 0.080 for a five-year productivity trend). The trend for Fox Sparrow was flat (absolute $r < 0.5$) but showed wide interannual fluctuation (*SE* of the slope > 0.080). Trends for four species (Arctic Warbler, Swainson's Thrush, Orange-crowned Warbler, and American Tree Sparrow) showed substantial ($r > 0.5$) increases, that of Arctic Warbler being nearly significant. The remaining species, Boreal Chickadee, showed a substantial ($r < -0.5$) but non-significant decline. Overall, as indicated by *PrT* values, trends for seven species and all species pooled were positive whereas trends for four species were negative.

Productivity trends for nine species plus all species pooled at the two western stations (Strangler Hill and Buhach Creek) during the five-year period 1997-2001 are shown in Figure 4b. The trend for Arctic Warbler could not be determined because no young birds were caught at these two stations during the five-year period. Trends for four of the remaining eight species (Orange-crowned Warbler, Fox Sparrow, White-crowned Sparrow, and Common Redpoll), as well as all species pooled, were fairly stable (absolute $r < 0.5$ and *SE* of the slope < 0.080 for a five-year productivity trend). The trend for American Tree Sparrow was flat (absolute $r < 0.5$) but showed wide interannual fluctuation (*SE* of the slope > 0.080). Trends for two species (Gray-cheeked Thrush and Wilson's Warbler) showed substantial ($r > 0.5$) but non-significant increases. The remaining species, Alder Flycatcher, showed a substantial ($r < -0.5$) but non-significant decline. Overall, as indicated by *PrT* values, trends for five species and all species pooled were positive whereas trends for three species were negative.

Among the six species found at both the eastern and western stations for which productivity trends could be estimated, the five-year (1997-2001) trends of only two species (Orange-crowned Warbler and White-crowned Sparrow) were in the same direction in both areas. Although Orange-crowned Warbler showed a substantial trend at the eastern stations but non-substantial trend at the western stations, the difference in the magnitude of these trends was small and unlikely of biological importance. In contrast, the trends of four species were in opposite directions in the two groups. Two of the four species showing opposite productivity trends (Fox Sparrow and Common Redpoll) had fairly flat trends (absolute $r < 0.5$) in both areas, indicating that the observed difference was not severe. The trend for Wilson's Warbler was negative at the four eastern stations but substantially positive at the two western stations, and the trend for American Tree Sparrow was substantially positive at the eastern stations but negative at the western stations, suggesting differing population dynamics between the two areas in these two species. Interestingly, however, the productivity trends for all species pooled were very similar (non-substantially positive) in both areas, despite the differences noted among individual species.

Productivity trends for the 11 study species and all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the first five-year period (1992-1996) are shown in Figure 5. Trends for seven of the 11 species, as well as all species pooled, were fairly stable (absolute $r \le 0.5$ and *SE* of the slope ≤ 0.080 for a five-year productivity trend). The trends for Boreal Chickadee and Fox Sparrow were flat (absolute $r \le 0.5$) but showed wide interannual fluctuation (*SE* of the slope > 0.080). The trends for Common Redpoll showed a substantial ($r > 0.5$) but non-significant increase. The remaining species, Wilson's Warbler, showed a substantial ($r < -0.5$) and significant decline. Overall, as indicated by *APC* values, productivity trends for six species and all species pooled were negative, whereas trends for five species were positive.

Comparison of the first five-year period (1992-1996; Fig. 5) with the second five-year period (1997-2001; Fig. 4a) at the four eastern stations indicates that four species and all species pooled reversed the direction of their productivity trend during these two periods, whereas seven species maintained the same trend direction. Three of the four species that reversed productivity trends (Orange-crowned Warbler, Yellow-rumped Warbler, and American Tree Sparrow) and all species pooled had negative trends in 1992-1996 and positive trends in 1997-2001. Boreal Chickadee had a positive trend in 1992-1996 but a negative trend in 1997-2001. Among the seven species that maintained the same trend direction, four (Arctic Warbler, Swainson's Thrush, White-crowned Sparrow, and Common Redpoll) were positive and two (Wilson's Warbler, Fox Sparrow, and Dark-eyed Junco) were negative. Interestingly, although the trend for all species pooled changed sign between the two sets of years, the magnitude of the actual difference was rather small. A comparison of *r* values indicates that productivity trends were more positive (or less negative) during 1997-2001 than during 1992-1996 for nine of eleven species plus all species pooled. The reverse was true for only Boreal Chickadee and Common Redpoll.

Productivity trends for the 11 study species and all species pooled at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) during the entire ten-year period (1992-2001) are shown in Figure 6a. Trends for seven of the 11 species (Orange-crowned, Yellow-rumped, and Wilson's warblers, American Tree and White-crowned sparrows, Dark-eyed Junco, and Common Redpoll) as well as all species pooled, were fairly stable (absolute $r \le 0.5$ and *SE* of the slope < 0.020 for a ten-year productivity trend). The trend for Fox Sparrow was flat (absolute $r \le 0.5$) but showed wide interannual fluctuation (*SE* of the slope > 0.020).

Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial ($r > 0.5$) and significant or highly significant increases. The remaining species, Boreal Chickadee, showed a substantial ($r < -0.5$) but non-significant decline in productivity. Overall, as indicated by *PrT* values, productivity trends for six species and all species pooled were positive whereas productivity trends for five species were negative.

Finally, productivity trends for these same 11 species and all species pooled during the entire ten-year period (1992-2001) for all six stations (the four eastern stations during the entire period and the two western stations during 1997-2001 only) are shown in Figure 6b. A comparison of Figures 6a and 6b indicate that few differences in direction, magnitude, or degree of fluctuation of productivity trends resulted from adding the two eastern stations to the second half of the ten-year period. The only differences in direction noted involved two species with essentially stable productivity trends: the non-substantial decrease in Wilson's Warbler productivity became non-substantially positive when the western stations were added, suggesting a greater decline in the productivity of this species at the eastern stations than at the western stations, as indicated above), and the non-substantial increase in American Tree Sparrow became non-substantially negative when the western stations were added, suggesting greater decline in the productivity of this species at the western stations than at the eastern stations, also as indicated above). Interestingly, these two changes involved the same species that varied in magnitude of population trend (Figs. 3a and 3b) when the same comparison was made, only the changes of the trends were in the opposite directions. The only change in magnitude involved Orange-crowned Warbler, in which a stable (but positive) productivity trend became substantially (but non-significantly) positive when the western stations were added, indicating a more positive trend at the western than at the eastern stations. The increase in productivity of all species pooled became nearly substantial when the western stations were added, indicating greater increases of landbird productivity at the western than at the eastern stations of Denali. This is also opposite to the changes observed in population size (Figs. 3a and 3b).

Again, as noted in previous reports, both numbers of young captured and productivity for all species pooled showed an alternating cycle of declines and increases through 1997, decreasing in even-numbered years and increasing in odd-numbered years, the opposite of the consistent alternating cycle noted for adults captured. But this cycle was disrupted between 1997 and 2001, when all three parameters showed changes in the same direction, increases in 1998, decreases in 1999 and 2000, and increases in 2001.

E. Five- and ten-year mean population size and productivity values — Table 8 gives mean annual numbers of individual adults captured (an index of adult population size), numbers of young captured, and proportions of young in the catch (an index of productivity) during the five-year period 1997-2001 for each of the six stations (Table 8a) and during the ten-year period 1992-2001 for each of the four long-running stations operated during that entire ten-year period (Table 8b). Examination of all-species-pooled values in Table 8a indicates that adult population sizes were substantially higher at the three western, scrubby and riparian stations (Strangler Hill, Buhach Creek, and Igloo Creek; mean 192.8 adults captured) than at the three eastern, spruce-forested stations (Mile Seven, Permafrost, and Rock Creek; mean 84.6 adults captured). By contrast, productivity values averaged somewhat lower at the three western (mean 0.463) than at the three eastern stations (mean 0.050). Adult population sizes showed a higher five-year (Table 8a) than ten-year (Table 8b) mean at each of the four long-running stations, indicating larger adult population sizes during the second half of the study. Similarly, the five-year mean for young captured was higher than the ten-year mean at each of the four stations. Productivity values varied, however, showing very slightly higher five-year than ten-year means at Igloo Creek and Mile Seven and the opposite at Permafrost and Rock Creek. Overall, the five-year mean productivity value was 0.48 and the ten-year value was a very similar 0.49. This suggests that reproductive output was higher during the second half of the study due to greater numbers of breeding adults with a similar level of productivity.

F. Relationship between annual change in productivity and annual change in adult captures the following year — To see whether or not productivity has had a direct effect on adult population size the following year, we examined the relationship between constant-effort changes in productivity during one between-year comparison (see Figure 6) with changes in adult captures during the following between-year comparison (see Figure 3), for the eleven study species and all species pooled at Denali (Figure 7). The slopes of these correlations, hereafter termed "productivity/population correlations" along with their standard errors (*SE*, in parentheses), the correlation coefficient (*r*), and the significance of the correlation (*P*) for each of the 11 study species and all species pooled are included in Figure 7. For comparison, we include data from just the four long-running stations (Fig. 7a) and data from all six stations combined (Fig. 7b).

Using data from just the four long-running stations (Fig. 7a), eight of the eleven species (all but Swainson's Thrush, Fox Sparrow, and Common Redpoll), as well as all species pooled, showed positive productivity/population correlations, i.e., changes in productivity one year resulted in corresponding changes in population size the following year. These correlations were relatively weak (absolute $r < 0.5$) for six of these eight species (Boreal Chickadee, Arctic, Orange-crowned, and Wilson's warblers, American Tree Sparrow, and Dark-eyed Junco) as well as for all three species showing negative correlations. The remaining two species (Yellow-rumped Warbler and White-crowned Sparrow), as well as all species pooled, showed substantial ($r > 0.5$) and significant productivity/population correlations. Thus, overall, there was a moderately strong relationship between these two parameters, supporting the concept that, for most species, changes in productivity one year bring about corresponding changes in population size the next. For many species and years (especially early in the 10-year study period), this relationship occurred in an alternating (positive and negative) pattern reflecting a density-dependent effect, as mentioned above.

A comparison of Tables 7a and 7b indicates few differences when the five-years of data (1997-2001) from the two western stations were included in the regressions. For only one species (Swainson's Thrush) did the direction of the slope change (from weakly negative to weakly positive), resulting in nine positive slopes and only two negative slopes. Changes in magnitude and/or significance were recorded for two species after addition of data from the two western stations: the weak but positive correlation became substantial and significantly positive for Wilson's Warbler, and the weak but negative correlation became substantial and significantly negative for Fox Sparrow. The substantial positive correlation for all species pooled also changed from significant to nearly significant after addition of the two stations.

Productivity as Correlated with Southern Oscillation Index

To assess the degree to which global climate patterns may affect landbird productivity, we compared annual productivity values (mean value for all species pooled from the four long-running stations) with the mean monthly Southern Oscillation Index (SOI) for January-December of each year. We found a non-significant negative relationship for all species pooled between productivity at Denali and SOI (Figure 8**A**): in general, the more La-Niña-like the conditions the lower the productivity. A comparison between SOI and year during the ten-year period showed a significant positive increase (Figure 8**B**), in part due to a strong El Niño early in the study period (1992-1993) and a strong La Niña late in the period (1999-2000). Figure 8**C** combines these two correlations and shows expected productivity values (according to the correlation depicted in Figure 8**A**) as a function of year (according to the annual SOI indices). We found that, given changes in SOI between 1992 and 2001, we would expect to see a slight annual productivity decline at Denali for all species pooled of -0.006**.** This compares to the slight actual increase in productivity at Denali for all species pooled of +0.004 (Fig. 8**D**; see also Fig. 6a).

Figures 9 and 10 show relationships of productivity with SOI for two species showing opposite productivity trends (see Fig. 6a), Swainson's Thrush and Wilson's Warbler, respectively. As expected, these two species show opposite effects of SOI: for Swainson's Thrush, the effect was positive and highly significant (Fig. 9**A**), whereas for Wilson's Warbler it was negative and significant (Fig. 10**A**). Thus, when the positive trend between SOI and year (Figs. 9**B** and 10**B**) was accounted for, we expected the productivity trend to be positive for Swainson's Thrush (Fig. 9**C**) and negative for Wilson's Warbler (Fig. 10**C**), in both cases by a rate of 0.021 per year. This compared rather favorably with the actual increase in productivity of Swainson's Thrush of +0.046 per year (Fig. 9**D**), and very favorably with the actual decrease in Wilson's Warbler of -0.020% per year (Fig. 10**D**).

Estimates of Adult Survivorship

Estimates of adult survival and recapture probability could be obtained for ten of the eleven study species breeding in Denali National Park (Tables 9 and 10). Estimates of survival probability could not be obtained for Common Redpoll, because insufficient numbers of individual adults banded in 1992-2000 were recaptured in subsequent years. For comparison, we modeled survival in two ways: first, using ten years (1992-2001) of data from just the four long-running eastern stations (Tables 9a and 10a), and then with the addition of five years (1997-2001) of data from the two western stations (Tables 9b and 10b).

Because of the existence of floaters, failed breeders, and dispersing adults, transient models, which calculate the proportion of residents in the population, produce less biased estimates of adult survivorship than do non-transient models, provided there are sufficient data (four years or more) to estimate a proportion of residents less than 1.0. Thus, we only present the results of transient models. Table 9a indicates that using data only from the four long-running stations, the time-constant transient model (*φpτ*) was selected over all time-dependent transient models (by having a $QAIC_C$ that was at least 2.0 $QAIC_C$ units lower than any other model) for nine of the ten species. For White-crowned Sparrow the model showing time-dependence in capture probability was equivalent to (within 2.0 $QAIC_C$ units of) the time-constant model. $\Delta QAIC_C$ (see Methods), a measure of the degree to which adult survival varied with time over the ten-year period, ranged from 4.7 in Arctic Warbler (indicating considerable time-dependence in survival) to 14.7 and 14.8 in Fox Sparrow and Yellow-rumped Warbler, respectively (indicating very little time dependence in survival), and averaged 11.4 for the ten species.

Table 10a presents the maximum-likelihood estimates of annual adult survival probability, recapture probability, and the proportion of residents for the time-constant models selected in Table 9a (data from the four long-running stations only), for each study species. The estimates for survival probability ranged from a low of 0.355 for Arctic Warbler to a high of 0.591 for Boreal Chickadee, and averaged 0.475. Time-constant estimates of recapture probability varied from 0.220 for Yellow-rumped Warbler to 0.625 for American Tree Sparrow with a mean of 0.440. The time-constant estimates for the proportion of residents among newly captured adults ranged from 0.352 for Wilson's Warbler to 1.000 for Boreal Chickadee and averaged 0.548. The time-dependent model for White-crowned Sparrow indicated that capture probability varied from a low of 0.158 in 1995 to highs of 0.688 in 2001 and 0.660 in 1996; values for all other years were between 0.330 and 0.510.

When data from all six stations were included (Tables 9b and 10b), survival estimates were obtained for one additional species, Gray-cheeked Thrush, for which the time-constant model was also selected (Table 9b). For Gray-cheeked Thrush, $\Delta QAIC_C$ was found to be 35.9, adult survival was estimated at 0.639, capture probability was 0.784, and proportion of residents was 0.641 (Table 10b).

For the remaining ten species, comparison of models using data from only the four long-running stations (Tables 9a and 10a) with those using data from all six stations combined (Tables 9b and 10b) revealed very similar results. In both cases the only time-dependent model selected involved time dependence in recapture probability for White-crowned Sparrow. $\Delta QAIC_C$ values were also similar, ranging from 4.2 to 14.8 (mean 10.9) using data from all six stations, as compared with 4.7 to 14.8 (mean 11.4) using data ONLY from the four long-running stations. The $\Delta QAIC_C$ value for only one species, Wilson's Warbler, differed by more than 1.1 units, being 12.6 at the four stations and 9.9 when all six stations were combined. When all six stations were combined, mean survival was 0.475 (compared with 0.475 for the four long-running stations only), mean capture probability was 0.424 (compared to 0.440), and mean proportion of residents was 0.564 (compared to 0.548). No species showed a difference of more than 2.3% (in Swainson's Thrush) for survival, more than 17.9% (in American Tree Sparrow) for capture probability, or more than 36.5% (in Fox Sparrow) for proportion of residents. Finally, results of the time-dependent models for capture probability in White-crowned Sparrow were also similar when the two western stations were added, with 1995, 1999, and 2000 having the three lowest capture-probability values and 1993, 1996, and 2001 having the three highest values using either data set.

Productivity Indices and Adult Survival Rates as a Function of Body Mass

Figure 11 shows productivity indices and adult survival rate estimates recorded at Denali National Park and throughout North America as a function of mean body mass (log transformed) for ten study species using data from all six stations combined. The purpose of this figure is to determine which species at Denali show higher or lower productivity or survival than might be expected given their body mass. Two regression lines are presented, one (solid) for all ten Denali species and one (dashed) using data from 210 (productivity) and 89 (survival) species in North America for which these parameters could be estimated using MAPS data from stations distributed across the continent. Species with larger body mass generally show lower productivity and higher survival than species with smaller body mass, which explains the negative and positive slopes, respectively, of the regression lines based on all North American species.

For productivity, the negative regression line based on data from the ten species at Denali was flatter than the line based on data from North America as a whole. We believe that this may be because of the very low productivity of Denali's Arctic Warbler population. Mean productivity, however, was higher at Denali than in North America as a whole, reflecting a continent-wide trend of higher productivity at more northerly latitudes, presumably due to more abundant food resources during the summer and lower brood parasitism and nest predation rates. For survival, the two lines were similar in both slope and mean value, indicating that survival rates (by body mass) are similar at Denali to those found throughout North America.

Five of the ten species shown in Figure 11 (in lowercase letters) had generally stable population trends over the ten year at Denali National Park. Interestingly these species all showed expected survival rates and expected or higher than expected productivity indices (Table 11). Both of the species with increasing population trends, Boreal Chickadee and Yellow-rumped Warbler (in regular uppercase letters), had higher-than-expected survival rates and expected or lower than expected productivity. Of the three species with declining populations (shown in bold uppercase letters), Arctic Warbler appeared to have lower-than-expected adult survival and productivity, Wilson's Warbler appeared to have lower-than-expected adult survival but expected or higher-than-expected productivity, and Swainson's Thrush appeared to have lower-than-expected productivity and expected or higher-than-expected survival.

DISCUSSION OF RESULTS

Overall, population sizes of adult birds tended to decrease slightly at Denali National Park during the ten years 1992-2001. Population trends, for example, were negative for seven of eleven study species and for all species pooled. The negative trend for all species pooled was a substantial and nearly significant -2.1% per year when data from all six stations were combined. As compared with 2000, however, adult populations of all species pooled in 2001 showed a substantial but non-significant increase of 18.0%.

Despite the slightly declining overall trend in all species pooled, several species showed pronounced ten-year increases or decreases in their breeding populations. These include significant and highly significant increases, respectively, in Boreal Chickadee and Yellow-rumped Warbler, significant declines in Arctic Warbler and Swainson's Thrush, a substantial and nearly significant decline in Wilson's Warbler when data from all six stations were pooled, and a significant decline in American Tree Sparrow over the four eastern stations. In order to investigate possible causes for these population trends and those of the other study species at Denali, we: (1) compared 1997-2001 population trends between the eastern and western stations and, for the eastern stations, between 1992-1996 and 1997-2000; (2) made similar comparisons of productivity trends; (3) examined productivity/population correlations and relationships between productivity and the Southern Oscillation Index; and (4) compared actual productivity indices and adult survival rate estimates at Denali National Park with expected values based on relationships of these parameters with body mass both at Denali National Park and across all of North America.

Among the seven species found at both the eastern and western stations, meaningful differences in the five-year (1997-2001) population trends were noted for only two species, and both of these differences could be explained by differences in the annual population change for just one or two (of the five) years of data. Because of these differences, however, the population decline of Wilson's Warbler appeared to be more substantial at the two western stations (Strangler Hill and Buhach Creek) than at the four eastern stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek), while the reverse seemed to be the case with the population decline of American Tree Sparrow. Comparison of the first five-year period (1992-1996) with the second five-year period (1997-2001) at the four eastern stations indicated that trends were more negative (or less positive) during 1997-2001 than during 1992-1996 for seven of eleven species plus all species pooled. This could be cause for concern although, interestingly, a comparison of five-year and ten-year mean values indicates a greater reproductive output during the latter half of the study period.

Productivity trends were fairly stable for seven of eleven species as well as all species pooled, although productivity fluctuated widely for Fox Sparrow. Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial and significant increases, a third species (Orange-crowed Warbler) showed a substantial but non-significant increase, at least when data from all six stations were pooled, and a fourth species (Boreal Chickadee) showed a substantial but non-significant decline in productivity. Among the six species and all species pooled found at both the eastern and western stations for which five-year (1997-2001) productivity trends could be estimated, substantial differences were noted for only two species: the trend for Wilson's Warbler was negative at the four eastern stations but substantially positive at the two western stations, and the trend for American Tree Sparrow was substantially positive at the eastern stations but negative at the western stations. Comparison of the first five-year period with the second five-year period at the four eastern stations indicates that productivity trends were more positive during 1997-2001 than in 1992-1996 for nine of eleven species plus all species pooled. For many species and for all species pooled, productivity showed a substantial and significant increase between 2000 and 2001 (+0.177 for all species pooled), resulting in a change from one of the lowest productivity values recorded for all species pooled during the ten-year period in 2000 to the highest value recorded for all species pooled in 2001. This very high productivity value in 2001 represent an encouraging turnaround in productivity from recent years, and caused ten-year (1992-2001) productivity trends in several species to be positive as compared with negative nine-year (1992-2000) trends for those same species (see last year's report).

A good measure of the effect of productivity on population size is the relationship between changes in productivity one year with changes in adult population size the following year, the "productivity/population correlation." Nine of the eleven species (all but Fox Sparrow and Common Redpoll), as well as all species pooled, showed positive productivity/population correlations when data from all six stations were pooled. The positive correlations were significant or near significant for Yellow-rumped and Wilson's warblers and White-crowned Sparrow, as well as for all species pooled. Thus, overall, there was a moderately strong relationship between these two parameters, supporting the concept that changes in productivity one year bring about corresponding changes in population size the next.

From 1992 through 1998, the positive productivity/population correlation was manifest by an alternating cycle of declines and increases, with productivity decreasing in even-numbered years and increasing in odd-numbered years (Figure 6a), followed by the same pattern of decreases and increases in numbers of adults captured the following year (Figure 3a). This alternating, two-year population dynamic has been noted at other MAPS stations and we believe it relates to density-dependent effects on productivity and recruitment along with lower productivity of first-time breeders. Larger populations in a given year show poorer productivity due to more competition and a greater proportion of inexperienced, first-time breeders. This poor productivity then results in decreased recruitment and fewer breeding birds the following year, which in turn have higher productivity due to less competition and a higher proportion of experienced (two-year-old or older) breeders. This dynamic was clearly in effect during 1992-1998, but was disrupted at Denali during the 1999-2001 seasons, when both population size and productivity showed changes in the same direction (negative during the 1998-1999 and 1999-2000 comparisons, and positive during the 2000-2001 comparison; Figs. 3a and 6a).

Similar disruptions of this alternating cycle at other MAPS stations have appeared to be related to unusually favorable or unfavorable weather, and it is possible that the severe La Niña event of 1999-2000 caused this disruption. To examine the possibility that global climate patterns can affect productivity at Denali, we compared annual productivity values with mean monthly SOI values and found an overall negative relationship between productivity at Denali and SOI: productivity for all species pooled was higher during El Niño than during La Niña conditions. Thus it is likely that the severe La Niña event of 1999-2000, resulting in the highest SOI values during the ten-year period, caused productivity to be lower than expected and disrupted the density-dependent effect. SOI during 2001 was closer to the ten-year mean for this value, and productivity responded by increasing substantially. This may signal the return to the density-dependent dynamic until the next severe La Niña or El Niño event. The dramatic increase in productivity in 2001 also accounts for the discrepancy between productivity trend as predicted by the effects of SOI (-0.006 per year) with that actually recorded at Denali (+0.004 per year). Similar analyses were performed for two individual species showing opposite productivity trends, Swainson's Thrush (positive) and Wilson's Warbler (negative). Productivity for both species was significantly or highly significantly related to SOI; the relationship was positive for Swainson's Thrush and negative for Wilson's Warbler. In both cases the predicted productivity trends (+0.021 and -0.021, respectively) were similar to the actual productivity trends (+0.046 and -0.020), with the actual productivity trend for Swainson's Thrush being somewhat higher than the predicted trend.

We have recently completed analyses using 1992-2000 MAPS data that show how global climate patterns affect landbird productivity in Pacific Northwest national forests (Nott et al. in press). For those analysis, we included other global climate indices such as the Equatorial Southern Precipitation Index (ESPI, another measure of La Niña and El Niño events) and the North Atlantic Oscillation (NAO). Those analyses showed that the El Niño/Southern Oscillation had a strong effect (higher productivity during El Niño conditions) on species wintering in or migrating through western Mexico, but had much smaller effects on temperate-wintering species. In both groups of species, however, increased productivity seems to be caused by conditions on the wintering grounds or migration route rather than on the breeding grounds. This may explain why Denali's Wilson's Warblers (which winter in Mexico and Central America) have such a strong negative relationship between productivity and SOI, while temperate-wintering Denali species generally show much weaker negative relationships between productivity and SOI. Other researchers (Sillett et al. 2000) have documented the opposite effect (lower productivity during El Niño conditions) on species wintering in the West Indies. Swainson's Thrush is unique among the 11 Denali study species for which we have ten years of data in that it migrates east of the Rocky Mountains and presumably across the Gulf of Mexico to reach its wintering grounds in South America. The fact that its productivity shows a significant positive relationship with SOI, suggests that it may be influenced by weather events in a similar manner to species wintering in the West Indies. Additional years of productivity data on Denali's Alder Flycatchers and Gray-cheeked Thrushes (for which we now have five years of data from the two western stations) could shed additional light on this possibility, because they both also winter in South America. Further pursuing this line of enquiry, it would be desirable to obtain data on Denali's Blackpoll Warblers, as they also winter in South America and undergo a trans-Atlantic migration to reach their wintering grounds. We currently capture only about five individuals of this species per year (not enough to obtain reliable indices or estimates), mostly at Mile Seven, but with a few also at Permafrost and Strangler Hill.

It is also possible that the North Atlantic Oscillation might affect productivity of species breeding in Denali, as we have shown that it has a strong effect on productivity of temperate wintering species in the Pacific Northwest (Nott et al. In press). Yet another index, the Pacific Decadal Oscillation (PDO), measures a different Pacific Ocean climate cycle that shifts every 25 years. This cycle underwent a major shift between 1999 and 2001, which might also explain the higher-than-expected productivity observed in 2001. When 15 years of data have been collected, we plan to model productivity and survivorship as a function of SOI, ESPI, NAO, PDO, and other global climate cycles to more fully understand how various climate cycles and the weather that they produce affect the vital rates of the study species at Denali National Park.

We have now found that, with ten years of data, reasonably precise estimates of adult survival probabilities using the transient model could be obtained for ten study species breeding in Denali National Park. The mean precision of survival-rate estimates for nine species using ten years of data (mean CV=17.1%; Table 10a; and mean CV=16.1% using data from all six stations, Table 10b) was improved over that from nine years (mean CV=17.8%), and notably improved over that from eight (mean CV=23.8%), seven (mean CV=26.5%), and six years of data (mean CV=30.4%), suggesting that maximum precision may not be obtained until 12 or more years of data are available from the six stations in the Park. This is in agreement with simulations completed as part of an evaluation of the statistical properties of MAPS data (Rosenberg et al. 1996, 1999). As we accumulate more years of data at Denali, the transient model will provide increasingly precise estimates of adult survival rates, particularly for those species (e.g., Arctic, Orange-crowned, and Wilson's warblers) that are long-distance migrants and/or that have transient summer populations in Alaska. With more years of data, relatively minor temporal effects on survival probabilities may also become more apparent, although it is likely that up to twenty years of data will be necessary to determine actual temporal trends in adult survivorship.

With a few exceptions, the addition of data from 1997-2001 from the two western stations to the entire ten-year's of data (1992-2001) from the four eastern stations had only minimal effects on population trends, productivity trends, productivity/population correlations, or adult survival-rate estimates. This provides evidence that the population dynamics of Denali's landbirds are relatively uniform over the entire road corridor of the Park. Therefore, for the ensuing discussion we used data from all six stations combined. Based on the lack of substantial variation found in analyses reported here, we will likely simplify future reports by only examining the results from all six stations combined.

To more fully evaluate what parameters may be driving the population trends of ten study species at Denali National Park, we included all available information on each species, including relationships of productivity and survival as a function of body mass, to assess whether or not productivity and/or survival was as expected, lower than expected, or higher than expected. Common Redpoll was excluded from these analyses because survival rates could not be obtained from mark-recapture models due to the species' lack of site-fidelity. Five of the ten species (Orange-crowned Warbler, American Tree Sparrow, Fox Sparrow, White-crowned Sparrow, and Dark-eyed Junco) showed relatively stable population dynamics at Denali, having non-significant population and productivity trends and expected adult survival rates and expected or higher-than-expected productivity given their body mass (Figures 3 and 6, Table 11). For four of these five species (all but Fox Sparrow), the productivity/population correlations were positive and for all five $\Delta QAIC_C$ was quite high, suggesting that there was relatively little annual variation in survival and that annual variation in population trends was driven primarily by annual variation in productivity. Fox Sparrow showed a negative productivity/population correlation, which was significant when data from all six stations were included, suggesting that populations decrease in the year following years of high productivity and vice versa. Fox Sparrow also had a high

$\Delta QAIC_C$, suggesting that annual adult survival rates were relatively constant. We can offer no explanation for this apparent anomaly, except to suggest that it may result from greatly increased density-dependent overwintering mortality of first year birds following years of high productivity.

For each of the remaining five species, our data suggest causes for the observed population trends. Although productivity appeared to be lower than expected in Boreal Chickadee (perhaps substantially low considering that cavity-nesting species typically have high productivity for their body mass), survival was consistently (time-independent) and substantially higher than expected, which likely explains the increases in adult population size observed for this species. Similarly, the population increase of Yellow-rumped Warbler also appears to be explained by consistent (time-independent) high adult survival, as discussed in detail in last year's report (DeSante et al. 2001b). Productivity of Yellow-rumped Warbler appeared to be about as expected or slightly lower than expected. In contrast, the population decline in Arctic Warbler appears to be explained by a combination of low productivity and both low and time-dependent survival, again as discussed in last year's report. The population decline in Wilson's Warbler also appears to be caused by low adult survival, although in this case, survival appeared to be more consistently low (less time-dependent) than for Arctic Warbler. Productivity in Wilson's Warbler appeared to be about as expected or, perhaps, even slightly higher than expected. In yet further contrast, the population decline in Swainson's Thrush appears to be explained by low productivity, as adult survival rates appear to be about as expected or even higher than expected.

Thus, we are able to identify likely proximate demographic causes of population trends for each of the five species that showed the greatest ten-year population trends at Denali National Park, and all five showed differing combinations of parameters that appear to be affecting their populations. The one population parameter that we have not been able to measure adequately is first-year survival, that is, the survival of young birds between fledging and breeding the following year. This is because young birds typically disperse substantial distances from their natal site to their site of first breeding. In future analyses we will attempt to index first-year survival through a combination of two methods: (1) by using data that distinguish captures of one-year-old adults (second year birds, SYs) from older adults (after-second-year birds, ASYs), and (2) by modeling temporal symmetry in mark-recapture data (that is, by running survival analyses in the reverse direction) to estimate annual recruitment (and thus to make inferences regarding survival) of one-year-old birds (Nichols and Hines in press). Once these analyses have been performed, we will be in a position to examine differences in adult and juvenal survival according to geographic location, climate, and habitat considerations.

Assimilating all of our results, annual variations in productivity generally appear to be more of a factor in causing year-to-year changes in adult population sizes at Denali than does annual variations in overwinter survival of adults. Evidence for this includes the positive productivity/ population correlation for nine of eleven species, an effect which was significant for two species and all species pooled, and the relatively small amount of time-dependence observed in adult survival rates. Indeed, for most species with relatively stable populations, the trend in global climate during the 1990's seems to have caused slightly decreasing trends in productivity which, in turn, have caused slight population declines. In contrast, however, for the species with pronounced population changes, average overall values of adult survival rates appear to affect overall population trends for more species (Boreal Chickadee, Arctic Warbler, Yellow-rumped Warbler, and Wilson's Warbler) than do average overall values of productivity (Arctic Warbler, Swainson's Thrush). If, indeed, survival of first year birds has as large or larger of an influence on bird populations at Denali as adult survival, as we speculate above, then good productivity is needed to provide an adequate pool of juvenile birds to balance their high mortality during migration and winter. Management practices to protect or increase the reproductive potential of birds would then be of paramount importance in maintaining healthy bird populations in Denali. On the other hand, high rates of first year mortality may limit the benefit that further increases in productivity could provide. In this respect it is interesting that three species with higher than expected productivity and expected adult survival (American Tree Sparrow, White-crowned Sparrow, Dark-eyed Junco) only show relatively stable rather than increasing population trends. The higher than expected productivity in these species is apparently balanced by high mortality of first-year birds.

Ten years of MAPS data from Denali National Park have consistently shown higher breeding bird densities in willow and scrub habitats than in spruce forest habitats, but slightly higher productivity in forested habitats. This suggests that the best way to optimize both productivity and population sizes of birds in Denali National Park may be to maintain the high quality of a mosaic of habitats. There is nothing new about this concept, but it is rewarding to see some of the mechanics behind it. In previous years, the population dynamics at the Permafrost station seem to be somewhat different than at the other Denali stations. 2001 was no exception, with Permafrost showing the largest decrease from 2000 in adult population size and the largest increase in productivity. This kind of between-station variation begs additional investigation and further underscores the need to maintain the quality of all habitats in Denali National Park and Preserve.

At this point it must be stressed that the six currently operated MAPS stations sample a small and really unrepresentative portion of the Park that lies entirely on north side of the Alaska Range. It is likely that the population dynamics of landbirds could vary dramatically in other portions of the park from what we have found here. In particular, the population dynamics of landbirds south of the Alaska Range could be strikingly different, because they would be influenced more by maritime conditions than the birds north of the Range. We would welcome opportunities to establish some pilot MAPS in other areas of the Park, if the logistical difficulties could be overcome.

Previous extensive analyses conducted on 1992-1996 data (DeSante et al. 1997) indicated that the indices and estimates of primary demographic parameters (productivity and adult survivorship) of common landbird species produced by the MAPS Program in Denali National Park could adequately predict the relative short-term population trends of those species. These results have now been extended more broadly by analyses of data from other national parks and national forests (DeSante et al. 1999). In this report we have demonstrated how MAPS data can be used to measure and assess the effects of productivity and survivorship as driving forces of population trends at Denali, both overall and at the individual species level. In future analyses, we hope to include estimates of recruitment of yearling birds and indices of first-year survival in order to fully understand what parameters are most affecting population changes in each study species. As a result, the indices and estimates of primary demographic parameters produced by MAPS are likely to be extremely useful for the management and conservation of landbirds at Denali National Park and Preserve and, in combination with similar data from other areas, across all of North America. We conclude that the MAPS protocol is very well-suited to provide one component of Denali's Long-term Ecological Monitoring Program.

Finally, in addition to analyses involving SOI and other global climate indices, we have initiated two broad-scale analyses to help us further understand the population dynamics of landbirds and potential management actions to reverse population declines. First, by modeling spatial variation in vital rates as a function of spatial variation in population trends we are beginning to examine the proximate demographic causes of population trends within a species on a continental scale (DeSante et al. 2001a). Among Gray Catbird populations, for example, we found that adult survival-rate estimates varied appropriately between areas of increasing vs. decreasing population trends while productivity indices were independent of area, suggesting that low survivorship was driving spatial differences in population trends in this species. Second, we have found that patterns of landscape structure detected within a two- to four-kilometer radius area of each station are good predictors, not only of the numbers of birds of each species captured but, more importantly, of their productivity levels as well (Nott 2000b). That study revealed the existence of threshold values of woodland/forest patch size above which productivity levels could be maximized, thus providing an extremely powerful tool to identify and formulate management actions aimed at increasing landbird populations. With appropriate funding we hope to be able to undertake such analyses when 15 years of data have been obtained, that is, after the 2006 field season.

CONCLUSIONS AND RECOMMENDATIONS

(1) Ten-year (1992-2001) trends in adult population size at Denali National Park were determined from constant-effort changes in indices of adult population size obtained from mist net capture data for eleven study species and all species pooled. Overall, population sizes of adult birds tended to decrease slightly over the ten years. Population trends were negative, for example, for seven of eleven study species and for all species pooled. The negative trend for all species pooled was a substantial and nearly significant -2.1% per year when data from all six stations were combined. As compared with 2000, however, adult populations of all species pooled in 2001 showed a substantial but non-significant increase of 18.0%.

(2) Despite the slightly declining overall trend in all species pooled, several species showed pronounced ten-year increases or decreases in their breeding populations. These included significant and highly significant increases, respectively, for Boreal Chickadee and Yellow-rumped Warbler, significant declines for Arctic Warbler and Swainson’s Thrush, a substantial and nearly significant decline for Wilson’s Warbler when data from all six stations were pooled,

and a significant decline for American Tree Sparrow over the four eastern stations. Trends in the populations of the other six species appeared rather stable, although generally with a slightly decreasing tendency.

(3) Among the seven species found at both the two western (Strangler Hill and Buhach Creek) and four eastern (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) stations, meaningful differences in the five-year (1997-2001) population trends were noted for only two species, and both of these differences could be explained by differences in the annual population changes for just one or two (of the five) years of data. Comparison of the first five-year period (1992-1996) with the second five-year period (1997-2001) at the four eastern stations indicated that trends were more negative (or less positive) during 1997-2001 than during 1992-1996 for seven of eleven species plus all species pooled. This could be cause for concern although, interestingly, a comparison of five-year with ten-year mean values indicated a greater reproductive output during the latter half of the study period.

(4) Productivity trends over the ten year 1992-2001 were fairly stable for seven of eleven species as well as for all species pooled, although productivity fluctuated widely for Fox Sparrow. Excellent productivity in 2001 (the highest recorded to date and a significant 0.177 higher than 2000) caused several species and all species pooled to show positive ten-year (1992-2001) productivity trends as compared with negative nine-year (1992-2000) trends. Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial and significant increases, a third species (Orange-crowned Warbler) showed a substantial but non-significant increase (at least when data from all six stations were pooled), and a fourth species (Boreal Chickadee) showed a substantial but non-significant decline. Among the six species and all species pooled found at both the eastern and western stations for which five-year (1997-2001) productivity trends could be estimated, meaningful differences were noted for only two species. Comparison of the first five-year period with the second five-year period at the four eastern stations indicated that productivity trends were more positive during 1997-2001 than during 1992-1996 for nine of eleven species plus all species pooled. Most of this difference, however, was caused by the very high productivity in 2001.

(5) Nine of eleven study species (all but Fox Sparrow and Common Redpoll), as well as all species pooled, showed positive "productivity/population correlations", indicating that a change in productivity one year results in a corresponding change in population size the following year. These positive relationships were significant or nearly significant for three species and for all species pooled.

(6) From 1992 through 1998, the positive productivity/population correlation was manifest at Denali by an alternating cycle of declines and increases, with productivity decreasing in even-numbered years and increasing in odd-numbered years, followed by the same pattern of decreases and increases in numbers of adults captured the following year. We suggest that this pattern was caused by a density-dependent effect on productivity along with low productivity of first-time breeders. This dynamic was disrupted during the 1999-2001 seasons, when both productivity

and population size showed changes in the same direction (negative during the 1998-1999 and 1999-2000 comparisons, and positive during the 2000-2001 comparison).

(7) To examine the possibility that global climate patterns are affecting productivity at Denali we regressed annual productivity indices on mean monthly Southern Oscillation Index (SOI) values and found an overall negative relationship between productivity at Denali and SOI, with productivity being higher in El Niño years than La Niña years. Thus it is likely that the severe La Niña event of 1999-2000, resulting in the highest SOI values during the ten-year period, caused productivity to be lower than expected and disrupted the density-dependent effect. Accounting for the significant positive increase in SOI with year during the ten-year study period, the predicted trend in productivity for all species pooled based on these correlations was -0.006 per year, compared with the observed productivity trend for all species pooled at Denali of +0.004 per year. Similar analyses were performed for two individual species showing significant, but opposite, relationships to SOI, Swainson's Thrush (positive) and Wilson's Warbler (negative). In each case the predicted trends (+0.021 and -0.021, respectively) were similar to the actual trends (+0.046 and -0.020), with the actual productivity trend for Swainson's Thrush, like that for all species pooled, being somewhat higher than the predicted trend. The discrepancy between the predicted and actual productivity trends likely resulted from the very high productivity observed at Denali in 2001.

(8) We have recently completed analyses showing how global climate patterns affect landbird productivity in Pacific Northwest national forests (Nott et al. in press), using other global climate indices such as the El Niño/Southern Oscillation Precipitation Index (ESPI, another measure of La Niña and El Niño events) and the North Atlantic Oscillation (NAO). These analyses showed that the El Niño conditions greatly enhanced productivity of species that breed in Pacific Northwest forests and winter or migrate through western Mexican (apparently by producing favorable weather conditions on their wintering grounds and migration routes), but had a much smaller effect on the productivity of temperate-wintering species breeding in the Pacific Northwest. Other researchers (Sillett et al. 2000) have documented the opposite effect, that is, higher productivity during la Niña events, in Black-throated Blue Warblers breeding in New Hampshire and wintering in the West Indies. These results nicely explain differences among Denali's Wilson's Warblers (that winter in or migrate through Mexico), Swainson's Thrushes (that are trans-Gulf migrants that winters in South America), and temperate-wintering species in the responses of their productivity to the El Niño/Southern Oscillation. These results beg for additional data from Denali National Park on other species, such as Alder Flycatcher, Gray-cheeked Thrush, and Blackpoll Warbler, that also winter in South America.

(9) It is also likely that the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO), which measures another Pacific global climate cycle that shifts every 25 years, could also affect productivity of Denali's birds. This latter cycle underwent a major shift between 1999 and 2001, which might explain the higher-than expected productivity observed in 2001. We suggest that after 2006, when 15 years of data will be available (that will include ten years of data from the two eastern stations that capture substantial numbers of Alder Flycatchers and Gray-cheeked Thrushes), we model both annual productivity indices and annual survival-rate estimates as a

function of SOI, ESPI, NAO, PDO, and other global climate cycles, to more fully understand how climate affects productivity of the study species at Denali National Park.

(10) Reasonably precise estimates of annual adult survival and recapture probabilities and proportion of young among newly captured adults are now being obtained from modified Cormack-Jolly-Seber mark-recapture analyses (using the program SURVIV and both a between- and within-year transient model) from ten years (1992-2001) of MAPS data for eleven breeding species at Denali National Park. The precision of the estimates increased from 2000 to 2001 and should continue to increase for several more years as additional years of data accumulate. This will allow improved analyses of the effect of adult survivorship in influencing population trends. With more years of data, temporal effects on survival may also become more evident, although it is likely that as many as twenty years of data will be necessary to determine actual temporal trends in adult survivorship.

(11) In order to investigate possible causes for population trends of individual study species at Denali National Park, we examined trends in productivity, relationships between changes in productivity and changes in population the following year ("productivity/population correlation"), interannual variability in survival, and comparisons of adult survival rates and productivity indices with those expected based on relationships of these parameters with body mass, both at Denali and across North America. Five of ten species showed relatively stable population dynamics at Denali, having non-significant population trends and expected adult survival rates and expected or higher-than-expected productivity given their body mass. For each of the remaining five species, our data suggest explanations for the observed population trends, with high adult survival causing observed increases in Boreal Chickadee and Yellow-rumped Warbler, low (and time-dependent) adult survival and low productivity causing declines in Arctic Warbler, low adult survival causing declines in Wilson's Warbler, and low productivity (or possibly low first-year survival) causing declines in Swainson's Thrush.

(12) Thus it appears that, at Denali National Park, mean annual survivorship, which is probably affected primarily on the wintering grounds or migration routes, is a greater factor in driving landbird population trends (both increasing and decreasing) than is mean annual productivity. This might be expected considering the near pristine nature of the breeding habitat at Denali. In contrast, however, annual changes in population size appear to be driven by annual changes in productivity more than by annual changes in adult survival rates. Evidence for this includes the positive productivity/ population correlations for nine of eleven species, which were significant for two species and all species pooled, and the relatively small amount of time-dependence observed in adult survival rates. Climatological events may, in turn, be driving these annual variations in productivity at Denali.

(13) The one population parameter that we have not been able to measure adequately is first-year survival, that is, the survival of young birds between fledging and breeding the following year. In future analyses we will attempt to index first-year survival through a combination of two methods: (1) by using data that distinguish captures of one-year-old adults (second year birds, SYs) from older adults (after-second-year birds, ASYs), and (2) by modeling temporal symmetry

in mark-recapture data (that is, by running survival analyses in the reverse direction) to estimate annual recruitment (and thus to make inferences regarding survival) of one-year-old birds.

(14) In this report we demonstrate how MAPS data can be used to measure and assess the effects of productivity and survivorship as driving forces of population trends at Denali. In future analyses we will add estimates of recruitment of young and indices of first-year survival in order to fully understand which parameters are most affecting population changes in each study species. As a result, the indices and estimates of primary demographic parameters produced by MAPS will be extremely useful for the management and conservation of landbirds at Denali National Park and Preserve and, in combination with similar data from other areas, across all of North America. We conclude that the MAPS protocol is extremely well-suited as a component of Denali's Long-term Ecological Monitoring Program.

(15) Ten years of MAPS data from Denali National Park have consistently shown higher breeding bird densities in willow and scrub habitats than in spruce forest habitats, but slightly higher productivity in forested habitats. This suggests that the best way to optimize both productivity and population sizes of birds in Denali National Park may be to maintain the high quality of a mosaic of habitats. It must be stressed, however, that the six currently operated MAPS stations sample a small and really unrepresentative portion of the Park that lies entirely on north side of the Alaska Range. It is likely that the population dynamics of landbirds could vary dramatically in other portions of the park from what we have found here. In particular, the population dynamics of landbirds south of the Alaska Range could be strikingly different, because they would be influenced more by maritime conditions than the birds north of the Range. We would welcome opportunities to establish some pilot MAPS in other areas of the Park, if the logistical difficulties could be overcome.

(16) We have initiated two additional types of broad-scale analyses of MAPS data to help us further understand the population dynamics of landbirds and potential management actions to reverse population declines. First, by modeling spatial variation in vital rates as a function of spatial variation in population trends, we are able to identify the proximate demographic causes of population decline for species at multiple spatial scales. Second, we have found that patterns of landscape structure detected within a two- to four-kilometer radius area of each station are good predictors not only of the numbers of birds of each species captured but, more importantly, their productivity levels as well. Based on these analyses, threshold values of various landscape-level habitat characteristics, such as woodland/forest patch size, can be determined that will maximize productivity, thereby providing an extremely powerful tool to aid in formulating management actions aimed at reversing landbird population declines. With appropriate funding, we hope to be able to undertake such analyses of Denali data in conjunction with data from other more heavily managed landscapes in Alaska and elsewhere when 15 years of data have been obtained, that is, after the 2006 field season.

(17) Based on the above information, it is recommended that the MAPS Program continue to be included as an integral part of Denali's Long-term Ecological Monitoring Program, and that operation at the six currently active stations be sustained indefinitely into the future. We also

recommend that, if possible, additional stations be established in other areas of the park in order to gain a more comprehensive picture of landbird population dynamics at Denali National Park. We also recommend, if possible, siting these additional stations at locations where increased numbers of individuals of species targeted by Boreal Partners in Flight, such as Gray-cheeked Thrush, Blackpoll Warbler, and Golden-crowned Sparrow, could be captured.

(18) Finally, we recommend greatly reducing the extent and thoroughness of the MAPS annual reports submitted each year to the LTEM Program, and recommend providing comprehensive reports with additional analyses as described above at approximately five-year intervals.

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Table 1. Summary of the 2001 MAPS program in Denali National Park.

Station						2001 operation		
Name	Code	No.	Major Habitat Type	Latitude-longitude	Avg. Elev. (m)	Total number of net-hours[1]	No. of periods	Inclusive dates
Strangler Hill	STHI	17731	Alder/birch scrub hillside	63°26'50"N,150°48'30"W	686	360.0 (269.2)	6	6/15-8/04
Buhach Creek	BUCR	17730	Willow/tundra scrub	63°25'20"N,150°26'40"W	884	315.8 (258.7)	6	6/14-8/05
Igloo Creek	IGCR	17705	Riparian willow scrub	63°35'40"N,149°36'30"W	945	333.7 (283.5)	6	6/13-8/07
Mile Seven	MISE	17703	Spruce forest, spruce/birch scrub, wet willow scrub	63°43'00"N,149°04'50"W	838	358.0 (326.0)	6	6/16-8/02
Permafrost	PERM	17704	Mature spruce forest, riparian alder, wet willow scrub	63°42'50"N,149°01'10"W	716	331.0 (320.7)	6	6/11-8/06
Rock Creek	ROCR	17706	Mature spruce forest, riparian alder woodland	63°43'30"N,148°58'00"W	686	333.3 (262.7)	6	6/10-8/01
ALL STATIONS COMBINED						2031.8 (1720.7)	6	6/10-8/07

[1] Total net-hours in 2001. Net-hours in 2001 that could be compared in a constant-effort manner to 2000 are shown in parentheses.

Table 2. Capture summary for the six individual MAPS stations operated in Denali National Park in 2001.
N = Newly Banded, U = Unbanded, R = Recaptures of banded birds.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek		
Species	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R
Solitary Sandpiper										1								
Three-toed Woodpecker													2		1			
Alder Flycatcher	9		3	1			2						1					
Gray Jay	4			1		1				2			2		2			1
Black-billed Magpie								3										
Black-capped Chickadee							19		5									
Boreal Chickadee										4		2	4		5	2		2
Ruby-crowned Kinglet	3		1							1			7					
Arctic Warbler				2		8	20	2	20				1					
Gray-cheeked Thrush	17		5													1		
Swainson's Thrush	3		2							1		1	5		10	10	1	3
Hermit Thrush							11		3									
American Robin	4						1			3								
Varied Thrush										2			3			2		
Bohemian Waxwing				1														
Orange-crowned Warbler	24	2	8	11		8	41		7	5		4	1			2		
Yellow Warbler				1		1							1					
Yellow-rumped Warbler							3			20		5	5			4		
Blackpoll Warbler	2									3								
Northern Waterthrush	1			2		1	2			1								
Wilson's Warbler	72	2	19	48	2	51	59	3	17	51		20	33	2	10	6		4
American Tree Sparrow	13		1	16		3	30		3	6		1	1					
Savannah Sparrow	4		1	8			1			1			1					
Fox Sparrow	29	1	12	3		1	2			2			2					
Lincoln's Sparrow										1								
White-crowned Sparrow	33	1	6	12	3	4	39		11	22		18	53		14			
Golden-crowned Sparrow				1														
Dark-eyed Junco	5						2			22	2	8	6		1	21		3

Table 2. (cont.) Capture summary for the six individual MAPS stations operated in Denali National Park in 2001.
N = Newly Banded, U = Unbanded, R = Recaptures of banded birds.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek		
Species	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R
White-winged Crossbill	2																	
Common Redpoll	34		11	16	1	13	10		2	5		1	4					
ALL SPECIES POOLED	259	6	69	123	6	91	242	8	68	153	2	60	132	2	43	48	1	13
TOTAL NUMBER OF CAPTURES		334			220			318			215			177			62	
NUMBER OF SPECIES	17	4	11	14	3	10	15	3	8	19	1	9	18	1	7	8	1	5
TOTAL NUMBER OF SPECIES		17			14			16			19			18			9	

Table 3. Numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the six individual MAPS stations operated in Denali National Park in 2001.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek		
Species	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.
Solitary Sandpiper																		
Three-toed Woodpecker													3.6	0.0	0.00			
Alder Flycatcher	15.0	0.0	0.00	1.9	0.0	0.00	3.6	0.0	0.00				1.8	0.0	0.00			
Gray Jay	5.0	1.7	0.25	0.0	1.9	1.00				1.7	1.7	0.50	1.8	3.6	0.67	1.8	0.0	0.00
Black-capped Chickadee							5.4	28.8	0.84									
Boreal Chickadee										6.7	1.7	0.20	12.7	0.0	0.00	5.4	0.0	0.00
Ruby-crowned Kinglet	0.0	5.0	1.00							1.7	0.0	0.00	5.4	7.3	0.57			
Arctic Warbler				3.8	0.0	0.00	25.2	18.0	0.42				0.0	1.8	1.00			
Gray-cheeked Thrush	15.0	16.7	0.53													0.0	1.8	1.00
Swainson's Thrush	3.3	3.3	0.50							1.7	0.0	0.00	9.1	7.3	0.44	12.6	5.4	0.30
Hermit Thrush							12.6	9.0	0.42									
American Robin	0.0	6.7	1.00				1.8	0.0	0.00	5.0	0.0	0.00						
Varied Thrush										3.4	0.0	0.00	3.6	1.8	0.33	3.6	0.0	0.00
Bohemian Waxwing				0.0	1.9	1.00												
Orange-crowned Warbler	21.7	23.3	0.52	19.0	5.7	0.23	12.6	62.9	0.83	6.7	1.7	0.20	0.0	1.8	1.00	3.6	0.0	0.00
Yellow Warbler				1.9	0.0	0.00							0.0	1.8	1.00			
Yellow-rumped Warbler							0.0	5.4	1.00	18.4	16.8	0.48	7.3	1.8	0.20	7.2	0.0	0.00
Blackpoll Warbler	1.7	1.7	0.50							3.4	1.7	0.33						
Northern Waterthrush	0.0	1.7	1.00	0.0	3.8	1.00	0.0	3.6	1.00	0.0	1.7	1.00						
Wilson's Warbler	31.7	91.7	0.74	58.9	41.8	0.42	39.6	71.9	0.65	26.8	58.7	0.69	18.1	45.3	0.71	5.4	5.4	0.50
American Tree Sparrow	1.7	20.0	0.92	19.0	13.3	0.41	3.6	52.1	0.94	0.0	10.1	1.00	0.0	1.8	1.00			
Savannah Sparrow	0.0	6.7	1.00	7.6	7.6	0.50	0.0	1.8	1.00	1.7	0.0	0.00	0.0	1.8	1.00			
Fox Sparrow	15.0	38.3	0.72	3.8	1.9	0.33	3.6	0.0	0.00	0.0	3.4	1.00	0.0	3.6	1.00			
Lincoln's Sparrow										0.0	1.7	1.00						
White-crowned Sparrow	15.0	45.0	0.75	13.3	9.5	0.42	19.8	55.7	0.74	21.8	25.1	0.54	23.6	81.6	0.78			
Golden-crowned Sparrow				0.0	1.9	1.00												
Dark-eyed Junco	1.7	6.7	0.80				0.0	3.6	1.00	10.1	28.5	0.74	5.4	5.4	0.50	7.2	32.4	0.82

Table 3. (cont.) Numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the six individual MAPS stations operated in Denali National Park in 2001.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek		
Species	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.	Ad.	Yg.	Prop. Yg.
White-winged Crossbill	0.0	3.3	1.00															
Common Redpoll	45.0	11.7	0.21	30.4	0.0	0.00	18.0	0.0	0.00	5.0	3.4	0.40	5.4	1.8	0.25			
ALL SPECIES POOLED	171.7	283.3	0.62	159.6	89.3	0.36	145.7	312.9	0.68	114.0	155.9	0.58	97.9	168.6	0.63	46.8	45.0	0.49
NUMBER OF SPECIES	12	16		10	10		11	11		14	13		12	15		8	4	
TOTAL NUMBER OF SPECIES		17			14			15			18			18			9	

Table 4. Summary of results for all six Denali National Park MAPS stations combined in 2001.

Species	Birds captured: Newly banded	Un-banded	Recap-tured	Birds/600net-hours: Adults	Young	Prop. Young
Solitary Sandpiper	1			0.0	0.0	0.00
Three-toed Woodpecker	2		1	0.6	0.0	0.00
Alder Flycatcher	13		3	3.8	0.0	0.00
Gray Jay	9		4	1.8	1.5	0.46
Black-billed Magpie		3				
Black-capped Chickadee	19		5	0.9	4.7	0.84
Boreal Chickadee	10		9	4.1	0.3	0.07
Ruby-crowned Kinglet	11		1	1.2	2.1	0.64
Arctic Warbler	23	2	28	4.7	3.2	0.41
Gray-cheeked Thrush	18		5	2.7	3.2	0.55
Swainson's Thrush	19	1	16	4.4	2.7	0.38
Hermit Thrush	11		3	2.1	1.5	0.42
American Robin	8			1.2	1.2	0.50
Varied Thrush	7			1.8	0.3	0.14
Bohemian Waxwing	1			0.0	0.3	1.00
Orange-crowned Warbler	84	2	27	10.6	15.9	0.60
Yellow Warbler	2		1	0.3	0.3	0.50
Yellow-rumped Warbler	32		5	5.6	4.1	0.42
Blackpoll Warbler	5			0.9	0.6	0.40
Northern Waterthrush	6		1	0.0	1.8	1.00
Wilson's Warbler	269	9	121	29.8	53.2	0.64
American Tree Sparrow	66		8	3.8	16.2	0.81
Savannah Sparrow	15		1	1.5	3.0	0.67
Fox Sparrow	38	1	13	3.8	8.3	0.68
Lincoln's Sparrow	1			0.0	0.3	1.00
White-crowned Sparrow	159	4	53	15.7	36.0	0.70
Golden-crowned Sparrow	1			0.0	0.3	1.00
Dark-eyed Junco	56	2	12	4.1	13.0	0.76
White-winged Crossbill	2			0.0	0.6	1.00
Common Redpoll	69	1	27	17.4	3.0	0.15
ALL SPECIES POOLED	957	25	344	122.8	177.5	0.59
TOTAL NUMBER OF CAPTURES		1326				
NUMBER OF SPECIES	29	9	21	23	26	
TOTAL NUMBER OF SPECIES		30			28	

Table 5. Percentage changes between 2000 and 2001 in the numbers of individual ADULT birds captured at six constant-effort MAPS stations in Denali National Park.

							All six stations combined				
								No. adults			
Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	n[1]	2000	2001	% change	SE[2]
Three-toed Woodpecker					+100.0		1	1	2	+100.0	
Alder Flycatcher	+14.3	0.0	++++ [3]		0.0		4	9	11	+22.2	15.2
Gray Jay				++++ [3]	0.0	-50.0	3	3	3	0.0	57.7
Black-capped Chickadee			+200.0				1	1	3	+200.0	
Boreal Chickadee				-20.0	+133.3	+50.0	3	10	14	+40.0	50.3
Ruby-crowned Kinglet				++++	0.0		2	3	4	+33.3	66.7
Arctic Warbler		0.0	-14.3				2	16	14	-12.5	3.1
Gray-cheeked Thrush	+100.0						1	4	8	+100.0	
Swainson's Thrush	0.0			++++	-16.7	+500.0	4	9	14	+55.6	81.9
Hermit Thrush			+100.0				1	3	6	+100.0	
American Robin			++++	+50.0	-100.0		3	3	4	+33.3	69.4
Varied Thrush				++++	0.0	0.0	3	4	6	+50.0	75.0
Bohemian Waxwing							0	0	0		
Orange-crowned Warbler	+57.1	+12.5	+100.0	+100.0		++++ [3]	5	20	32	+60.0	25.3*
Yellow Warbler		++++[3]					1	0	1	++++[3]	
Yellow-rumped Warbler	-100.0			+175.0	+100.0	-57.1	4	15	18	+20.0	67.1
Blackpoll Warbler	0.0			0.0			2	3	3	0.0	88.9
Northern Waterthrush							0	0	0		
Wilson's Warbler	+30.0	0.0	+100.0	+77.8	+42.9	+50.0	6	65	90	+38.5	21.3
American Tree Sparrow	++++ [3]	-27.3	-50.0	-100.0			4	17	10	-41.2	20.3
Savannah Sparrow	-100.0	+100.0		++++			3	6	5	-16.7	85.5
Fox Sparrow	+14.3	0.0	+100.0				3	10	12	+20.0	12.0
Lincoln's Sparrow							0	0	0		
White-crowned Sparrow	-14.3	-30.0	+25.0	-14.3	+116.7		5	45	48	+6.7	20.8
Golden-crowned Sparrow							0	0	0		
Dark-eyed Junco				+100.0	-40.0	-62.5	3	16	12	-25.0	37.2

Table 5. (cont.) Percentage changes between 2000 and 2001 in the numbers of individual ADULT birds captured at six constant-effort MAPS stations in Denali National Park.

Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	All six stations combined: n[1]	No. adults 2000	No. adults 2001	% change	SE[2]
Common Redpoll	+160.0	-31.6	-18.2	-57.1	-57.1		5	54	54	0.0	37.5
ALL SPECIES POOLED	+37.7	-9.9	+35.2	+28.8	+20.0	-4.2	6	317	374	+18.0	9.8
No. species that increased[4]	7(1)	3(1)	8(2)	10(5)	5(0)	4(1)				16(1)	
No. species that decreased[5]	3(2)	3(0)	3(0)	4(1)	4(1)	3(0)				4(0)	
No. species remained same	2	4	0	1	4	1				3	
TOTAL NUMBER OF SPECIES	12	10	11	15	13	8				23	
Proportion of increasing (decreasing) species	0.583	(0.300)	0.727	0.667	0.385	(0.375)				0.696	
Sig. of increase (decrease)[6]	0.387	(0.945)	0.113	0.151	0.867	(0.855)				0.047 **	

[1] Number of stations at which at least one adult bird was captured in either year.
[2] Standard error of the % change in the number of adult birds captured.
[3] Increase indeterminate (infinite) because no adult was captured during 2000.
[4] No. of species for which adults were captured in 2001 but not in 2000 are in parentheses.
[5] No. of species for which adults were captured in 2000 but not in 2001 are in parentheses.
[6] Statistical significance of the one-sided binomial test that the proportion of increasing (decreasing) species is not greater than 0.50.
*** P < 0.01; ** 0.01 # P < 0.05; * 0.05 # P < 0.10.

Table 6. Percentage changes between 2000 and 2001 in the numbers of individual YOUNG birds captured at six constant-effort MAPS stations in Denali National Park.

								All six stations combined			
								No. young			
Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	n[1]	2000	2001	% change	SE[2]
Three-toed Woodpecker							0	0	0		
Alder Flycatcher							0	0	0		
Gray Jay	0.0	++++[3]		++++[3]	++++[3]		4	1	5	+400.0	541.6
Black-capped Chickadee			++++[3]	-100.0		-100.0	3	2	10	+400.0	750.0
Boreal Chickadee				-50.0	-100.0		2	3	1	-66.7	22.2
Ruby-crowned Kinglet	++++[3]			-100.0	++++		3	1	7	+600.0	1053.6
Arctic Warbler			+42.9		++++		2	7	11	+57.1	28.6
Gray-cheeked Thrush	+800.0	-100.0				++++	3	2	10	+400.0	396.9
Swainson's Thrush	0.0				++++	+200.0	3	3	9	+200.0	230.9
Hermit Thrush			++++				1	0	5	++++[3]	
American Robin	++++						1	0	3	++++	
Varied Thrush					++++	-100.0	2	1	1	0.0	200.0
Bohemian Waxwing		++++					1	0	1	++++	
Orange-crowned Warbler	++++	++++	+450.0	-66.7	0.0		5	10	49	+390.0	207.9
Yellow Warbler					++++		1	0	1	++++	
Yellow-rumped Warbler	-100.0		++++	+50.0	++++	-100.0	5	11	13	+18.2	62.1
Blackpoll Warbler	0.0			++++			2	1	2	+100.0	200.0
Northern Waterthrush	0.0	++++	++++	++++			4	1	5	+400.0	541.6
Wilson's Warbler	0.0	-22.2	+680.0	+400.0	+2400.0	++++	6	71	150	+111.3	100.1
American Tree Sparrow	+1000.0	+250.0	+633.3	+20.0	-91.7		5	23	47	+104.3	146.8
Savannah Sparrow	+100.0	++++	++++		++++		4	1	7	+600.0	692.8
Fox Sparrow	+466.7	++++	-100.0	++++	++++		5	4	22	+450.0	175.7*
Lincoln's Sparrow			-100.0	++++			2	1	1	0.0	200.0
White-crowned Sparrow	+666.7	+100.0	+180.0	+116.7	+200.0	-100.0	6	37	113	+205.4	45.9***
Golden-crowned Sparrow		++++		-100.0			2	1	1	0.0	200.0
Dark-eyed Junco	+50.0		++++	+40.0	-62.5	+260.0	5	25	40	+60.0	63.9

Table 6. (cont.) Percentage changes between 2000 and 2001 in the numbers of individual YOUNG birds captured at six constant-effort MAPS stations in Denali National Park.

Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	All six stations combined: n[1]	No. young 2000	No. young 2001	% change	SE[2]
Common Redpoll	++++	-100.0		-66.7	++++		4	10	8	-20.0	96.8
ALL SPECIES POOLED	+155.1	+10.3	+369.7	+84.1	+144.7	+92.3	6	216	522	+141.7	48.2**
No. species that increased[4]	10(4)	9(7)	11(6)	10(5)	12(10)	4(2)				20(4)	
No. species that decreased[5]	1(1)	3(2)	2(2)	6(3)	3(1)	4(4)				2(0)	
No. species remained same	5	0	0	0	1	0				3	
TOTAL NUMBER OF SPECIES	16	12	13	16	16	8				25	
Proportion of increasing (decreasing) species	0.625	0.750	0.846	0.625	0.750	0.500				0.800	
Sig. of increase (decrease)[6]	0.227	0.073 *	0.011 **	0.227	0.038 **	0.637				0.002 ***	

[1] Number of stations at which at least one young bird was captured in either year.
[2] Standard error of the % change in the number of young birds captured.
[3] Increase indeterminate (infinite) because no young was captured during 2000.
[4] No. of species for which young were captured in 2001 but not in 2000 are in parentheses.
[5] No. of species for which young were captured in 2000 but not in 2001 are in parentheses.
[6] Statistical significance of the one-sided binomial test that the proportion of increasing (decreasing) species is not greater than 0.50.
*** *P* < 0.01; ** 0.01 # *P* < 0.05; * 0.05 # *P* < 0.10

Table 7. Absolute changes between 2000 and 2001 in the PROPORTION OF YOUNG in the catch at six constant-effort MAPS stations in Denali National Park.

							All six stations combined			
							Prop. young			
Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	n[1]	2000	2001	Absol. change	SE[2]
Three-toed Woodpecker					0.000		1	0.000	0.000	0.000	
Alder Flycatcher	0.000	0.000	+-+-+[3]		0.000		4	0.000	0.000	0.000	0.000
Gray Jay	0.000	+-+-+[3]		+-+-+[3]	+0.667	0.000	5	0.250	0.625	+0.375	0.288
Black-capped Chickadee			+0.769	+-+-+		+-+-+[3]	3	0.667	0.769	+0.103	0.333
Boreal Chickadee				-0.086	-0.250	0.000	3	0.231	0.067	-0.164	0.089
Ruby-crowned Kinglet	+-+-+[3]			-1.000	+0.571		3	0.250	0.636	+0.386	0.357
Arctic Warbler		0.000	+0.121		+-+-+[3]		3	0.304	0.440	+0.136	0.070
Gray-cheeked Thrush	+0.329	+-+-+				+-+-+	3	0.333	0.556	+0.222	0.197
Swainson's Thrush	0.000			+-+-+	+0.444	-0.167	4	0.250	0.391	+0.141	0.186
Hermit Thrush			+0.455				1	0.000	0.455	+0.455	
American Robin	+-+-+		+-+-+	0.000	+-+-+		4	0.000	0.429	+0.429	0.360
Varied Thrush				+-+-+	+0.333	-0.333	3	0.200	0.143	-0.057	0.185
Bohemian Waxwing		+-+-+					1	-----[4]	1.000	+-+-+[3]	
Orange-crowned Warbler	+0.500	+0.250	+0.180	-0.400	0.000	+-+-+	6	0.333	0.605	+0.272	0.231
Yellow Warbler		+-+-+			+-+-+		2	-----	0.500	+-+-+	
Yellow-rumped Warbler	+-+-+		+-+-+	-0.150	+0.200	-0.364	5	0.423	0.419	-0.004	0.127
Blackpoll Warbler	0.000			+0.333			2	0.250	0.400	+0.150	0.262
Northern Waterthrush	0.000	+-+-+	+-+-+	+-+-+			4	1.000	1.000	0.000	0.000
Wilson's Warbler	-0.051	-0.063	+0.327	+0.252	+0.589	+0.500	6	0.522	0.625	+0.103	0.102
American Tree Sparrow	-0.083	+0.313	+0.357	+0.444	0.000		5	0.575	0.825	+0.250	0.244
Savannah Sparrow	+0.800	+0.429	+-+-+	+-+-+	+-+-+		5	0.143	0.583	+0.441	0.162*
Fox Sparrow	+0.380	+0.333	-0.500	+-+-+	+-+-+		5	0.286	0.647	+0.361	0.089**
Lincoln's Sparrow			+-+-+	+-+-+			2	1.000	1.000	0.000	0.000
White-crowned Sparrow	+0.493	+0.197	+0.181	+0.220	+0.062	+-+-+	6	0.451	0.702	+0.251	0.114*
Golden-crowned Sparrow		+-+-+		+-+-+			2	1.000	1.000	0.000	0.000
Dark-eyed Junco	0.000		+-+-+	-0.069	-0.115	+0.473	5	0.610	0.769	+0.160	0.118

Table 7. (cont.) Absolute changes between 2000 and 2001 in the PROPORTION OF YOUNG in the catch at six constant-effort MAPS stations in Denali National Park.

								All six stations combined			
								Prop. young			
Species	Strangler Hill	Buhach Creek	Igloo Creek	Mile Seven	Perma-frost	Rock Creek	n[1]	2000	2001	Absol. change	SE[2]
Common Redpoll	+0.188	-0.269	0.000	-0.050	+0.250		5	0.156	0.129	-0.027	0.089
ALL SPECIES POOLED	+0.153	+0.046	+0.301	+0.089	+0.175	+0.169	6	0.405	0.583	+0.177	0.050**
No. species that increased	6	5	7	4	8	2				16	
No. species that decreased	2	2	1	6	2	3				4	
No. species remained same	6	2	0	1	4	2				5	
TOTAL NUMBER OF SPECIES[5]	14	9	8	11	14	7				25	
Proportion of increasing (decreasing) species	0.429	0.555	0.875	0.364	0.571	0.286				0.640	
Sig. of increase (decrease)[6]	0.788	0.500	0.035 **	0.887	0.395	0.938				0.115	

[1] Number of stations at which at least one aged bird was captured in either year.
[2] Standard error of the change in the proportion of young.
[3] The change in the proportion of young is undefined at this station because no aged individual of the species was captured in one of the two years.
[4] Proportion of young not given because no aged individual of the species was captured in the year shown.
[5] Species for which the change in the proportion of young is undefined are not included.
[6] Statistical significance of the one-sided binomial test that the proportion of increasing (decreasing) species is not greater than 0.50.
*** $P < 0.01$; ** 0.01 # $P < 0.05$; * 0.05 # $P < 0.10$

Table 8a. Mean numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the six individual MAPS stations operated in Denali National Park averaged over the five years, 1997-2001. Data are included only from stations that lie within the breeding range of the species.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek			All stations pooled		
Species	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.
Sharp-shinned Hawk																0.4	0.0	0.00	0.1	0.0	0.00
Solitary Sandpiper																					
Three-toed Woodpecker													1.5	0.4	0.17				0.2	0.1	0.17
Olive-sided Flycatcher				0.0	0.7	1.00													0.0	0.1	1.00
Western Wood-Pewee							0.0	0.3	1.00										0.0	0.1	1.00
"Traill's" Flycatcher	15.6	1.8	0.07	5.0	0.0	0.00	1.1	0.3	0.25				1.1	0.8	0.25	0.4	0.0	0.00	3.8	0.5	0.10
Hammond's Flycatcher	0.4	0.0	0.00				0.0	0.3	1.00	0.0	0.3	1.00							0.1	0.1	0.67
Northern Shrike										0.3	0.0	0.00							0.1	0.0	0.00
Gray Jay	1.0	1.1	0.75	0.0	0.4	1.00	0.7	0.4	0.33	0.7	1.0	0.67	1.5	1.1	0.33	1.6	2.6	0.53	0.9	1.1	0.56
Black-capped Chickadee							3.9	8.9	0.50	0.0	0.4	1.00	0.0	0.4	1.00	1.1	0.8	0.44	0.8	1.8	0.63
Boreal Chickadee	0.0	0.4	1.00				0.0	0.4	1.00	4.2	1.8	0.23	5.6	1.4	0.25	4.8	1.4	0.17	2.5	0.9	0.31
Ruby-crowned Kinglet	0.7	1.3	0.50							0.3	0.4	0.50	3.2	3.9	0.56				0.7	1.0	0.54
Arctic Warbler	0.3	0.0	0.00	4.3	0.0	0.00	42.9	17.0	0.30	0.4	0.0	0.00	0.0	0.4	1.00				8.2	3.0	0.28
Townsend's Solitaire																					
Gray-cheeked Thrush	11.6	6.4	0.32	0.8	0.4	0.33	0.3	0.0	0.00							0.0	0.4	1.00	2.1	1.2	0.33
Swainson's Thrush	2.2	3.0	0.65				0.3	1.1	0.75	1.8	0.0	0.00	9.6	3.0	0.20	7.3	7.1	0.52	3.5	2.3	0.38
Hermit Thrush							5.8	2.8	0.32				0.0	0.3	1.00	1.4	1.1	0.43	1.2	0.7	0.35
American Robin	0.4	1.3	0.50				0.4	0.0	0.00	2.1	0.4	0.25	2.2	0.0	0.00	0.8	0.8	0.33	1.0	0.4	0.21
Varied Thrush	0.0	0.3	1.00							2.1	0.0	0.00	2.2	0.7	0.21	1.9	2.2	0.60	1.0	0.5	0.37
Bohemian Waxwing	0.4	0.0	0.00	0.4	0.4	0.50													0.1	0.1	0.33
Orange-crowned Warbler	25.2	16.6	0.28	24.2	16.3	0.27	18.2	24.7	0.53	7.4	6.1	0.35	1.6	3.1	0.78	1.4	0.7	0.44	13.0	11.5	0.42
Yellow Warbler	1.1	1.1	0.50	6.1	2.6	0.26	0.3	0.3	0.50				0.0	0.7	1.00				1.3	0.8	0.42
Yellow-rumped Warbler	3.5	1.8	0.30				0.0	1.1	1.00	7.3	7.0	0.39	9.7	4.9	0.15	9.1	3.9	0.25	4.9	3.1	0.35
Blackpoll Warbler	0.8	2.1	0.67							2.9	1.4	0.31	0.8	0.0	0.00				0.7	0.6	0.40
Northern Waterthrush	0.7	2.6	0.85	0.0	1.8	1.00	1.0	1.4	0.75	0.0	1.4	1.00	0.0	0.3	1.00				0.3	1.3	0.86
Wilson's Warbler	35.4	52.3	0.54	85.4	88.3	0.50	43.0	51.1	0.50	25.2	34.8	0.55	18.5	23.7	0.48	5.1	6.1	0.46	35.1	42.7	0.54
American Tree Sparrow	3.7	15.0	0.82	19.6	22.5	0.50	10.9	21.0	0.60	3.2	10.7	0.78	0.4	5.6	0.75	0.0	0.4	1.00	6.3	12.8	0.66
Savannah Sparrow	2.2	3.8	0.64	11.1	10.6	0.43	0.3	1.7	0.92	0.3	0.0	0.00	0.0	0.4	1.00				2.2	2.8	0.51
Fox Sparrow	10.5	17.7	0.60	5.4	1.1	0.23	5.4	2.9	0.25	0.0	1.0	1.00	0.0	1.5	1.00	0.0	0.7	1.00	3.5	4.2	0.50
Lincoln's Sparrow							0.0	1.1	1.00	0.0	0.7	1.00	0.0	0.4	1.00				0.0	0.4	1.00
White-crowned Sparrow	19.2	35.3	0.60	22.5	21.1	0.46	23.9	31.9	0.57	21.6	15.1	0.40	24.8	43.0	0.56	0.0	1.2	1.00	18.7	24.9	0.56

Table 8a. (cont.) Mean numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the six individual MAPS stations operated in Denali National Park averaged over the five years, 1997-2001. Data are included only from stations that lie within the breeding range of the species.

	Strangler Hill			Buhach Creek			Igloo Creek			Mile Seven			Permafrost			Rock Creek			All stations pooled		
Species	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.
Golden-crowned Sparrow				0.4	0.4	0.50	1.4	0.3	0.17	0.0	0.4	1.00							0.3	0.2	0.47
Dark-eyed Junco	1.4	5.3	0.81	0.0	0.4	1.00	0.0	0.7	1.00	8.9	15.0	0.61	8.8	11.7	0.56	13.8	23.3	0.57	5.5	9.4	0.61
White-winged Crossbill	0.0	1.9	1.00							1.9	0.4	0.17	0.4	0.4	0.50				0.4	0.4	0.50
Common Redpoll	26.8	11.1	0.25	48.8	18.1	0.22	21.5	2.6	0.09	5.1	2.1	0.43	16.9	5.3	0.20	0.4	0.0	0.00	19.8	6.5	0.22
ALL SPECIES POOLED	163.2	182.2	0.50	233.8	185.2	0.42	181.5	172.4	0.47	95.7	100.3	0.50	108.6	113.5	0.50	49.4	52.6	0.50	138.3	135.3	0.48
NUMBER OF SPECIES	21	21		13	15		18	22		18	19		17	23		14	15		30	31	
TOTAL NUMBER OF SPECIES		24			17			24			24			25			18			33	

[1] Years for which the proportion of young was undefined (no aged birds were captured in the year) are not included in the mean proportion of young.

Table 8b. Mean numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the four long running MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) operated in Denali National Park averaged over the ten years, 1992-2001. Data are included only from stations that lie within the breeding range of the species.

	Igloo Creek			Mile Seven			Permafrost			Rock Creek			All stations pooled		
Species	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.
Sharp-shinned Hawk										0.2	0.0	0.00	0.0	0.0	0.00
Solitary Sandpiper															
Three-toed Woodpecker							1.4	0.2	0.07	0.4	0.0	0.00	0.4	0.0	0.07
Olive-sided Flycatcher				0.1	0.0	0.00	0.1	0.0	0.00				0.1	0.0	0.00
Western Wood-Pewee	0.0	0.2	1.00										0.0	0.0	1.00
"Traill's" Flycatcher	0.8	0.2	0.13	0.3	0.1	0.33	0.8	0.4	0.17	0.3	0.0	0.00	0.5	0.2	0.29
Hammond's Flycatcher	0.0	0.2	1.00	0.0	0.2	1.00	0.0	0.1	1.00	0.0	0.1	1.00	0.0	0.2	1.00
Northern Shrike	0.1	0.0	0.00	0.2	0.0	0.00							0.1	0.0	0.00
Gray Jay	0.4	0.3	0.67	1.3	1.0	0.46	1.9	1.2	0.32	1.8	1.7	0.42	1.3	1.1	0.42
Black-capped Chickadee	3.3	5.0	0.38	0.0	0.2	1.00	0.0	0.2	1.00	0.7	0.4	0.33	1.0	1.4	0.45
Boreal Chickadee	0.0	0.2	1.00	3.3	1.6	0.31	4.0	2.5	0.41	4.4	1.0	0.15	2.9	1.3	0.32
Ruby-crowned Kinglet				0.3	0.2	0.33	2.8	3.1	0.43	0.0	0.5	1.00	0.8	0.9	0.50
Arctic Warbler	42.7	16.5	0.27	0.2	0.1	0.50	0.3	0.2	0.33	0.1	0.0	0.00	10.8	4.2	0.27
Townsend's Solitaire	0.0	0.1	1.00										0.0	0.0	1.00
Gray-cheeked Thrush	0.4	0.0	0.00	0.3	0.0	0.00	0.3	0.0	0.00	0.0	0.2	1.00	0.2	0.0	0.17
Swainson's Thrush	0.5	0.5	0.38	1.3	0.1	0.14	9.1	2.3	0.17	9.4	5.7	0.39	5.0	2.1	0.29
Hermit Thrush	3.7	1.9	0.38	0.1	0.5	0.67	0.0	0.5	1.00	1.0	0.8	0.46	1.2	0.9	0.49
American Robin	0.4	0.0	0.00	2.0	0.2	0.14	2.1	0.1	0.13	0.9	0.5	0.42	1.4	0.2	0.10
Varied Thrush	0.1	0.0	0.00	1.7	0.1	0.08	1.6	0.5	0.23	1.7	1.8	0.55	1.3	0.6	0.29
Orange-crowned Warbler	16.7	20.8	0.53	5.2	3.9	0.25	1.2	2.3	0.70	0.9	0.4	0.33	6.0	6.8	0.52
Yellow Warbler	0.2	0.2	0.50				0.0	0.4	1.00				0.0	0.1	0.83
Yellow-rumped Warbler	0.0	0.5	1.00	5.7	4.0	0.28	8.3	6.0	0.30	6.7	3.8	0.33	5.1	3.5	0.38
Blackpoll Warbler				1.7	0.8	0.29	0.5	0.1	0.17				0.6	0.2	0.29
Northern Waterthrush	0.5	1.3	0.85	0.0	1.1	1.00	0.0	0.3	1.00	0.0	0.3	1.00	0.1	0.7	0.91
Wilson's Warbler	35.8	43.4	0.51	22.8	31.8	0.56	18.6	24.2	0.52	4.4	10.4	0.55	20.5	27.6	0.55
American Tree Sparrow	13.2	18.4	0.54	3.7	10.9	0.75	0.7	8.6	0.86	0.0	0.8	1.00	4.4	9.7	0.67
Savannah Sparrow	0.4	1.9	0.87	0.4	1.6	0.69	0.0	0.3	1.00				0.2	1.0	0.84
Fox Sparrow	5.0	2.9	0.26	0.4	0.8	0.67	0.0	1.0	1.00	0.0	0.4	1.00	1.3	1.3	0.37
Lincoln's Sparrow	0.0	0.8	1.00	0.0	1.1	1.00	0.1	0.5	0.83				0.0	0.6	0.96
White-crowned Sparrow	20.0	27.0	0.55	23.6	16.3	0.40	20.8	39.3	0.58	0.0	1.0	1.00	16.1	21.0	0.55

Table 8b. (cont.) Mean numbers of aged individual birds captured per 600 net-hours and proportion of young in the catch at the four long running MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) operated in Denali National Park averaged over the ten years, 1992-2001. Data are included only from stations that lie within the breeding range of the species.

	Igloo Creek			Mile Seven			Permafrost			Rock Creek			All stations pooled		
Species	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.	Ad.	Yg.	Prop.[1] Yg.
Golden-crowned Sparrow	0.8	0.3	0.33	0.1	0.2	0.50							0.2	0.1	0.47
Dark-eyed Junco	0.0	0.4	1.00	6.1	9.3	0.51	8.9	8.1	0.44	10.4	18.8	0.58	6.3	9.2	0.56
White-winged Crossbill				0.9	0.2	0.17	0.2	0.2	0.50	0.1	0.0	0.00	0.3	0.1	0.10
Common Redpoll	18.7	2.4	0.10	5.5	2.2	0.31	13.0	4.3	0.21	0.7	0.9	0.35	9.4	2.5	0.20
ALL SPECIES POOLED	163.8	145.5	0.45	87.2	88.5	0.49	96.7	106.8	0.51	44.1	49.4	0.51	98.0	97.8	0.49
NUMBER OF SPECIES	20	23		24	25		21	26		17	19		27	26	
TOTAL NUMBER OF SPECIES		27			28			28			24			30	

[1] Years for which the proportion of young was undefined (no aged birds were captured in the year) are not included in the mean proportion of young.

Table 9a. Summary statistics for survival analyses with temporally variable survival and recapture probabilities and proportions of residents among newly captured adults in transient models using ten years (1992-2001) of mark-recapture data from the four eastern MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) at Denali National Park. $QAIC_C$[1] and (GOF)[2] are presented for all models.

	Transient Models								
Species	$\varphi p \tau$[3]	$\varphi_t p \tau$[4]	$\varphi p_t \tau$[5]	$\varphi p \tau_t$[6]	$\varphi_t p_t \tau$[7]	$\varphi_t p \tau_t$[8]	$\varphi p_t \tau_t$[9]	$\varphi_t p_t \tau_t$[10]	$\Delta QAIC_C$[11]
Boreal Chickadee	71.4* (1.000)	85.7 (1.000)	85.5 (1.000)	86.9 (1.000)	108.9 (1.000)	111.1 (1.000)	110.2 (1.000)	139.5 (1.000)	14.3
Arctic Warbler	97.9* (1.000)	102.6 (1.000)	107.1 (1.000)	108.2 (1.000)	110.7 (1.000)	113.9 (1.000)	119.0 (1.000)	121.5 (1.000)	4.7
Swainson's Thrush	87.8* (0.999)	98.9 (1.000)	97.1 (1.000)	100.1 (0.999)	104.9 (1.000)	114.7 (1.000)	113.4 (1.000)	118.7 (1.000)	11.1
Orange-crowned Warbler	66.9* (1.000)	75.9 (1.000)	73.0 (1.000)	78.7 (1.000)	83.7 (1.000)	89.7 (1.000)	87.1 (1.000)	97.0 (1.000)	9.0
Yellow-rumped Warbler	54.1* (1.000)	68.9 (1.000)	64.6 (1.000)	66.7 (1.000)	78.3 (1.000)	83.9 (1.000)	77.4 (1.000)	93.6 (1.000)	14.8
Wilson's Warbler	106.8* (1.000)	119.4 (1.000)	120.2 (1.000)	118.0 (1.000)	132.0 (1.000)	126.4 (1.000)	130.6 (1.000)	137.1 (1.000)	12.6
American Tree Sparrow	68.4* (1.000)	80.5 (1.000)	80.9 (1.000)	76.0 (1.000)	91.1 (1.000)	92.5 (1.000)	92.5 (1.000)	103.2 (1.000)	12.1
Fox Sparrow	44.9* (0.995)	59.6 (0.996)	62.5 (1.000)	67.3 (0.995)	117.9 (0.999)	131.4 (0.999)	127.1 (1.000)	388.6 (1.000)	14.7
White-crowned Sparrow	141.0* (0.995)	150.3 (0.996)	142.9* (1.000)	150.9 (0.995)	154.4 (0.999)	157.9 (0.999)	153.8 (1.000)	164.0 (1.000)	9.3
Dark-eyed Junco	75.9* (1.000)	87.5 (1.000)	88.6 (1.000)	87.4 (1.000)	101.3 (1.000)	100.7 (1.000)	103.3 (1.000)	113.2 (1.000)	11.6

Table 9a (cont.). Summary statistics for survival analyses with temporally variable survival and recapture probabilities and proportions of residents among newly captured adults in transient models using ten years (1992-2001) of mark-recapture data from the four eastern MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) at Denali National Park. $QAIC_C$[1] and (GOF)[2] are presented for all models.

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[1] Akaike Information Criterion ($QAIC_C$) given as -2(log-likelihood) + 2(number of estimable parameters) with corrections for small sample sizes and overdispersion of data.

[2] Goodness-of-fit is a measure of how well the actual distribution of data fits the theoretical distribution calculated using the estimates provided by the model. The larger the value provided by the GOF test the better the model describes the data.

[3] $\varphi p \tau$ Model: Transient model with temporally-constant survival probability, recapture probability, and proportion of residents (invariable from year to year).

[4] $\varphi_t p \tau$ Model: Transient model with temporally-variable survival probability; and temporally-constant recapture probability and proportion of residents.

[5] $\varphi p_t \tau$ Model: Transient model with temporally-variable recapture probability; and temporally-constant survival probability and proportion of residents.

[6] $\varphi p \tau_t$ Model: Transient model with temporally-variable proportion of residents; and temporally-constant survival and recapture probabilities.

[7] $\varphi_t p_t \tau$ Model: Transient model with temporally-variable survival and recapture probabilities; and temporally-constant proportion of residents.

[8] $\varphi_t p \tau_t$ Model: Transient model with temporally-variable survival probability and proportion of residents; and temporally-constant recapture probability.

[9] $\varphi p_t \tau_t$ Model: Transient model with temporally-variable recapture probability and proportion of residents; and temporally-constant survival probability.

[10] $\varphi_t p_t \tau_t$ Model: Transient model with temporally-variable survival probability, recapture probability, and proportion of residents.

[11] $\Delta QAIC_C$ is defined as the difference in $QAIC_C$ between the $\varphi p \tau$ model and the $\varphi_t p \tau$ model.

* The chosen models are the model with the lowest $QAIC_C$ and the models with $QAIC_C$s within 2.0 units of the model with the lowest $QAIC_C$.

Table 9b. Summary statistics for survival analyses with temporally variable survival and recapture probabilities and proportions of residents among newly captured adults in transient models using ten years (1992-2001) of mark-recapture data from all six MAPS stations at Denali National Park. $QAIC_C$[1] and (GOF)[2] are presented for all models.

Species	Transient Models								
	$\varphi p \tau$[3]	$\varphi_t p \tau$[4]	$\varphi p_t \tau$[5]	$\varphi p \tau_t$[6]	$\varphi_t p_t \tau$[7]	$\varphi_t p \tau_t$[8]	$\varphi p_t \tau_t$[9]	$\varphi_t p_t \tau_t$[10]	$\Delta QAIC_C$[11]
Boreal Chickadee	71.4* (1.000)	85.7 (1.000)	85.5 (1.000)	86.9 (1.000)	108.9 (1.000)	111.1 (1.000)	110.2 (1.000)	139.5 (1.000)	14.3
Arctic Warbler	97.4* (1.000)	101.6 (1.000)	105.8 (1.000)	108.0 (1.000)	109.7 (1.000)	113.4 (1.000)	118.1 (1.000)	120.9 (1.000)	4.2
Gray-cheeked Thrush	28.1* (1.000)	64.0 (1.000)	64.3 (1.000)	67.3 (1.000)	278.1 (1.000)	431.2 (1.000)	431.7 (1.000)	n/a	35.9
Swainson's Thrush	91.0* (0.999)	102.8 (0.999)	99.5 (1.000)	105.4 (0.999)	110.1 (1.000)	118.7 (0.999)	117.5 (1.000)	125.6 (1.000)	11.8
Orange-crowned Warbler	86.2* (1.000)	96.3 (1.000)	92.0 (1.000)	99.2 (1.000)	102.9 (1.000)	110.9 (1.000)	105.9 (1.000)	118.2 (1.000)	10.1
Yellow-rumped Warbler	54.1* (1.000)	68.9 (1.000)	64.6 (1.000)	66.7 (1.000)	78.3 (1.000)	83.9 (1.000)	77.4 (1.000)	93.6 (1.000)	14.8
Wilson's Warbler	127.6* (1.000)	137.5 (1.000)	136.1 (1.000)	137.1 (1.000)	148.2 (1.000)	145.3 (1.000)	147.0 (1.000)	153.7 (1.000)	9.9
American Tree Sparrow	80.1* (1.000)	91.6 (1.000)	89.9 (1.000)	89.1 (1.000)	98.6 (1.000)	103.4 (1.000)	101.0 (1.000)	108.4 (1.000)	11.5
Fox Sparrow	61.0* (1.000)	72.8 (1.000)	73.0 (1.000)	75.2 (1.000)	92.5 (1.000)	90.3 (1.000)	95.2 (1.000)	119.9 (1.000)	11.8
White-crowned Sparrow	151.4* (0.970)	160.4 (0.975)	152.6* (0.997)	157.9 (0.986)	162.2 (0.997)	165.0 (0.995)	160.1 (0.999)	169.3 (0.999)	9.0
Dark-eyed Junco	77.4* (1.000)	88.8 (1.000)	90.4 (1.000)	88.9 (1.000)	102.8 (1.000)	101.4 (1.000)	104.8 (1.000)	114.4 (1.000)	11.4

Table 9b. (cont.). Summary statistics for survival analyses with temporally variable survival and recapture probabilities and proportions of residents among newly captured adults in transient models using ten years (1992-2001) of mark-recapture data from all six MAPS stations at Denali National Park. $QAIC_C$[1] and (GOF)[2] are presented for all models.

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[1] Akaike Information Criterion ($QAIC_C$) given as -2(log-likelihood) + 2(number of estimable parameters) with corrections for small sample sizes and overdispersion of data.

[2] Goodness-of-fit is a measure of how well the actual distribution of data fits the theoretical distribution calculated using the estimates provided by the model. The larger the value provided by the GOF test the better the model describes the data.

[3] $\varphi p \tau$ Model: Transient model with temporally-constant survival probability, recapture probability, and proportion of residents (invariable from year to year).

[4] $\varphi_t p \tau$ Model: Transient model with temporally-variable survival probability; and temporally-constant recapture probability and proportion of residents.

[5] $\varphi p_t \tau$ Model: Transient model with temporally-variable recapture probability; and temporally-constant survival probability and proportion of residents.

[6] $\varphi p \tau_t$ Model: Transient model with temporally-variable proportion of residents; and temporally-constant survival and recapture probabilities.

[7] $\varphi_t p_t \tau$ Model: Transient model with temporally-variable survival and recapture probabilities; and temporally-constant proportion of residents.

[8] $\varphi_t p \tau_t$ Model: Transient model with temporally-variable survival probability and proportion of residents; and temporally-constant recapture probability.

[9] $\varphi p_t \tau_t$ Model: Transient model with temporally-variable recapture probability and proportion of residents; and temporally-constant survival probability.

[10] $\varphi_t p_t \tau_t$ Model: Transient model with temporally-variable survival probability, recapture probability, and proportion of residents.

[11] $\Delta QAIC_C$ is defined as the difference in $QAIC_C$ between the $\varphi p \tau$ model and the $\varphi_t p \tau$ model.

* The chosen models are the model with the lowest $QAIC_C$ and the models with $QAIC_C$s within 2.0 units of the model with the lowest $QAIC_C$.

Table 10a. Estimates of adult survival and recapture probabilities and proportion of residents using both temporally variable and time-constant models for ten species breeding at the four eastern MAPS stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park obtained from ten years (1992-2001) of mark-recapture data.

Species	Num. sta[1]	Num. ind.[2]	Num. caps.[3]	Num. ret.[4]	Model[5]	$QAIC_C$[6]	Survival probability[7]	Surv. C.V.[8]	Recapture probability[9]	Proportion of residents[10]
Boreal Chickadee	3	56	88	17	$\varphi p \tau$	71.4	0.591 (0.105)	17.8	0.326 (0.120)	1.000 (0.427)
Arctic Warbler	1	231	417	47	$\varphi p \tau$	97.9	0.355 (0.056)	15.8	0.609 (0.106)	0.585 (0.153)
Swainson's Thrush	2	94	153	27	$\varphi p \tau$	87.8	0.550 (0.077)	14.0	0.480 (0.109)	0.511 (0.169)
Orange-crowned Warbler	2	122	196	18	$\varphi p \tau$	66.9	0.461 (0.097)	21.0	0.400 (0.138)	0.424 (0.182)
Yellow-rumped Warbler	3	116	148	11	$\varphi p \tau$	54.1	0.535 (0.132)	24.7	0.220 (0.118)	0.442 (0.255)
Wilson's Warbler	4	470	772	52	$\varphi p \tau$	106.8	0.383 (0.054)	14.1	0.412 (0.087)	0.368 (0.096)
American Tree Sparrow	2	87	185	25	$\varphi p \tau$	68.4	0.482 (0.076)	15.8	0.625 (0.123)	0.352 (0.135)
Fox Sparrow	1	24	48	8	$\varphi p \tau$	44.9	0.489 (0.137)	28.0	0.547 (0.217)	0.589 (0.372)
White-crowned Sparrow	3	330	601	80	$\varphi p \tau$	141.0	0.465 (0.046)	9.9	0.401 (0.065)	0.772 (0.153)
					$\varphi p_t \tau$	142.9	0.441 (0.046)	10.4	a0.503 (0.150)	0.787 (0.156)
									b0.415 (0.135)	
									c0.158 (0.077)	
									d0.660 (0.154)	
									e0.500 (0.149)	
									f0.409 (0.136)	
									g0.334 (0.111)	
									h0.349 (0.129)	
									i0.688 (0.208)	
Dark-eyed Junco	3	137	229	20	$\varphi p \tau$	75.9	0.441 (0.091)	20.6	0.380 (0.126)	0.437 (0.180)

Table 10a. (cont.). Estimates of adult survival and recapture probabilities and proportion of residents using both temporally variable and time-constant models for ten species breeding at the four eastern MAPS stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park obtained from ten years (1992-2001) of mark-recapture data.

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[1] Number of stations where the species was a regular or usual breeder at which adults of the species were captured.

[2] Number of adult individuals captured at stations where the species was a regular or usual breeder (i.e., number of capture histories).

[3] Total number of captures of adult birds of the species at stations where the species was a regular or usual breeder.

[4] Total number of returns. A return is the first recapture in a given year of a bird originally banded at the same station in a previous year.

[5] Models included are those chosen by $QAIC_C$ (those models marked with * in Table 9) plus the $\varphi p \tau$ model in all cases. See Table 9 for definitions of the models.

[6] Akaike Information Criterion ($QAIC_C$) given as -2(log-likelihood) + 2(number of estimable parameters) with corrections for small sample size and overdispersion of data.

[7] Survival probability presented as the maximum likelihood estimate (standard error of the estimate).

[8] The coefficient of variation for survival probability.

[9] Recapture probability presented as the maximum likelihood estimate (standard error of the estimate).

a The recapture probability in 1993 in a temporally variable model.
b The recapture probability in 1994 in a temporally variable model.
c The recapture probability in 1995 in a temporally variable model.
d The recapture probability in 1996 in a temporally variable model.
e The recapture probability in 1997 in a temporally variable model.
f The recapture probability in 1998 in a temporally variable model.
g The recapture probability in 1999 in a temporally variable model.
h The recapture probability in 2000 in a temporally variable model.
i The recapture probability in 2001 in a temporally variable model.

[10] The proportion of residents among newly captured adults presented as the maximum likelihood estimate (standard error of the estimate).

Table 10b. Estimates of adult survival and recapture probabilities and proportion of residents using both temporally variable and time-constant models for eleven species breeding at six MAPS stations in Denali National Park obtained from ten years (1992-2001) of mark-recapture data.

Species	Num. sta[1]	Num. ind.[2]	Num. caps.[3]	Num. ret.[4]	Model[5]	$QAIC_C$[6]	Survival probability[7]	Surv. C.V.[8]	Recapture probability[9]	Proportion of residents[10]
Boreal Chickadee	3	56	88	17	$\varphi p \tau$	71.4	0.591 (0.105)	17.8	0.326 (0.120)	1.000 (0.427)
Arctic Warbler	2	242	444	47	$\varphi p \tau$	97.4	0.348 (0.055)	15.8	0.600 (0.107)	0.587 (0.154)
Gray-cheeked Thrush	1	21	39	10	$\varphi p \tau$	28.1	0.639 (0.154)	24.1	0.784 (0.173)	0.641 (0.307)
Swainson's Thrush	3	98	160	29	$\varphi p \tau$	91.0	0.563 (0.076)	13.5	0.477 (0.104)	0.522 (0.165)
Orange-crowned Warbler	4	237	386	35	$\varphi p \tau$	86.2	0.460 (0.073)	15.9	0.423 (0.105)	0.425 (0.130)
Yellow-rumped Warbler	3	116	148	11	$\varphi p \tau$	54.1	0.535 (0.132)	24.7	0.220 (0.118)	0.442 (0.255)
Wilson's Warbler	6	762	1282	81	$\varphi p \tau$	127.6	0.377 (0.045)	11.9	0.409 (0.072)	0.398 (0.083)
American Tree Sparrow	4	144	259	29	$\varphi p \tau$	80.1	0.478 (0.073)	15.3	0.530 (0.116)	0.342 (0.118)
Fox Sparrow	3	58	109	16	$\varphi p \tau$	61.0	0.487 (0.108)	22.2	0.483 (0.159)	0.804 (0.342)
White-crowned Sparrow	5	433	738	89	$\varphi p \tau$	151.4	0.470 (0.045)	9.6	0.368 (0.060)	0.709 (0.135)
					$\varphi p_t \tau$	152.6	0.459 (0.046)	10.0	a0.514 (0.151)	0.709 (0.134)
									b0.424 (0.136)	
									c0.161 (0.078)	
									d0.668 (0.153)	
									e0.501 (0.150)	
									f0.387 (0.116)	
									g0.286 (0.086)	
									h0.252 (0.092)	
									i0.483 (0.144)	
Dark-eyed Junco	4	140	235	21	$\varphi p \tau$	77.4	0.442 (0.089)	20.1	0.402 (0.126)	0.412 (0.167)

Table 10b. (cont.) Estimates of adult survival and recapture probabilities and proportion of residents using both temporally variable and time-constant models for eleven species breeding at six MAPS stations in Denali National Park obtained from ten years (1992-2001) of mark-recapture data.

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[1] Number of stations where the species was a regular or usual breeder at which adults of the species were captured.

[2] Number of adult individuals captured at stations where the species was a regular or usual breeder (i.e., number of capture histories).

[3] Total number of captures of adult birds of the species at stations where the species was a regular or usual breeder.

[4] Total number of returns. A return is the first recapture in a given year of a bird originally banded at the same station in a previous year.

[5] Models included are those chosen by $QAIC_C$ (those models marked with * in Table 9) plus the $\varphi p \tau$ model in all cases. See Table 9 for definitions of the models.

[6] Akaike Information Criterion ($QAIC_C$) given as -2(log-likelihood) + 2(number of estimable parameters) with corrections for small sample size and overdispersion of data.

[7] Survival probability presented as the maximum likelihood estimate (standard error of the estimate).

[8] The coefficient of variation for survival probability.

[9] Recapture probability presented as the maximum likelihood estimate (standard error of the estimate).

a The recapture probability in 1993 in a temporally variable model.
b The recapture probability in 1994 in a temporally variable model.
c The recapture probability in 1995 in a temporally variable model.
d The recapture probability in 1996 in a temporally variable model.
e The recapture probability in 1997 in a temporally variable model.
f The recapture probability in 1998 in a temporally variable model.
g The recapture probability in 1999 in a temporally variable model.
h The recapture probability in 2000 in a temporally variable model.
i The recapture probability in 2001 in a temporally variable model.

[10] The proportion of residents among newly captured adults presented as the maximum likelihood estimate (standard error of the estimate).

Table 11. Relative values of vital rates (lower-than-expected, as-expected, higher-than-expected) for selected study species in Denali National Park in relation to the direction and significance of their adult population trends over the years 1992-2001.

Species	Direction & Significance of the trend[1]	Productivity	Survival Probability
Boreal Chickadee	+**	lower	higher
Arctic Warbler	-**	lower	lower
Swainson's Thrush	-*	lower	higher ?
Orange-crowned Warbler	+	expected	expected
Yellow-rumped Warbler	+***	lower ?	higher
Wilson's Warbler	-*	higher ?	lower
American Tree Sparrow	-	higher	expected
Fox Sparrow	-	expected	expected
White-crowned Sparrow	-	higher	expected
Dark-eyed Junco	+	higher	expected

[1] Direction and significance of the trends in adult population size as based on data from all six stations (Fig. 3b): + positive trend, - negative trend; *** $P < 0.01$, ** $0.01 \leq P < 0.05$, * $0.05 \leq P < 0.10$.

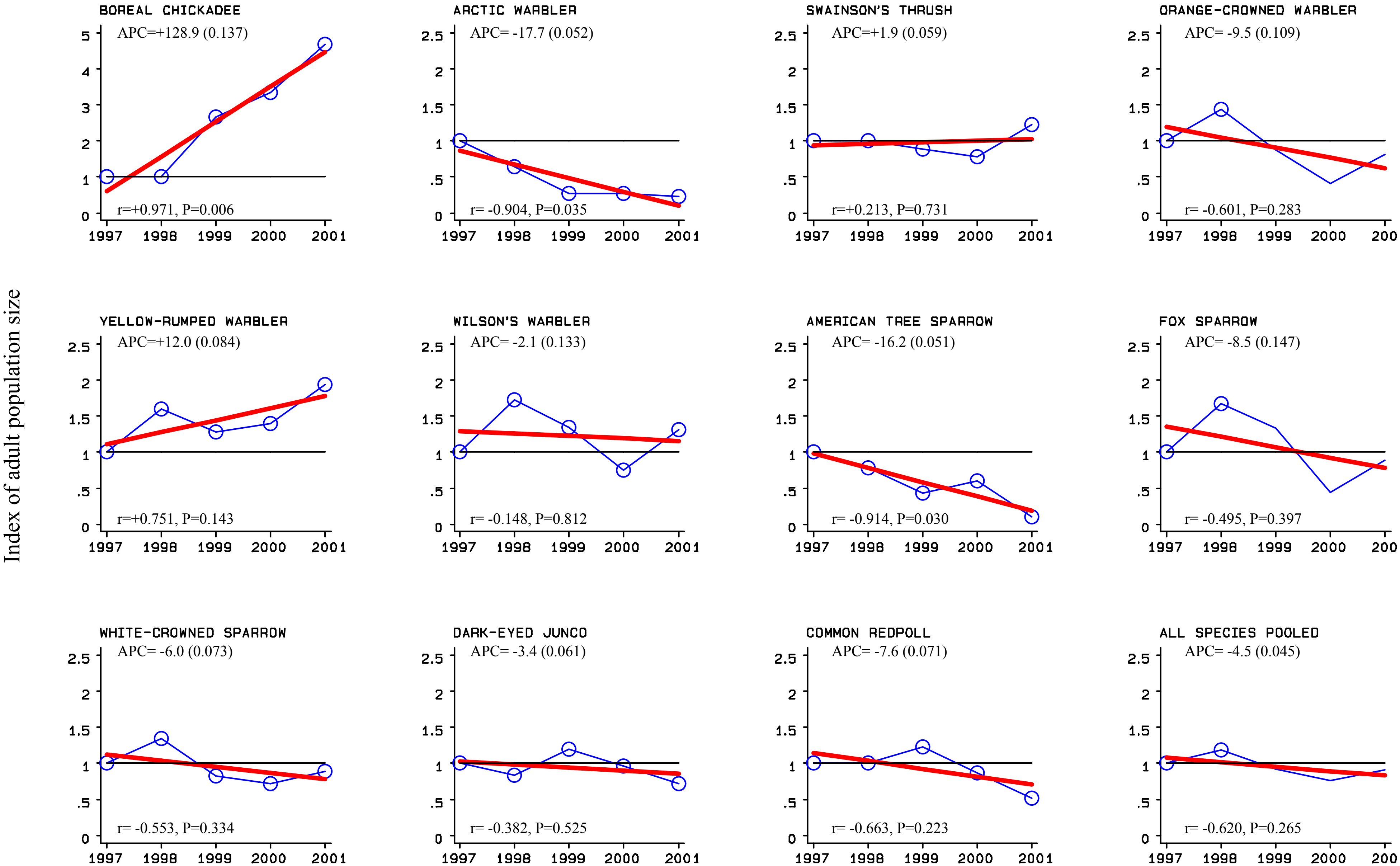

Figure 1a. Population trends for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the five years 1997-2001. The index of population size was arbitrarily defined as 1.0 in 1997. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. The annual percentage change in the index of adult population size was used as the measure of the population trend (*APC*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

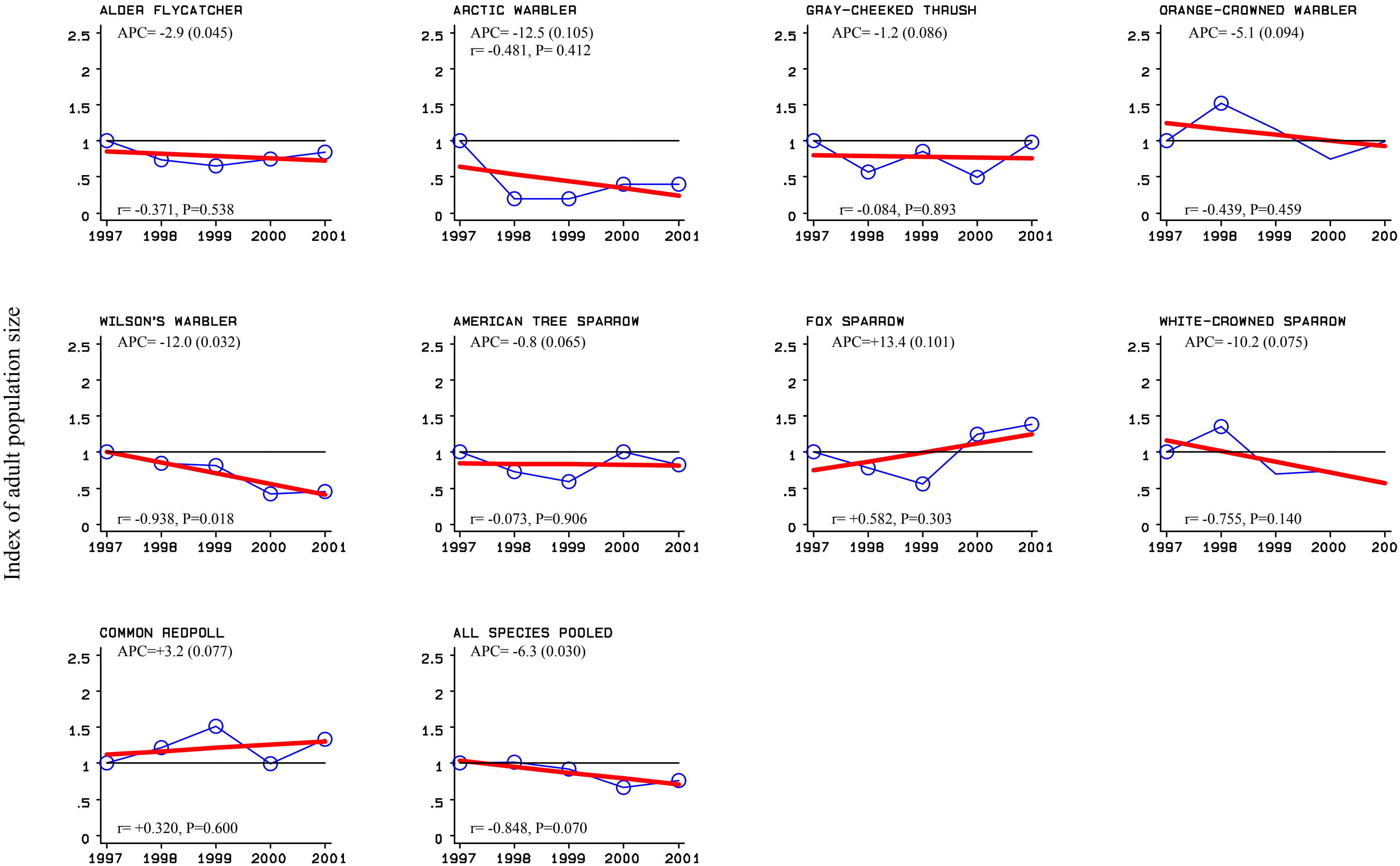

Figure 1b. Population trends for nine species and all species pooled at two stations (Strangler Hill, Buhach Creek) in Denali National Park over the five years 1997-2001. The index of population size was arbitrarily defined as 1.0 in 1997. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. The annual percentage change in the index of adult population size was used as the measure of the population trend (*APC*), and it and the standard error of the slope (in parentheses are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

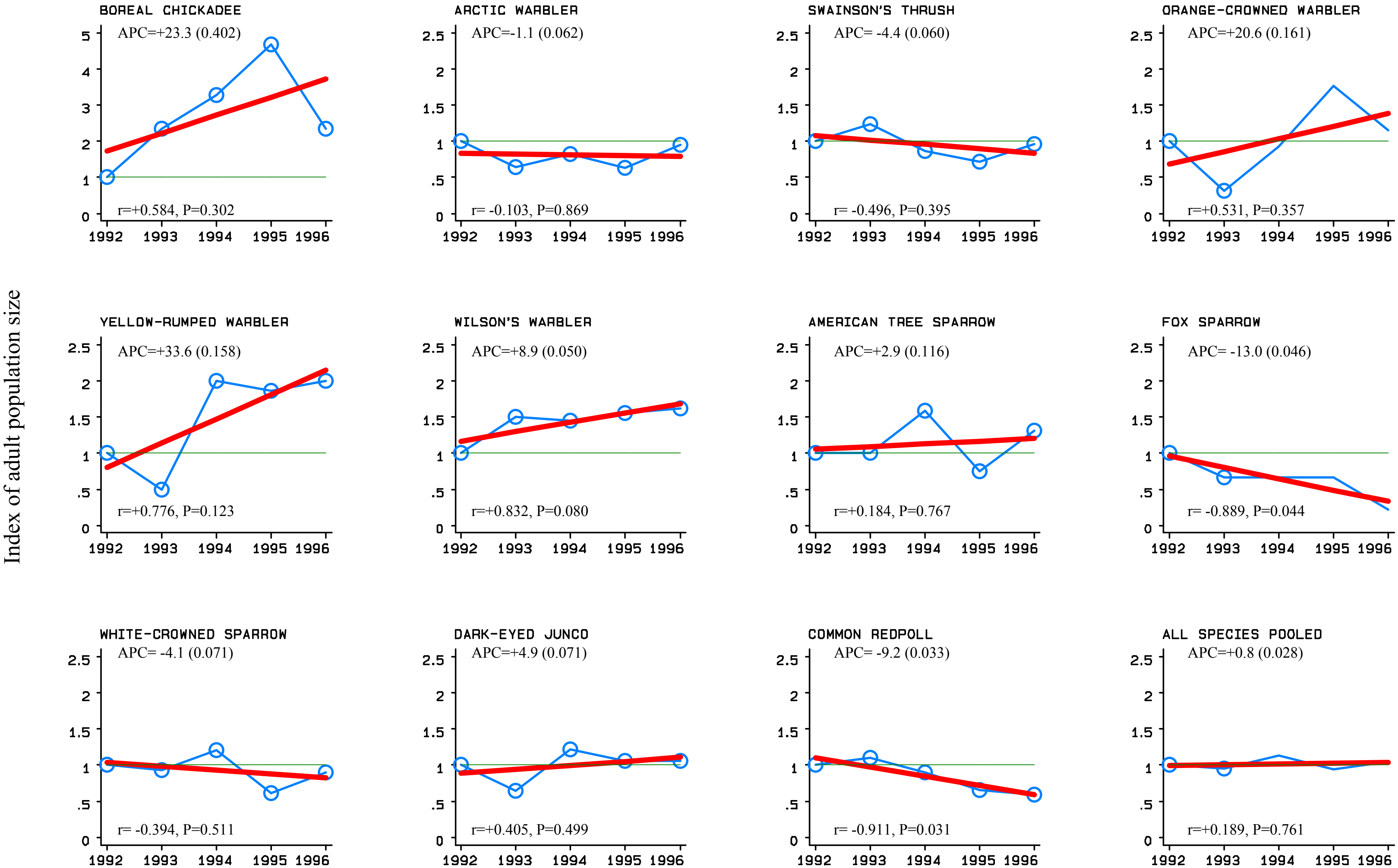

Figure 2. Population trends for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the five years 1992-1996. The index of population size was arbitrarily defined as 1.0 in 1992. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. The annual percentage change in the index of adult population size was used as the measure of the population trend (*APC*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

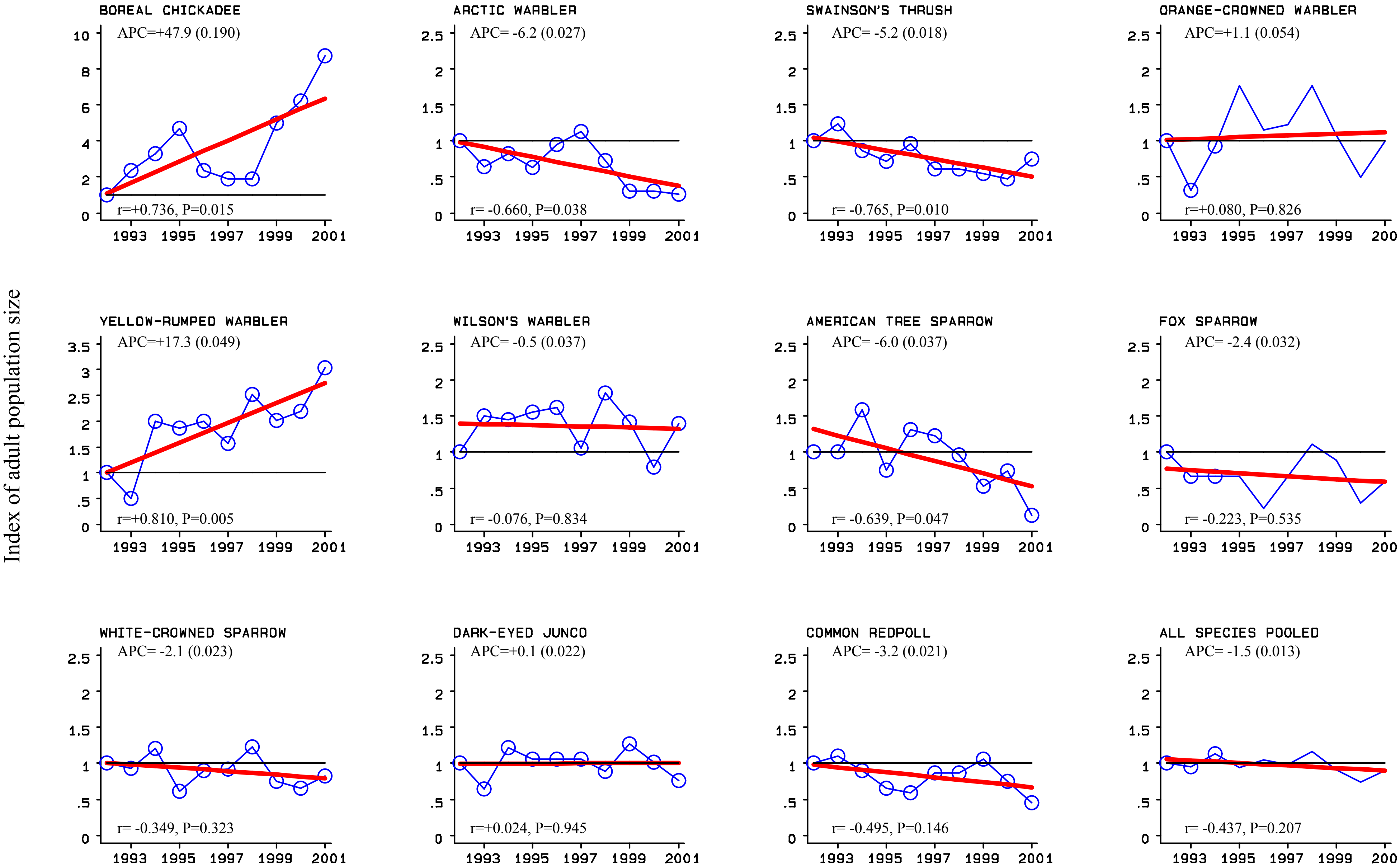

Figure 3a. Population trends for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the ten years 1992-2001. The index of population size was arbitrarily defined as 1.0 in 1992. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. The annual percentage change in the index of adult population size was used as the measure of the population trend (*APC*), and it and the standard error of the slope (in parenthesis) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

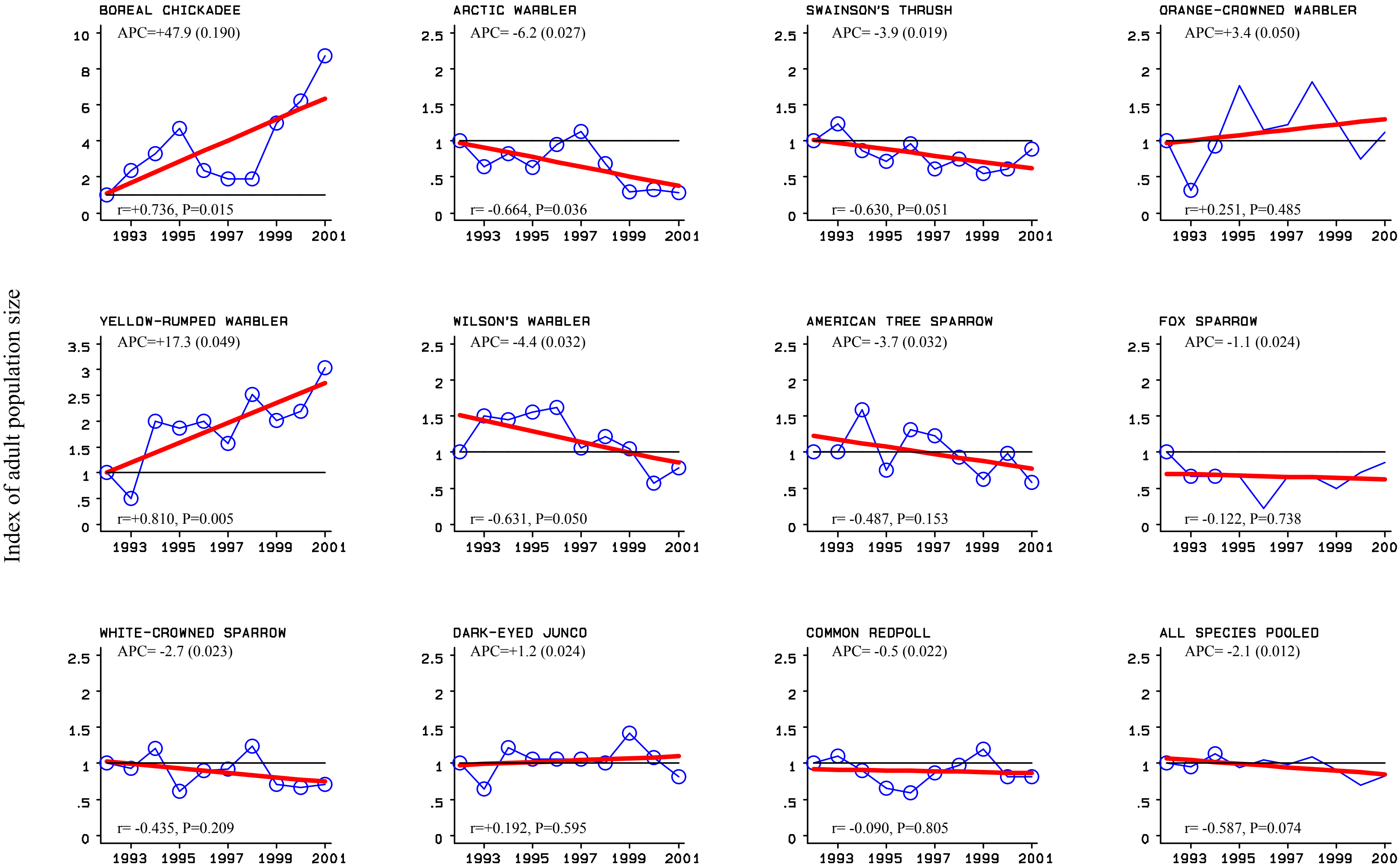

Figure 3b. Population trends for 11 species and all species pooled at all six stations in Denali National Park over the ten years 1992-2001. The index of population size was arbitrarily defined as 1.0 in 1992. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. The annual percentage change in the index of adult population size was used as the measure of the population trend (*APC*), and it and the standard error of the slope (in parenthesis) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

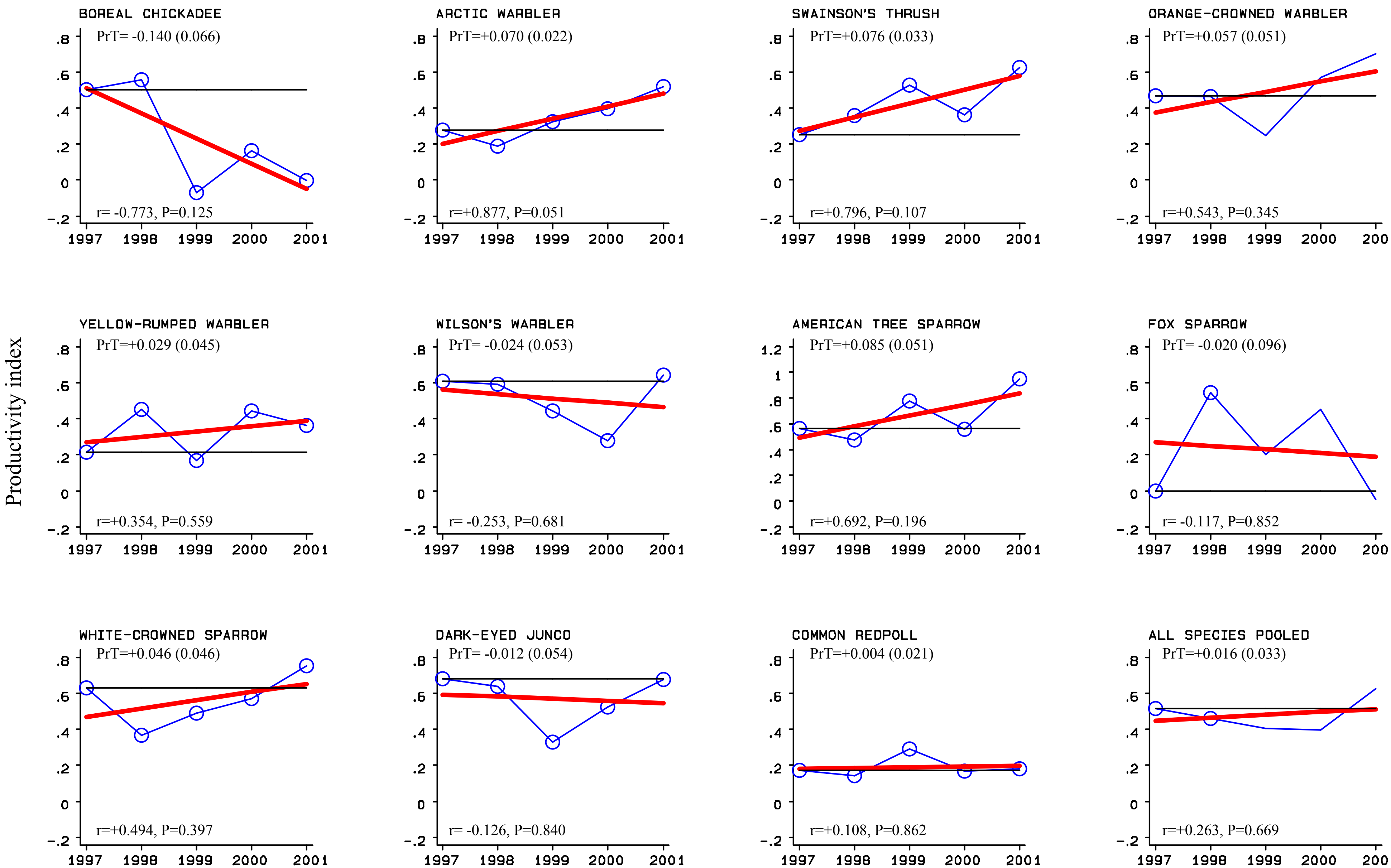

Figure 4a. Trend in productivity for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the five years 1997-2001. The productivity index was defined as the actual productivity value in 1997. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line for annual change in the index of productivity was used as the measure of the productivity trend (*PrT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

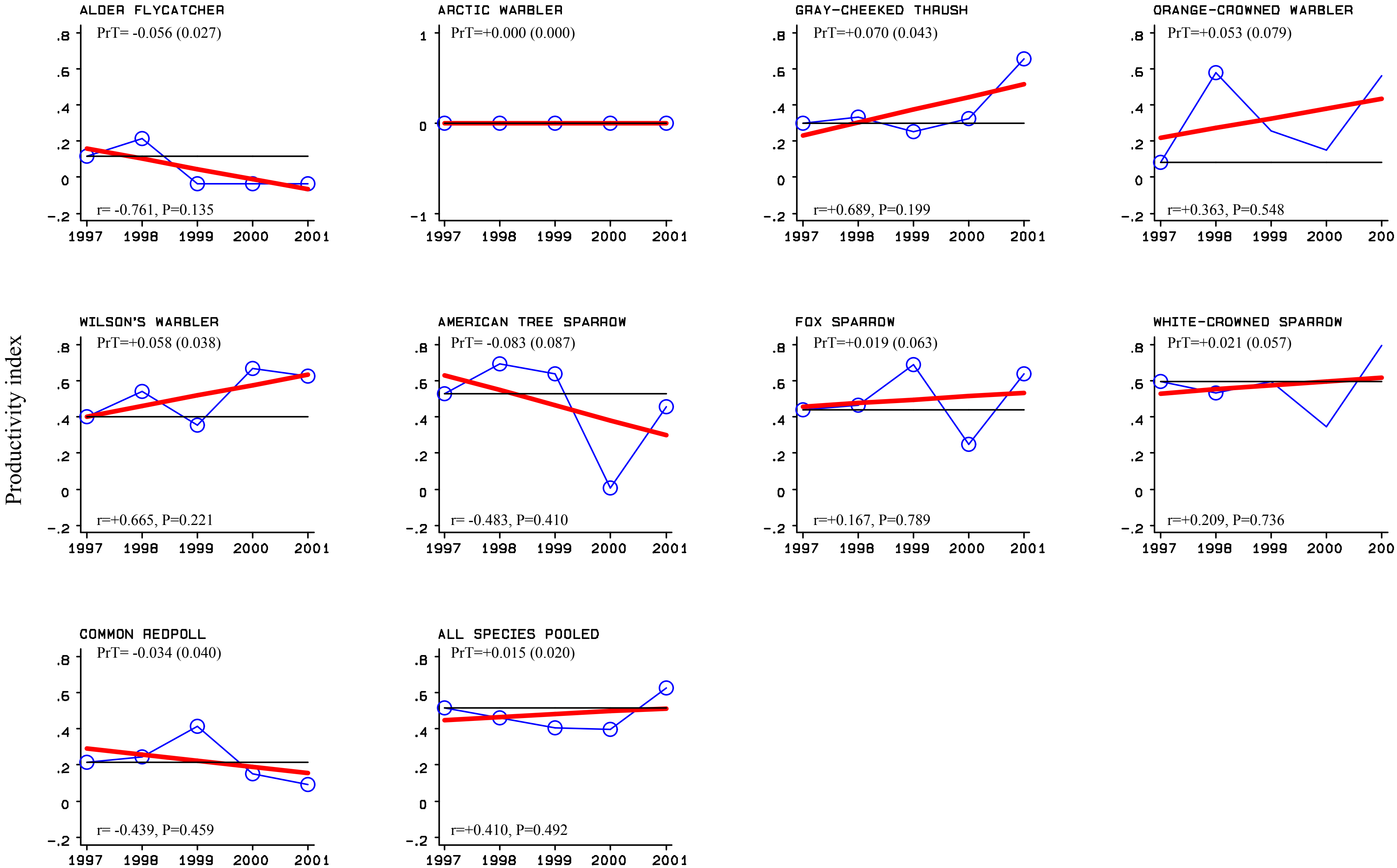

Figure 4b. Trend in productivity for nine species and all species pooled at two stations (Strangler Hill, Buhach Creek) in Denali National Park over the five years 1997-2001. The productivity index was defined as the actual productivity value in 1997. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line for annual change in the index of productivity was used as the measure of the productivity trend (*PrT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

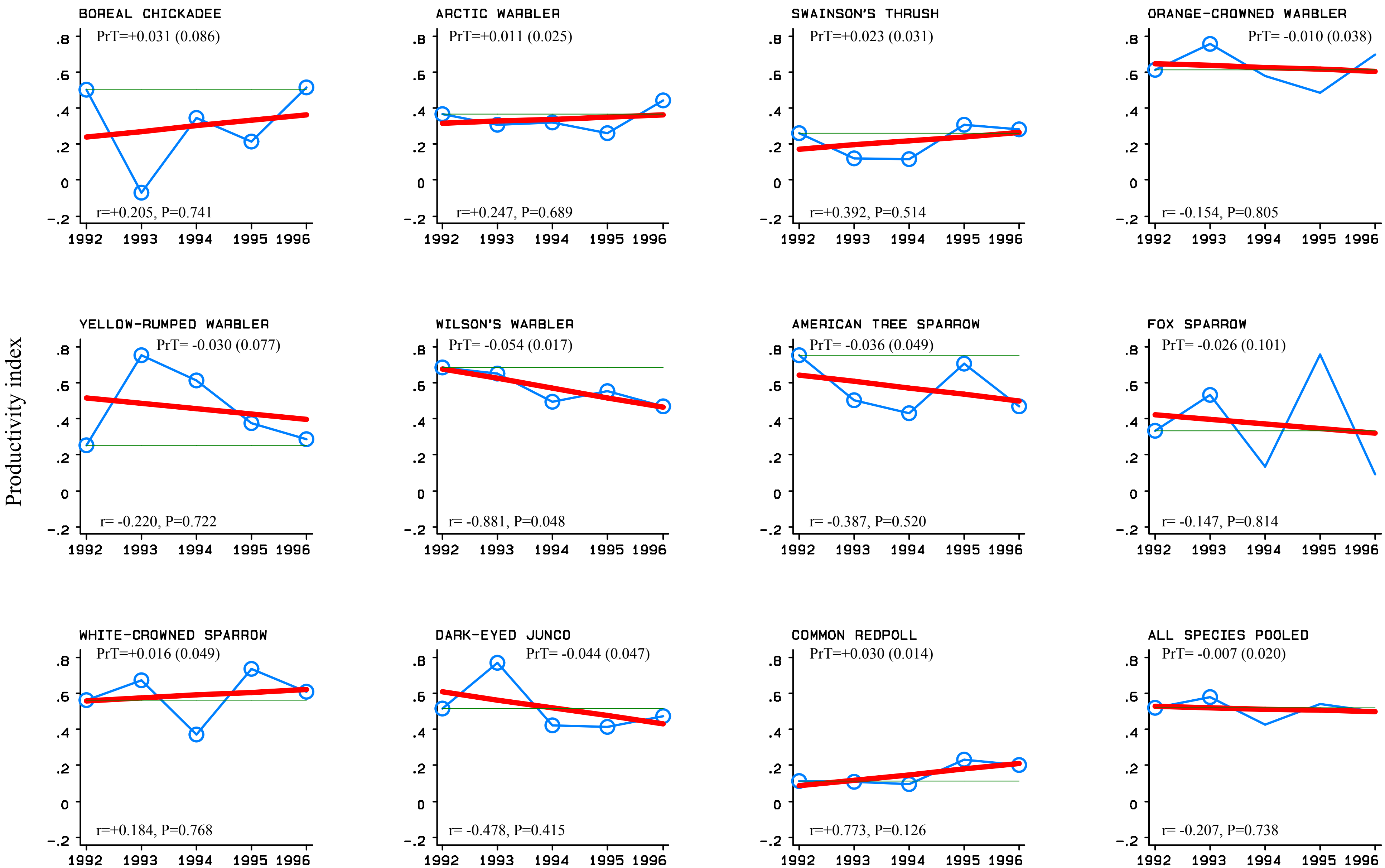

Figure 5. Trend in productivity for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the five years 1992-1996. The productivity index was defined as the actual productivity value in 1992. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line for annual change in the index of productivity was used as the measure of the productivity trend (*PrT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

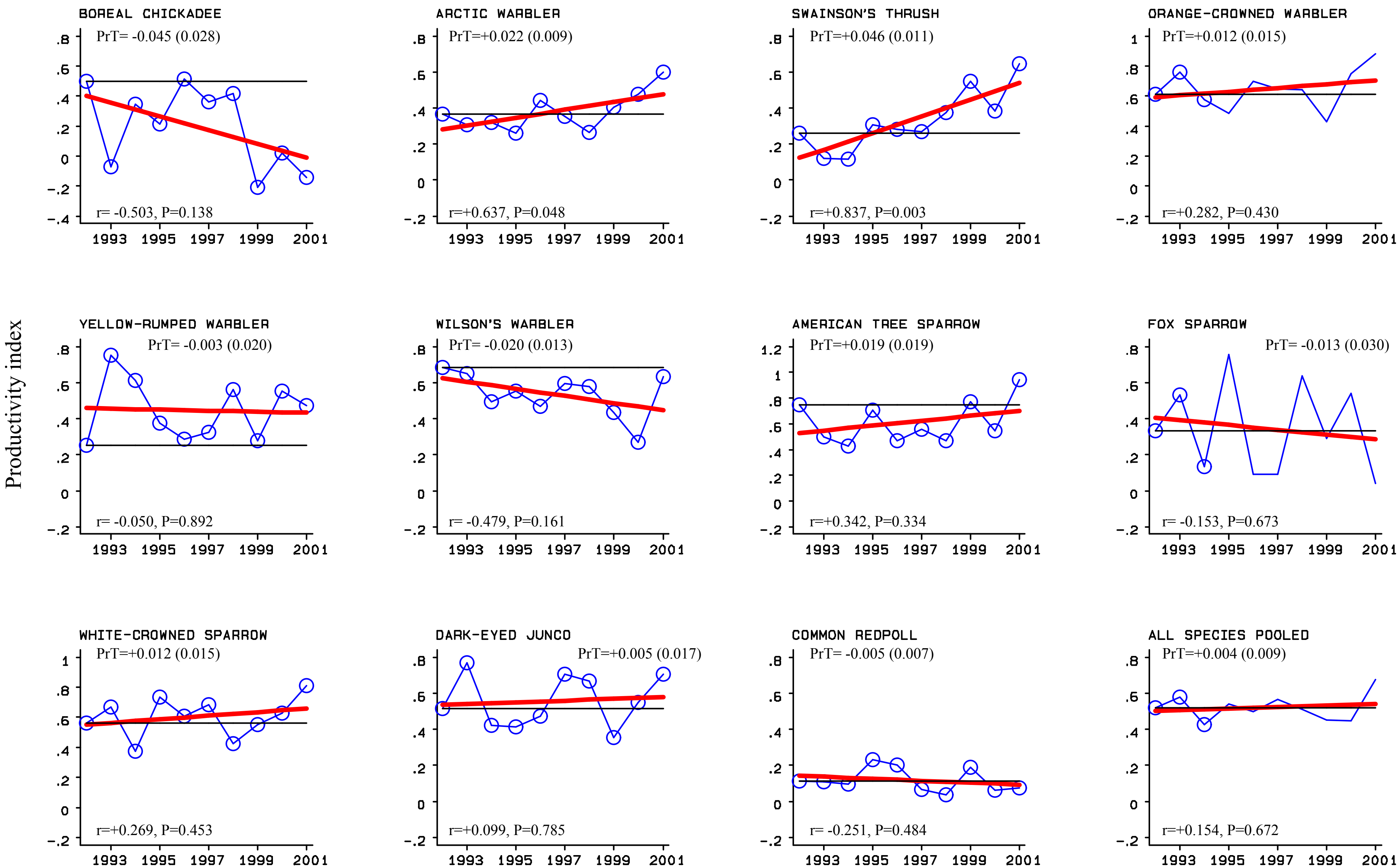

Figure 6a. Trend in productivity for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the ten years 1992-2001. The productivity index was defined as the actual productivity value in 1992. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line for annual change in the index of productivity was used as the measure of the productivity trend (*PrT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

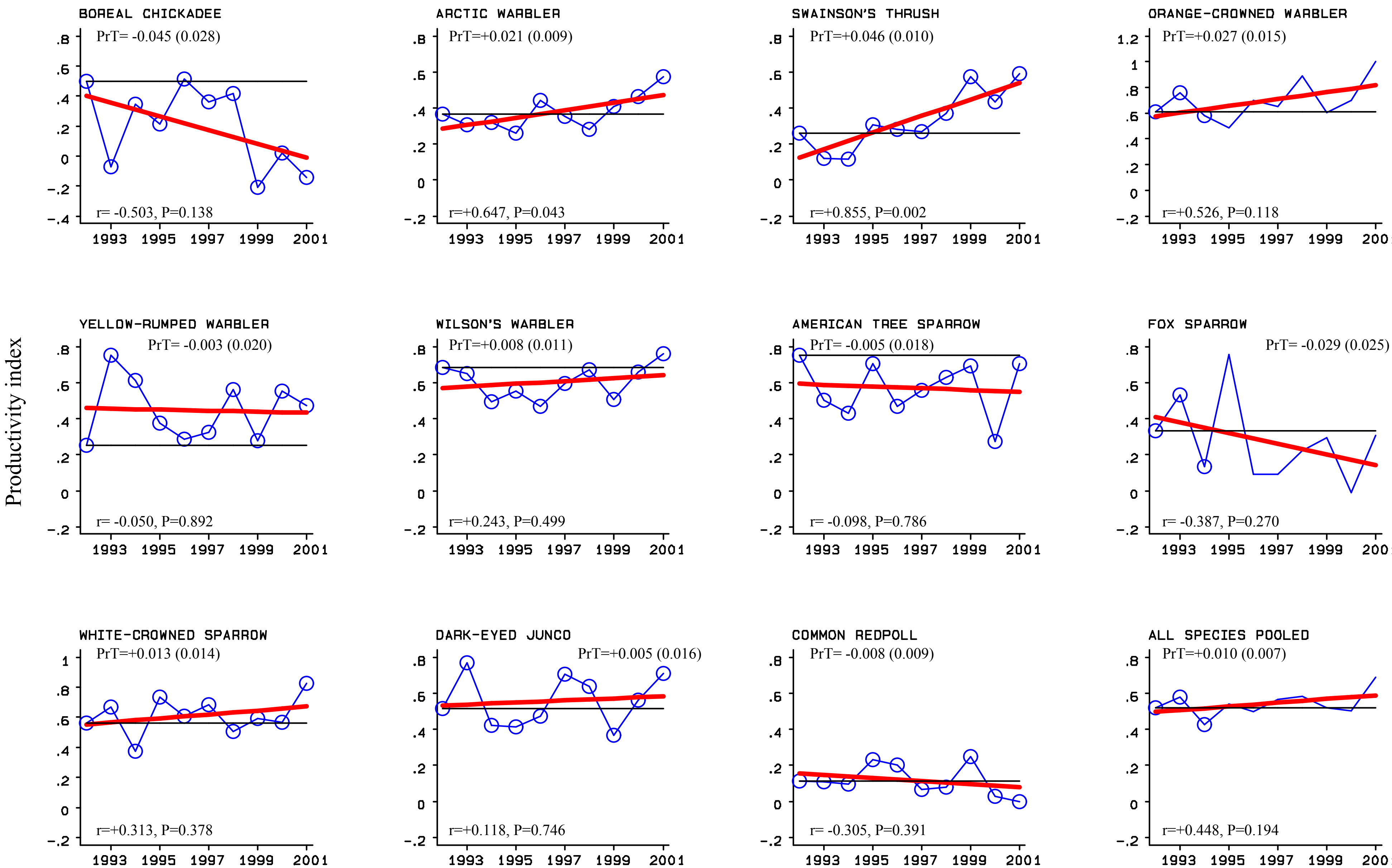

Figure 6b. Trend in productivity for 11 species and all species pooled at all six stations in Denali National Park over the ten years 1992-2001. The productivity index was defined as the actual productivity value in 1992. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line for annual change in the index of productivity was used as the measure of the productivity trend (*PrT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

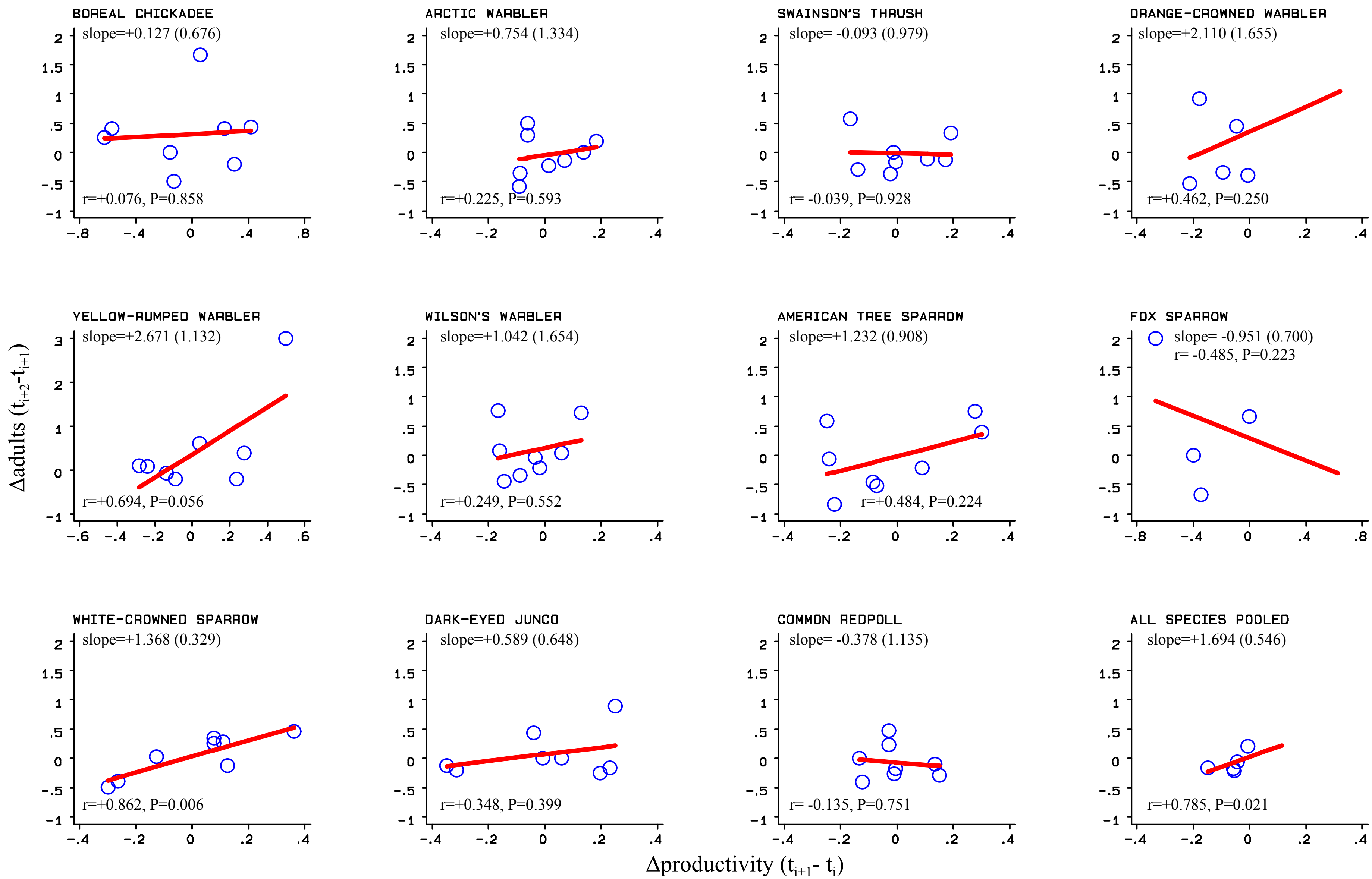

Figure 7a. The regression of the proportional change in the number of adults between year i+2 and year i+1 on the absolute change in productivity between year i+1 and year i ("productivity/population correlation") for 11 species and all species pooled at four stations (Igloo Creek, Mile Seven, Permafrost, Rock Creek) in Denali National Park over the years 1992-2001. The constant-effort between-year changes were obtained from data pooled from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line, the standard error of the slope (in parentheses), the correlation coefficient (*r*), and significance of the correlation coefficient (*P*) are presented on each graph.

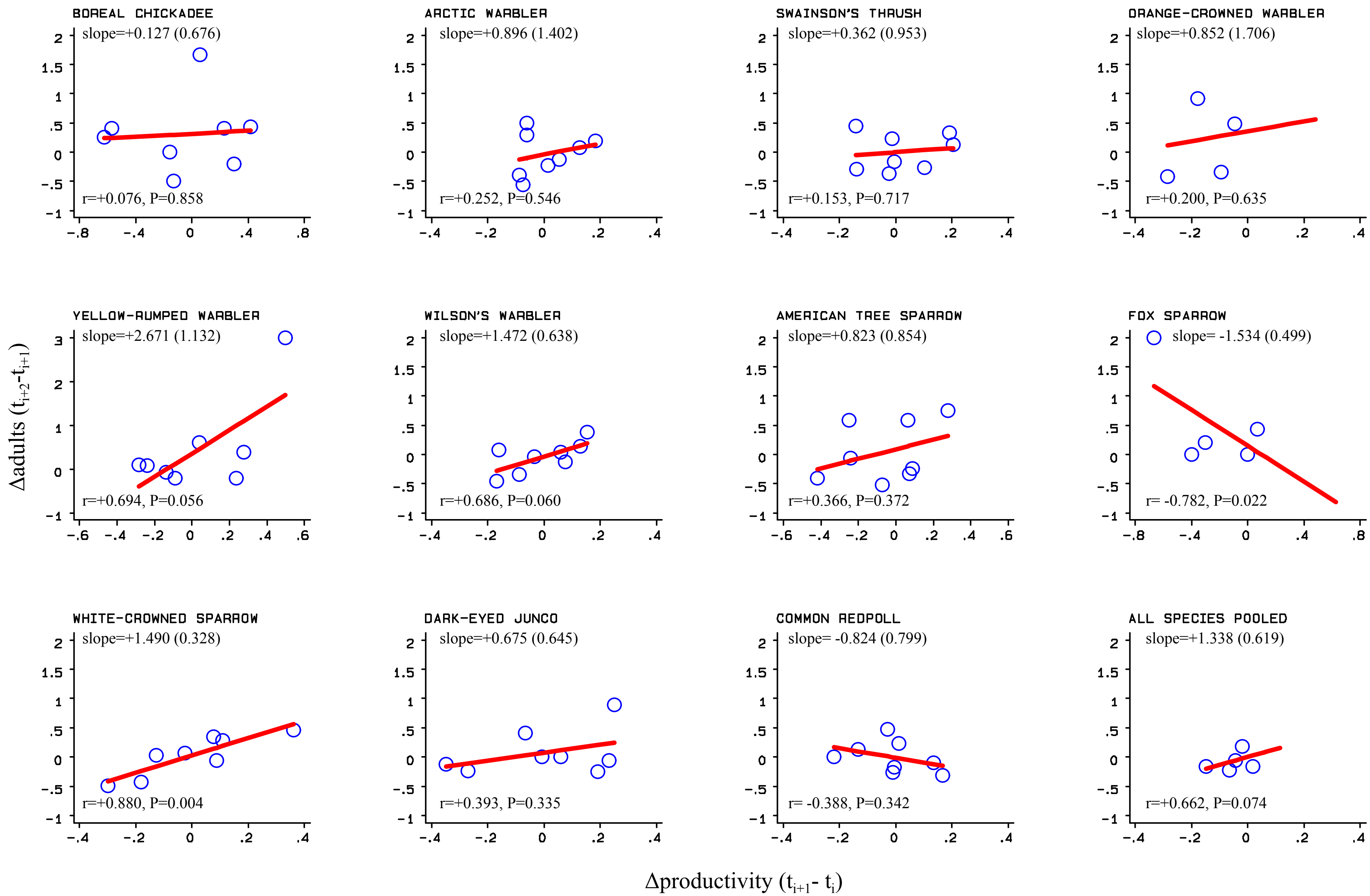

Figure 7b. The regression of the proportional change in the number of adults between year i+2 and year i+1 on the absolute change in productivity between year i+1 and year i ("productivity/population correlation") for 11 species and all species pooled at all six stations in Denali National Park over the years 1992-2001. The constant-effort between-year changes were obtained from data pooled from stations where the species was a regular or usual breeder and summer resident. The slope of the regression line, the standard error of the slope (in parentheses), the correlation coefficient (*r*), and significance of the correlation coefficient (*P*) are presented on each graph.

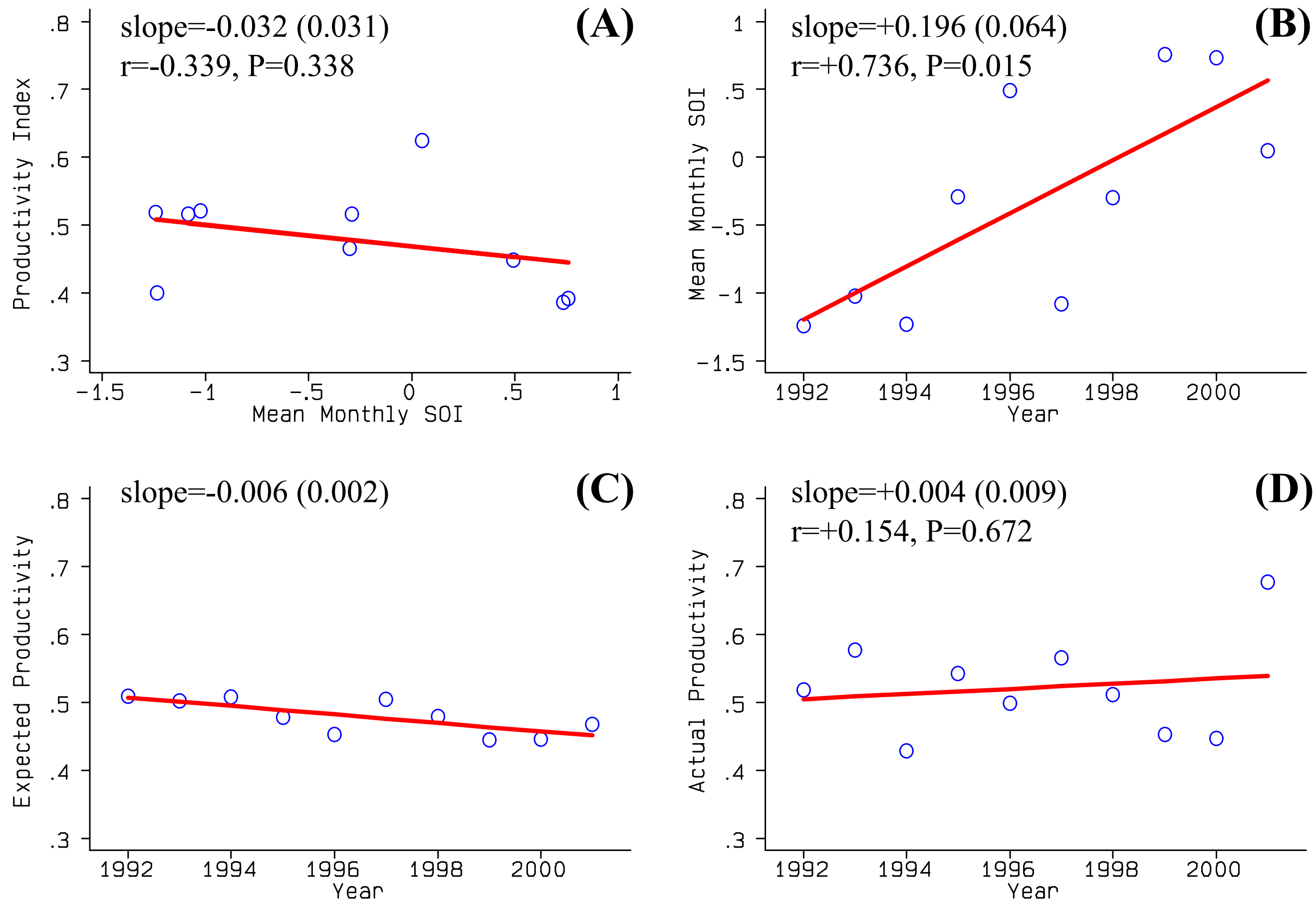

Figure 8. Effects of El Nino/Southern Oscillation (ENSO) on productivity of all species pooled at the four long running MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) operated in Denali National Park. (A) Annual productivity indices as a function of mean monthly Southern Oscillation Index (SOI; see text); (B) Mean monthly SOI as a function of year; (C) Expected annual productivity indices (based on relationships shown in A and B) as a function of year; (D) Actual trend in productivity indices.

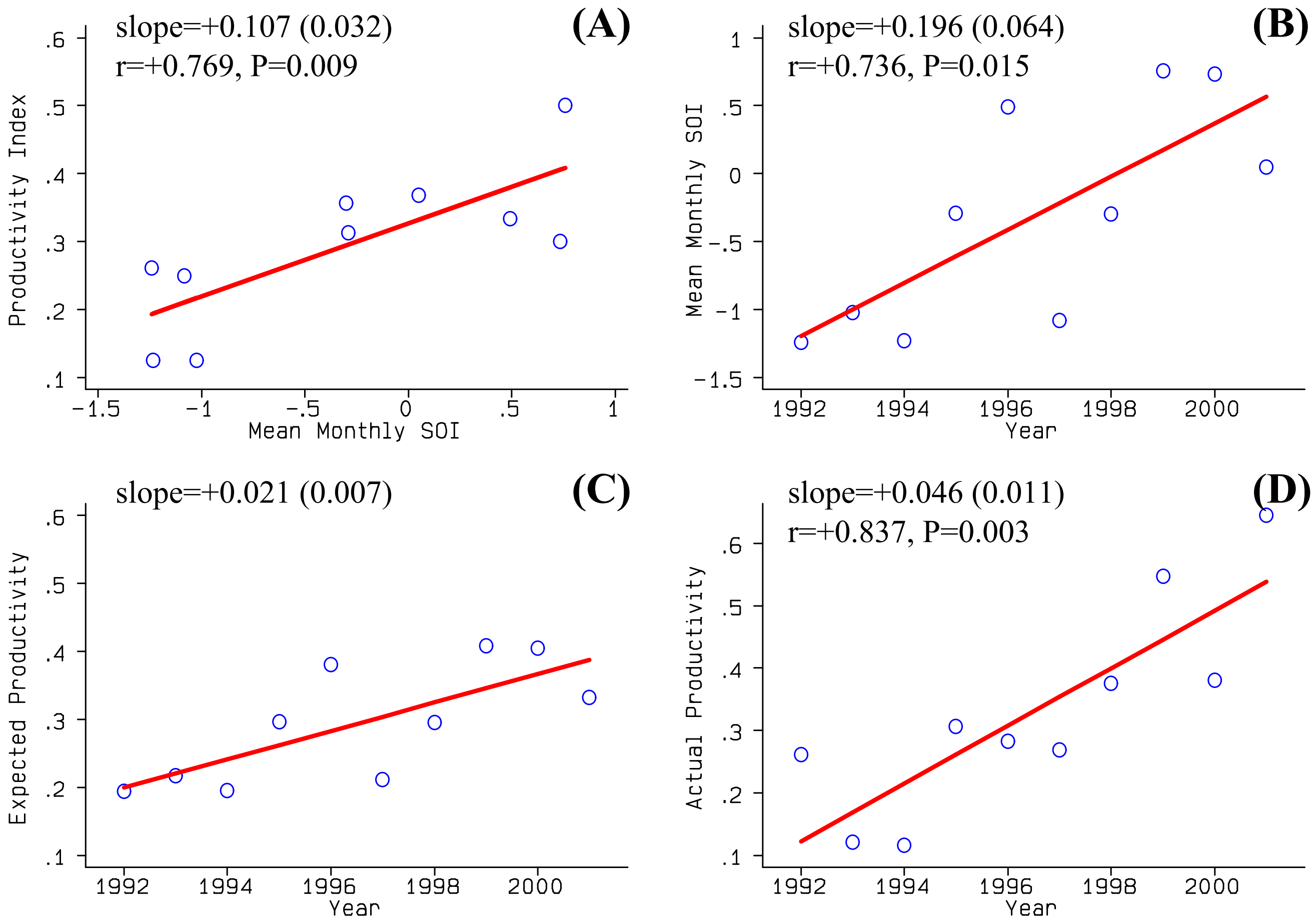

Figure 9. Effects of El Nino/Southern Oscillation (ENSO) on productivity of Swainson's Thrush at the four long running MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) operated in Denali National Park. (A) Annual productivity indices as a function of mean monthly Southern Oscillation Index (SOI; see text); (B) Mean monthly SOI as a function of year; (C) Expected annual productivity indices (based on relationships shown in A and B) as a function of year; (D) Actual trend in productivity indices.

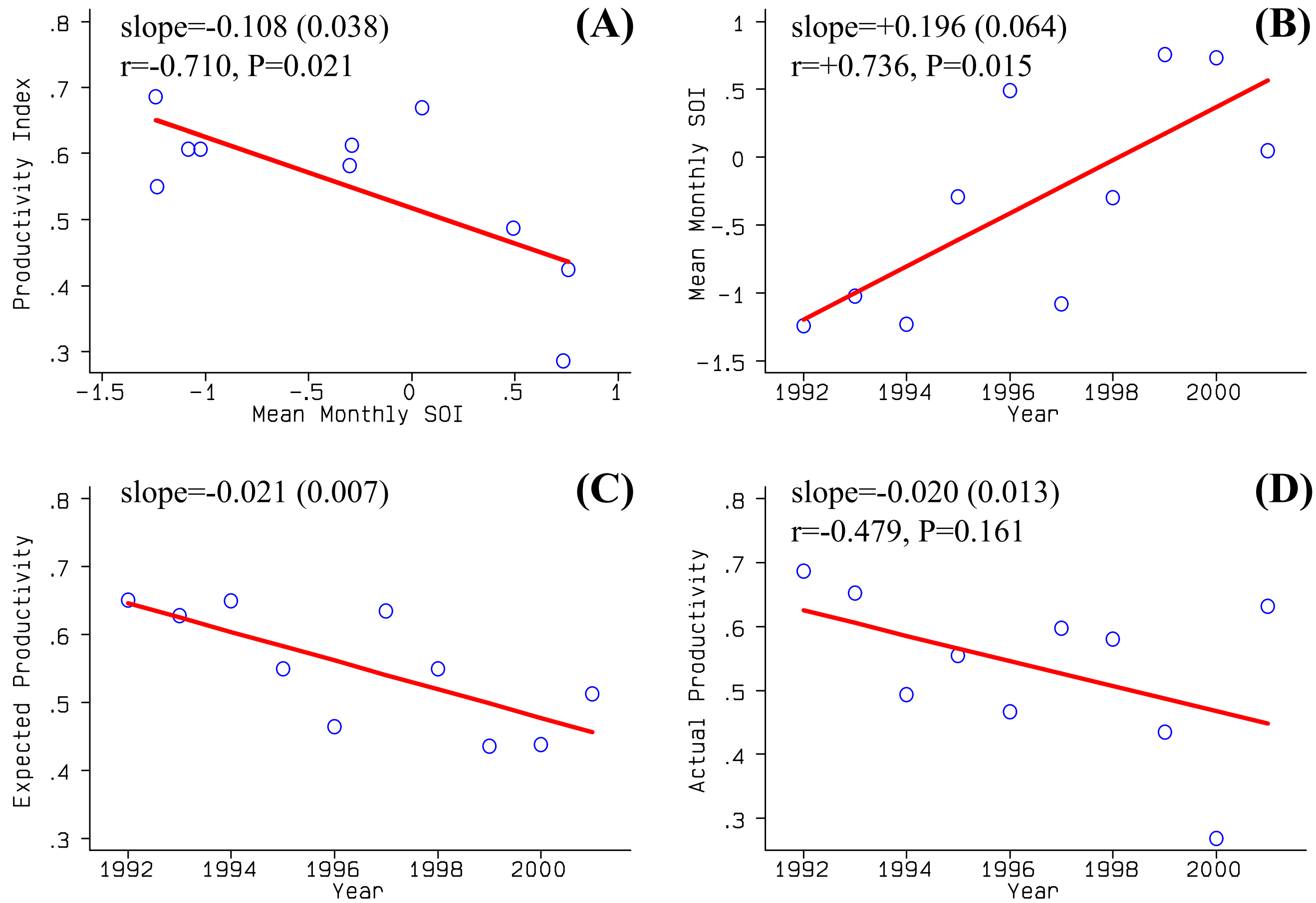

Figure 10. Effects of El Nino/Southern Oscillation (ENSO) on productivity of Wilson's Warbler at the four long running MAPS stations (Igloo Creek, Mile Seven, Permafrost, and Rock Creek) operated in Denali National Park. (A) Annual productivity indices as a function of mean monthly Southern Oscillation Index (SOI; see text); (B) Mean monthly SOI as a function of year; (C) Expected annual productivity indices (based on relationships shown in A and B) as a function of year; (D) Actual trend in productivity indices.

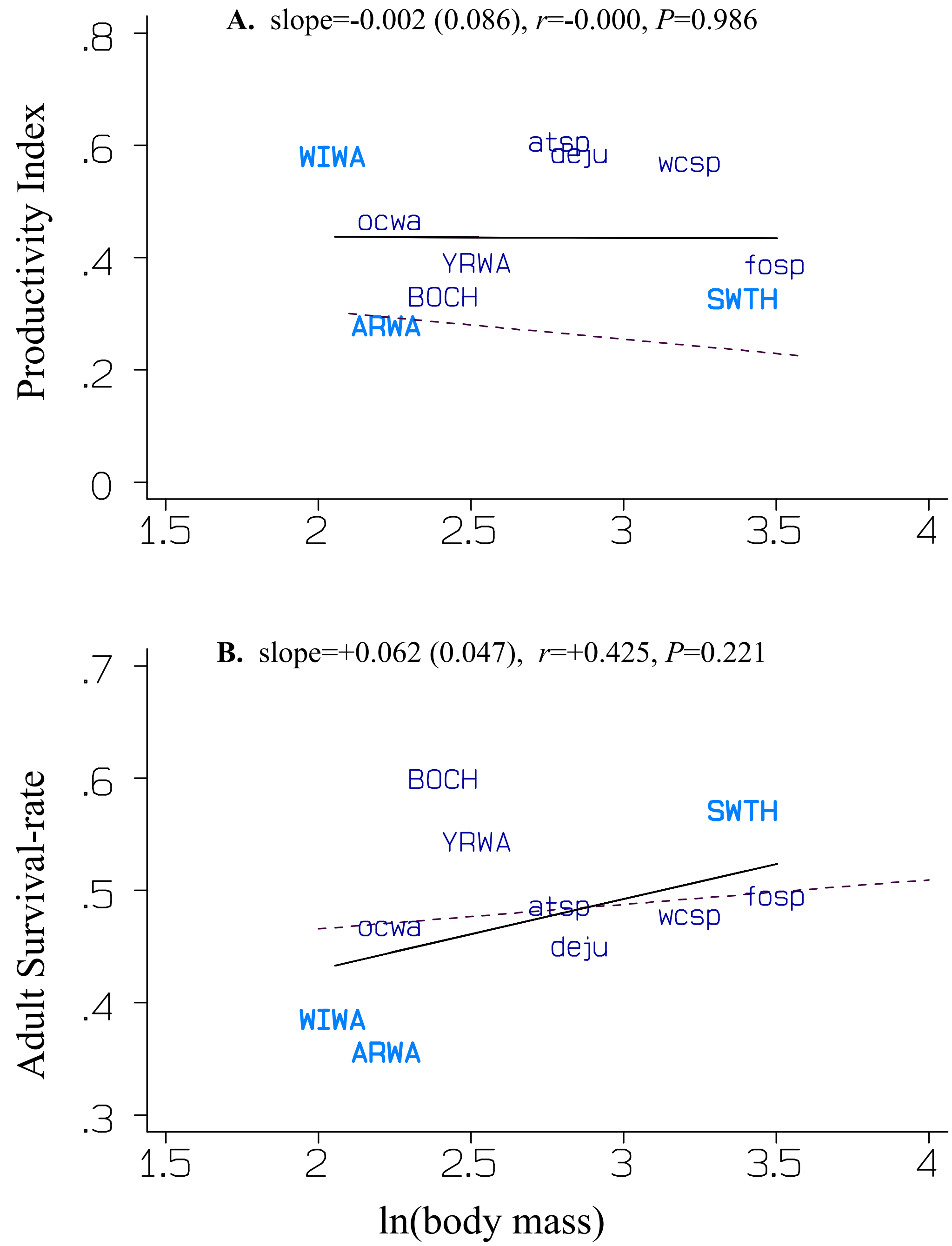

Figure 11. Regressions of productivity indices (**A**) and adult survival-rate estimates (**B**) at all six MAPS stations operated in Denali National Park on the natural log of body mass for ten selected study species for the ten years 1992-2001. Species whose four-letter codes are shown in bold uppercase letters (Arctic Warbler, Swainson's Thrush, Wilson's Warbler) showed substantially decreasing ($r < -0.5$) population trends; those in regular uppercase letters (BorealChickadee, Yellow-rumped Warbler) had substantially increasing ($r > 0.5$) population trends; and those in lowercase letters (Orange-crowned Warbler, American Tree Sparrow, Fox Sparrow, White-crowned Sparrow, Dark-eyed Junco) had stable trends (absolute $r < 0.5$). Regressions are shown for all ten study species in Denali (solid line) and for all species throughout all of North America (dashed line). The slope, the correlation coefficient r, and significance of the correlation P are presented for the Denali study species line.