THE 2000 ANNUAL REPORT OF THE MONITORING AVIAN PRODUCTIVITY AND SURVIVORSHIP (MAPS) PROGRAM IN DENALI NATIONAL PARK

FINAL REPORT

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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 crucial 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 in Denali National Park as part of the development of a 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 2000 in Denali National Park. Four of these were in the same locations where they were operated from 1992 to 1999; the other two were in the same locations where they were operated from 1997 to 1999. 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 512 birds of 26 species were banded at the six stations during the summer of 2000, various individuals were recaptured a total of 168 times, and 69 birds were captured and released unbanded. Thus, a total of 749 captures of 26 species was recorded. Analyses of constant-effort data indicated that both adult population sizes and numbers of young captured decreased from 1999 to 2000, as they did from 1998 to 1999. The number of adults captured decreased highly significantly, by -25.4% for all species pooled and productivity decreased by a very slight and non-significant absolute value of -0.004.

Overall, both population sizes and productivity tended to remain relatively constant at Denali National Park during the nine years 1992-2000, although some general declines have been noted; e.g., trends in both population size and productivity were negative for six of nine target species and all species pooled, and productivity was lower in 2000 than in any of the previous eight years. Despite relatively stable trends in many species at Denali National Park, a few species have shown pronounced increases or decreases in their breeding populations. These include a non-significant but pronounced decline in Arctic Warbler, a highly significant long-term decline in Swainson's Thrush, and a significant increase in Yellow-rumped Warbler.

Productivity trends were fairly stable for six of nine species, showed substantial and nearly significant increases for two species (Arctic Warbler and Swainson’s Thrush), and showed a substantial and significant decline for Wilson’s Warbler. Eight of nine species as well as all species pooled showed a positive “productivity/population correlation” (relationship between

changes in productivity one year and changes in population size the following year), which was significant for four species and for all species pooled, indicating that a change in productivity in one year usually results in a corresponding change in population size the following year.

We found a significant relationship between the strength of the productivity/population correlation and $\Delta QAIC_C$, a measure of interannual variability in survival. Thus, species with more interannual variation in survival showed weaker correlations between changes in productivity one year and changes in population size the next year. This relationship is very important as it validates that annual productivity indices and annual survival rate estimates from MAPS are useful for predicting the driving mechanisms causing year-to-year population changes in landbirds at Denali National Park.

From 1992 through 1997, 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, followed by the same pattern of decreases and increases in numbers of adults captured the following year. We believe that this pattern reflects a density-dependent effect on productivity and recruitment along with lower productivity of first-time breeders. This dynamic was disrupted at Denali during the 1998-2000 seasons, when all three parameters showed changes in the same direction (positive during the 1997-1998 comparison and negative during the 1998-1999 and 1999-2000 comparisons).

We compared annual productivity values with mean monthly Southern Oscillation Indices (SOI) and found a near-significant, negative relationship between productivity at Denali and SOI: productivity is 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 nine-year period, caused productivity to be lower than expected and disrupted the density-dependent effect. In the future, by integrating this correlation into station-specific data, we will further understand how populations vary, both in response to year-to-year, density-dependent effects and, over longer time frames, to variation in the El Niño-Southern Oscillation cycles (e.g., due to global climate change).

Accounting for the significant positive increase in SOI with year during the nine-year study period, the predicted annual percent decline (*APC*) in productivity was -1.0%. This compares very favorably to the observed *APC* in productivity at Denali, -1.1%, suggesting that the slight and general declines observed in both productivity and population size may be largely explained by global climate patterns during the 1990's.

Five of eight target species seemed to show relatively stable population dynamics at Denali, having non-significant (albeit mostly negative) population trends and expected or close-to-expected adult survival rates and productivity indices in relation to their body mass. For Arctic Warbler, assimilation of all data suggests that low survival in some years, combined with overall low productivity, may be driving the population decline in this species at Denali. For Swainson’s Thrush, our data suggest that poor productivity may be the main contributor to the population decline of this species at Denali. For Yellow-rumped Warbler, our data indicate that good overwinter survival by adults is the major cause of the population increase of this species at Denali, overcompensating for relatively low productivity. Thus, we are able to identify likely proximate demographic causes of population trends in the three species showing the greatest nine-year population changes at Denali, and all three showed differing combinations of parameters that appear to be affecting their populations.

A very interesting result of this report is the fact that productivity at Denali is much higher than that found in North America as a whole, whereas adult survival at Denali appears to be similar to that found in North America as a whole. In past reports we have postulated that survival rates generally might be lower at Denali than in the lower 48 United States. We now speculate that an inverse relationship between juvenile survival and latitude may be more pronounced than that between adult survival and latitude; in other words, juveniles fledging from Denali may have a lower chance of returning to breed than juveniles fledging from the lower 48 states, whereas adult survival appears to be more similar between these two areas. In future analyses we will attempt to index juvenile survival with data that separates captures of one-year-old birds (SYs) from older birds (ASYs), and by running survival analyses in reverse order to estimate annual recruitment (and thus make inferences regarding survival) of one-year-old birds.

Summarizing all of our results, interannual variation in productivity generally appears to be more of a factor in determining interannual variation in population trends at Denali than interannual variation in overwinter survival of adults. 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 three species with pronounced population changes, average overall values of adult survival rates appear to affect overall population trends about as often as average overall values of productivity. 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.

With nine years of data, reasonably precise estimates of adult survival probabilities using the transient model could be obtained for eight of nine target species breeding in Denali National Park. 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.

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 juvenal recruitment and indices of juvenile survival in order to fully understand which parameters are most affecting population changes in each target 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.

Finally, we have initiated two additional types of 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 able to identify the proximate demographic causes of population decline within a 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 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 when 12 years of data have been obtained, that is, after the 2003 field season.

We conclude that the MAPS protocol is very well-suited to provide one component of Denali's Long-term Ecological Monitoring Program, and recommend that the MAPS Program be continued in Denali National Park indefinitely into the future.

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.

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 target 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 affect primary demographic parameters directly and these effects 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.

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 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 effectiveness for monitoring demographic parameters of landbirds.

Now in its twelfth year (ninth 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 2000. 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 nine 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 target 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, and recruitment into the adult population 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 target species, population trends of the target 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 physiographic strata or Bird Conservation Regions) or specific locations (such as individual national parks, national forests, or military installations) 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 the landbirds of the Alaskan montane environment; and

(3) develop detailed written protocols for the long-term monitoring of landbird 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 Denali's landbirds as part of Denali's LTEM 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 latter 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 target species, in order to determine the proximate demographic factor (i.e., productivity or survivorship) causing the observed population trends. 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 target species. This will allow us to generate strong testable hypotheses regarding the ultimate environmental cause(s) of population decline. Even more importantly, it will allow us to identify and suggest conservation strategies, management actions, and habitat restoration practices aimed at reversing declining populations and maintaining stable or increasing populations of target species. We are confident that this approach will be fruitful, because we will be formulating actions to address the particular demographic parameters that are responsible for the population declines. The final step will be to evaluate the effectiveness of the management actions actually implements by continued monitoring of vital rates in an adaptive management context.

It is appropriate to point out the importance of primary demographic data on target 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 12 consecutive years of data have been collected, that is, after the 2003 breeding season.

Establishment and Operation of Stations

Four of the six MAPS stations in operation in Denali National Park in 2000 were established in 1992. These stations were established along a habitat gradient of forest cover from more heavily forested stations (Rock Creek and Permafrost) to less heavily forested stations (Mile Seven and Igloo Creek). In 1997, two new stations, Strangler Hill and Buhach Creek, were added to the four continuing stations, and these continued to be operated through 2000. 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, pseudo-random sample of two major types of montane habitat -- spruce forest edge and willow or dwarf birch scrub -- along the main road corridor in the northeastern portion of Denali National Park. The six stations, ordered along a gradient from less-heavily to more-heavily forested habitats are: (1) 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; (2) the Buhach Creek station, representing a mix of alder and willow scrub, located along the McKinley River south of the Denali Park road at milepost 69.8; (3) the Strangler Hill station, representing alder-birch scrub, also located along the McKinley River south of the Denali Park road at milepost 83.7; (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 2000 Denali MAPS Program

The 2000 Denali field biologist interns were Chris Kelly and Bryan Botson. Bryan had previously served as a MAPS intern for the Institute for Bird Populations. They received a comprehensive 14-day training course in mist-netting techniques from IBP biologists Amy McAndrews and Heather Howitt at the Stony Creek Preserve (The Nature Conservancy, Kaiser Unit), Glenn County, 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. Chris and Bryan were responsible for all of the MAPS data collected in Denali National Park during 2000.

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 2000 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 2000 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 2000 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 2000).

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 and survivorship analyses only if the species was classified as a regular (B) or usual (U) breeder at the station. Data from a station for a species classified as a occasional breeder (O), a transient (T), or a migrant (M) at the station were not included in these analyses.

A. Population-size and productivity analyses -- The proofed, verified, and corrected banding data from 2000 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 2000) 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 number of young birds captured and the proportion of young in the catch were used as indices of post-fledging productivity.

For all six stations we calculated changes between 1999 and 2000 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 nine-year trends in indices of adult population size and productivity for target species for which an average of at least seven individual adult birds were captured per year at all stations combined during the nine ears, 1992-2000. For trends in adult population size, we first calculated adult population indices for each species for each of the nine years based on an arbitrary starting index of 1.0 in 1992. 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 of these indices over the nine years. We used the slope of this regression to provide an estimate of the population trend (PT) for the species, which was defined as the average change per year over the nine-year period, 1992-2000, in the index of adult population size as determined from mist net capture-rate data. From PT we then calculated annual percent change (APC_{PT}) in the population as:

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

For this particular calculation, the 1992 value of PT has been set at one, thus, $APC_{PT} = PT /$ the predicted 1992 value of PT based on the regression. Trends in Productivity, PrT, were calculated in the same manner by starting with actual productivity values in 1992 and calculating each successive year’s value based on the constant-effort percentage changes in productivity between each pair of consecutive years. For trends in productivity, APC_{PrT} was calculated as:

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

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.* 2000). 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 on nine years of banding data (1992-2000) from those four stations operated during all nine years (Igloo Creek, Mile Seven, Permafrost, and Rock Creek; captures from the Lost Forest station, operated between 1993 and 1996, were included with those from Rock Creek since the centers of the two stations were no more than 1350 m apart, close enough for regular movements of birds between the two stations and thus necessitating their consideration as a single super-station for survivorship analyses.) The mark-recapture analyses were conducted on the target species for which an average of at least seven individual adults were captured per year at the four stations (plus Lost Forest) combined over the nine years, 1992-2000. Data from 1997-2000 from the Buhach Creek and Strangler Hill stations were not included in the survival analyses for this report.

Using SURVIV (White 1983), we estimated survivorship parameters for each of the target species using the 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). In previous years we also used a non-transient model; however, we have found that the transient model provides the most unbiased survivorship estimates for all species, provided there is sufficient years of data (four) to use it. The transient model calculates 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 target species captured at all stations at which they were classified as regular (B) or usual (U) breeders (see above).

The nine years of data, 1992-2000, available for assessing 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 did not examine spatial variability among stations, as data from individual stations are generally insufficient to provide survival estimates. 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; models showing $QAIC_C$'s within 2.0 $QAIC_C$ units of each other were considered effectively equivalent. 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 interannual 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 can assess whether or not productivity or survival of a given species at Denali is expected, lower than expected, or higher than expected based on body mass.

RESULTS

A total of 1,841.7 net-hours were accumulated at the six MAPS stations operated in Denali National Park in 2000 (Table 1). Data from 1,595.7 of these net-hours could be compared directly to 1998 data in a constant-effort manner.

Indices of Adult Population Size and Post-fledging Productivity

A. 2000 values -- The 2000 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. As in 1999, Buhach Creek produced the greatest number of total captures (197), while Rock Creek produced the smallest (52). Permafrost had the greatest species richness with 16 species, while species richness was poorest at Igloo Creek and Rock Creek with 10 species each.

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 2000 was greatest at the Buhach Creek station, followed in descending order by Strangler Hill, 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 2000 followed a similar sequence as the capture rate of adults, being highest at Buhach Creek and lowest at Rock Creek. The index of productivity at each station in 2000 (Table 3), as determined by the percentage of young in the catch, varied from 0.36 (Igloo Creek) to 0.46 (Mile Seven and Permafrost). As in most previous years, the capture rates of adult birds (the index of adult population size) were higher at the less heavily forested stations dominated by willow or birch/alder scrub, and the percentage of young in the catch (an index of post-fledging productivity) tended to be higher at the more forested stations.

Table 4 summarizes the banding results at all six 2000 Denali MAPS stations combined. Altogether, a total of 749 birds of 26 species were captured during the 2000 breeding season. Newly-banded birds comprised 68.4% of the total captures. Overall, Wilson's Warbler was the most frequently captured species, followed by White-crowned Sparrow, Common Redpoll, Dark-eyed Junco, American Tree Sparrow, Orange-crowned Warbler, Arctic Warbler, and Yellow-rumped Warbler. The eight most abundant breeding species at the six Denali MAPS stations in 2000 (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, American Tree Sparrow, Arctic Warbler, Dark-eyed Junco, and Yellow-rumped Warbler. 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 2000 (from Table 3):

Igloo Creek
Arctic Warbler
Wilson’s Warbler
Common Redpoll
White-crowned Sparrow
Orange-crowned Warbler

Mile Seven
White-crowned Sparrow
Wilson’s Warbler
Common Redpoll
Boreal Chickadee
Yellow-rumped Warbler
American Tree Sparrow

Buhach Creek
Wilson's Warbler
Common Redpoll
American Tree Sparrow
White-crowned Sparrow
Orange-crowned Warbler
Savannah Sparrow
Fox Sparrow

Permafrost
Wilson’s Warbler
Common Redpoll
Swainson’s Thrush
White-crowned Sparrow
Dark-eyed Junco

Strangler Hill
Wilson’s Warbler
Common Redpoll
Alder Flycatcher
Orange-crowned Warbler
Fox Sparrow
White-crowned Sparrow
Gray-cheeked Thrush
Savannah Sparrow

Rock Creek
Dark-eyed Junco
Yellow-rumped Warbler

The 2000 rankings are very similar to those for 1999, 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 1999 and 2000 — Constant-effort comparisons between 1999 and 2000 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 decreased by -25.4%, a highly significant difference (Table 5). Decreases between 1999 and 2000 were recorded for 15 of 27 species, a proportion not significantly different from 0.50 (Table 5; $P = 0.351$). The overall adult population size for all species pooled decreased at five of the six stations, by amounts ranging from -19.3% at Mile Seven to -40.3% at Permafrost, whereas it increased at Rock Creek by +31.6%. The proportion of decreasing (or increasing) species was not significantly greater than 0.50 at any station. Significant or near-significant decreases in the number of adults captured for all stations combined were recorded for three species, Orange-crowned Warbler, Wilson's Warbler, and Common Redpoll, while no such increases were recorded. The highly significant decrease in all species pooled coupled with the non-significant proportion of decreasing species overall reflects substantial declines in most of the more common species: the three species above as well as White-crowned Sparrow and Dark-eyed Junco.

The number of young birds captured of all species pooled at all six stations combined also decreased, by a non-significant -26.5% (Table 6). Decreases were recorded for 14 of 25 species, a proportion not significantly greater than 0.50. The number of young birds captured of all species pooled decreased at four of the six stations, by amounts ranging from -6.4% at Strangler Hill to -51.0% at Buchach Creek, and it increased at Mile Seven (+20.0%) and Permafrost (+11.8%). The proportion of decreasing species was nearly significantly greater than 0.50 at Buchach Creek. Two species (Fox Sparrow and Common Redpoll) showed significant decreases across all stations, whereas Yellow-rumped Warbler showed a significant increase in young captured across stations.

Productivity (the proportion of young in the catch) showed a very slight, absolute decrease of -0.004 from 1999 to 2000 for all species pooled and all stations combined; this decrease was not significant (Table 7). Decreases were recorded for 11 of 20 species, a proportion not significantly greater than 0.50. Three stations showed decreases in productivity between the two years, ranging from -0.078 at Buhach Creek to -0.100 at Igloo Creek, and it showed an absolute increase at three stations, by amounts ranging from +0.041 at Strangler Hill to +0.148 at Permafrost. Two species (Fox Sparrow and Common Redpoll) showed near-significant decreases in productivity from 1999 to 2000 for all stations combined, while one species (Gray Jay) showed a significant increase across stations.

Thus, adult breeding populations showed a substantial decline in 2000 as compared with 1999, which was generally station-wide and occurred with the most abundant breeding species at both forested and scrub stations. Numbers of young captured also showed a decline between 1999 and

2000, indicating that productivity remained poor in 2000 (very similar to that of 1999) despite drops in adult populations (which tend to result in increased productivity). These patterns in young captured and productivity appeared, in general, to be station-wide, indicating no real differences between breeding performance in forested vs. scrub stations (although productivity was slighter better in 2000 as compared with 1999 at the scrub stations than at the forested stations).

C. Nine-year trends in adult population size and productivity -- Table 8 presents annual indices and year-to-year changes in numbers of adult and young birds captured and proportion of young in the catch for all species pooled and for nine target species for which an average of at least seven individual adults were captured per year at all stations combined over the nine years 1992-2000. The annual indices presented in this table are based on all captures during periods five through ten in a given year, while the year-to-year changes are based only on constant-effort data from periods five through ten in accordance with updated MAPS protocols. Note that data from 1997-2000 includes two extra stations (Buhach Creek and Strangler Hill); thus, total numbers of adults and young showed increases between 1996 and 1997 that were not necessarily reflected by the constant-effort comparisons between those two years.

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; but this pattern 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 (see more detailed discussion below). All species pooled and Yellow-rumped Warbler showed decreases in five of eight between-year comparisons (although the warbler showed pronounced increases in two of the three remaining comparisons) whereas no species showed increases in as many as five comparisons.

"Chain" indices of adult population size for each of the nine years (1992-2000) are presented for each of the nine target species and for all species pooled in Figure 1. See Methods for an explanation of the calculations used to obtain the indices. We used the slope of the regression line for each species as an estimate of the mean annual population trend (*PT*) for that species. Estimates of *PT* and its standard error (*S.E.*, in parentheses), the annual percentage change (*APC*), the correlation coefficient (*r)*, and the significance of the linear trend (*P*) for each of the nine target species and all species pooled are included in Figure 1. These data indicate fairly consistent population trends over the nine years for all nine species and all species pooled, with the *S.E.* of the slope being < 0.1 in all cases. Trends for six of the nine species (Orange-crowned Warbler, Wilson's Warbler, American Tree Sparrow, White-crowned Sparrow, Dark-eyed Junco, and Common Redpoll) and all species pooled were fairly stable (absolute $r < 0.5$), although decreases were recorded for four of the six species. Trends for one species (Yellow-rumped Warbler) showed a substantial ® > 0.5) and significant increase. Finally, adult Arctic Warblers and Swainson's Thrushes each showed a substantial ® < -0.5) decline, which was not significant for the warbler but highly significant for the thrush. Overall, as indicated by *PT* values, trends for six species and all species pooled were negative whereas trends for only three species were positive. The annual percentage change (*APC*) in population between 1992 and 2000 varied from -7.3% for Swainson's Thrush to +15.7% for Yellow-rumped Warbler, and was -1.7% for all species pooled.

Table 8 indicates that, through 1997, both numbers of young captured and productivity for all species pooled showed an alternating cycle of declines and increases, 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 2000, when all three parameters showed changes in the same direction, increases in 1998 and decreases in 1999 and 2000. American Tree Sparrow and White-crowned Sparrow showed decreases in young captured in five of eight between-year comparisons and Common Redpoll showed increases in productivity in five of eight comparisons.

Figure 2 shows productivity trends (*PrT*) for the nine target species and all species pooled at Denali. See Methods for an explanation of the calculations used to obtain the indices. We used the slope of the regression line for each species as an estimate of the mean annual productivity trend for that species. Estimates of *PrT* and its standard error (*S.E.*, in parentheses), the annual percentage change (*APC*), the correlation coefficient (*r*), and the significance of the linear trend (*P*) for each of the nine target species and all species pooled are included in Figure 2. Productivity trends for six of the nine species (Orange-crowned Warbler, Yellow-rumped Warbler, American Tree Sparrow, White-crowned Sparrow, Dark-eyed Junco, and Common Redpoll), as well as all species pooled, were fairly stable (absolute $r < 0.5$). Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial $r > 0.5$) increases, which were nearly significant for both species. Finally, Wilson's Warbler showed a substantial $r < -0.5$) and significant decline in productivity trend. Overall, as indicated by *PrT* values, trends of six species and all species pooled were negative while trends of only three species were positive. The annual percentage change (*APC*) in productivity between 1992 and 2000 varied from -3.8% for Wilson's Warbler to +5.7% for Arctic Warbler and was -1.1% for all species pooled.

D. Relationship between annual change in productivity and annual change in adult captures the following year -- To see if productivity has had a direct effect on breeding population size the following year we examined the relationship between constant-effort changes in productivity during one between-year comparison (see Table 8) with changes in adult captures during the following between-year comparison, for the nine target species and all species pooled at Denali (Figure 3). The slopes of these correlations, hereafter termed "productivity/population correlations" along with their standard errors (*S.E.*, in parentheses), the correlation coefficient (*r*), and the significance of the linear trend (*P*) for each of the nine target species and all species pooled are included in Figure 3. For eight of the nine species (all but Common Redpoll), as well as all species pooled, the productivity/population correlation was positive, i.e., changes in productivity one year resulted in corresponding changes in population size the following year. These correlations were fairly flat (absolute $r < 0.5$) for Common Redpoll along with three other species (Arctic Warbler, American Tree Sparrow, and Dark-eyed Junco). The remaining five species (Swainson's Thrush, Orange-crowned Warbler, Yellow-rumped Warbler, Wilson's Warbler, and White-crowned Sparrow), as well as all species pooled, showed strong productivity/population correlations $r > 0.5$), which were significant for all species pooled and for four of the five species (all but Orange-crowned Warbler). Thus, overall, there was a strong relationship between these two parameters, supporting the concept that changes in productivity one year bring about corresponding changes in population size the next. For many species and years this relationship occurred in an alternating (positive and negative) pattern reflecting a density-dependent effect, as mentioned above.

Productivity as Correlated 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 mean monthly SOI indices for January-December of each year. We found a significant negative relationship between productivity at Denali and SOI (Figure 4A): the more La-Niña-like the conditions the lower the productivity. A comparison between SOI and year during the nine-year period showed a significant positive increase (Figure 4B), 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 4C combines these two correlations and plots expected productivity (according to the correlation depicted in Figure 4A) against year (according to the annual SOI). We found that this correlation was also significant and that, given changes in SOI between 1992 and 2000, we would expect to see an annual productivity decline (=*APC*) at Denali of -1.3%**.** This compares with an actual decline in productivity at Denali of -1.1% (Figure 2).

Estimates of Adult Survivorship

Estimates of adult survival and recapture probability could be obtained for eight of the nine target species breeding in Denali National Park using data only from periods five through ten (Tables 9 and 10). Estimates of survival probability could not be obtained for Common Redpoll because only one individual adult banded during 1992-1999 was ever recaptured in a subsequent year. We suspect this occurred because Common Redpolls have very low intrinsic site fidelity from year-to-year; thus, mark-recapture methods will be unable to provide estimates of between-year survival for this species.

Because of the existence of floaters, failed breeders, and dispersing adults, transient models, which calculate the proportion of residents in the population, will always produce less biased adult survivorship estimates than 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 9 indicates that the time-constant transient model ($\varphi P \tau$) 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 all eight species. $\Delta QAIC_C$ (see Methods), a measure of the degree to which adult survival has varied with time over the nine-year period, ranged from 3.4 in Arctic Warbler (indicating some time-dependence in survival) to 14.2 in Yellow-rumped Warbler (indicating little time dependence in survival), with a mean of 9.93.

Comparison of the results of Figure 3 with those of the adult survivorship models (Table 9) reveals a significant positive relationship between the strength of this productivity/population correlation (as measured by the *r*-value) and $\Delta QAIC_C$ (Figure 5). Thus, species with more interannual variation in survival showed a weaker correlation between productivity one year and population size the next year.

Table 10 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 9, for each target species. The estimates for survival probability ranged from a low of 0.353 for Arctic Warbler to a high of 0.599 for Yellow-rumped Warbler, and averaged 0.467. Time-constant estimates of recapture probability varied from 0.215 for Yellow-rumped Warbler to 0.657 for American Tree Sparrow with a mean of 0.429. The time-constant estimates for the proportion of the resident population ranged from 0.367 (Wilson's Warbler) to 0.769 (White-crowned Sparrow) and averaged 0.495.

Adult survival rates and productivity indices as a function of body mass

Figure 6 compares mean body mass (log transformed) with survival estimates recorded throughout North America and at Denali for the eight target species for which survival could be estimated (Table 9). The purpose of this figure is to see which species at Denali show higher or lower survival than might be expected given their body mass. Two regression lines are presented, one comparing all eight Denali species and one comparing 89 species in North America for which survival could be estimated using MAPS stations distributed across the continent. Species with larger body mass generally showed higher survival, which explains the positive slopes of the regression lines and supports the established premise that survival rates average higher in larger species. The slope of the line based on the eight species at Denali was very similar to that for North America as a whole, supporting the validity of this relationship; interestingly, however, it was not substantially lower at Denali than in North America, as we have postulated in past reports (see Discussion). Six of the eight species fall close to the line and thus have expected adult survival at Denali. Arctic Warbler appears to have lower adult survival at Denali than might be expected, whereas Yellow-rumped Warbler appears to have higher adult survival at Denali than might be expected.

Figure 7 makes the same comparison as Figure 6, plotting productivity (instead of survival) against body mass (log transformed). Three regression lines are presented, one comparing all eight Denali species, one comparing all species except Arctic Warbler, and one comparing 210 species in North America for which productivity could be estimated using MAPS stations distributed across the continent. For reasons discussed below, we believe that productivity values of Arctic Warbler at Denali may be lower than expected relative to body mass, and we thus examined this relationship without its inclusion. Both the regression line based on the remaining seven species at Denali and that based on all North American species show nearly the same downward slope, suggesting that smaller species have higher productivity. As mentioned above, productivity was also higher at Denali (and other northern latitudes) than in the rest of North America (Figure 7), apparently due to more abundant food resources during the summer and lower brood parasitism and nest predation rates. Note, however, that these two lines are nearly parallel, supporting the validity of this relationship once the difference in productivity by latitude is accounted for. Excluding Arctic Warbler, five of the seven species fall close to the line and thus have expected productivity at Denali. The remaining two species, Yellow-rumped

Warbler and Swainson's Thrush, appear to have lower productivity than might be expected at Denali.

Assuming stable bird populations and similar juvenal survival rates across species, the downward slope in Figure 6 should counterbalance the upward slope in Figure 7. Indeed, a comparison of individual species in Figures 6 and 7 indicate that, with the exception of Arctic Warbler, species with survival rates below the regression line tended to have productivity values of a similar magnitude above the line, and vice versa. This indicates that these comparisons may be useful in predicting the driving forces (adult survival vs. productivity) behind population trends at Denali. Certain species may have higher or lower productivity or survival than expected based on body mass, but this should be compensated by opposite changes of similar magnitude in the other parameter.

DISCUSSION OF RESULTS

Overall, both population sizes and productivity tended to remain relatively constant at Denali National Park during the nine years 1992-2000, although some general declines have been noted; e.g., trends in both population size (*PT*; Figure 1) and productivity (*PrT*; Figure 2) were negative for six of nine target species and all species pooled, and productivity was lower in 2000 than in any of the previous eight years (Table 8). As compared with 1999, adult breeding populations in 2000 showed a substantial decline which was generally station-wide and occurred with the most abundant breeding species at both forested and scrub stations. Numbers of young captured also showed an equal or slightly greater decline between 1999 and 2000; thus, productivity remained poor in 2000 as it was in 1999.

Despite relatively stable trends in many species at Denali National Park, a few species have shown pronounced increases or decreases in their breeding populations (Figure 1). These include a non-significant but pronounced decline in Arctic Warbler, a highly significant long-term decline in Swainson's Thrush, and a significant increase in Yellow-rumped Warbler. In order to investigate possible causes for these population trends and those of the other target species at Denali, we examined trends in productivity (Figure 2), productivity/population correlations (Figure 3), relationships between productivity and Southern Oscillation Index (Figure 4), $\Delta QAIC_C$ (a measure of interannual variability in survival; Table 9), and comparisons of adult survival and productivity values with those expected based on relationships of these parameters with body mass at Denali and across North America (Figures 6-7). These data are summarized for each of the eight target species (all except Common Redpoll, for which adult survival estimates could not be obtained) in Table 11.

Productivity trends (Figure 2) were fairly stable for six of nine species as well as all species pooled. Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial increases, which were nearly significant for both species, whereas Wilson's Warbler showed a substantial and significant decline in productivity trend. Five species and all species pooled showed *PT* values in the same direction as *PrT* values, whereas four species showed these two values trending in opposite directions (Table 11), suggesting that trends in productivity are not always correlated strongly with trends in population size. Indeed, the population trend for Swainson's Thrush was significantly negative whereas the productivity trend was almost significantly positive. This lack of correspondence indicates that other factors besides productivity may be driving population trends and/or, more importantly, that overall productivity in a given species may be too low to support the population (or is high enough to cause a population increase), despite of the direction of the productivity trend.

A better measure of the effects of productivity on population size is the relationship between changes in productivity one year with changes in breeding population size the following year, the "productivity/population correlation" (Figure 3). Eight of the nine species, as well as all species pooled, showed a positive productivity/population correlation, indicating that a change in productivity one year usually results in a corresponding change in population size the following year. These positive correlations ranged from nearly flat for three species, to substantial but non-significant for one species, to substantial and significant for four species (Table 11). For all species pooled this relationship was also significant. The one species with a negative relationship, Common Redpoll, has very low intrinsic site fidelity from year-to-year; thus, a year-to-year correlation between productivity and population size might not be expected.

The positive productivity/population relationship would be expected to be weaker in species with substantial interannual variation in overwinter survival. This is because the year-to-year effects of survival on population size will not necessarily correspond with those of productivity on population size. To see if this was the case, we compared the strength of the productivity/population correlation (as measured by its *r*-value) with $\Delta QAIC_C$, a measure of interannual variability in survival, and found a significant relationship among the eight species (all but Common Redpoll) for which survival could be estimated (Figure 5). Thus, species with more interannual variation in survival showed weaker correlations between productivity one year and population the next year. In Arctic Warbler, for example, our data show that survival was very poor during the winters of 1993-1994, 1996-1997, and 1998-1999 ($\varphi < 0.2$) compared with most of the other winters ($\varphi > 0.5$), and it appears that this variation in survival may sometimes override productivity as the most important factor driving year-to-year population changes. The significant relationship shown in Figure 5 is very important as it validates that annual productivity indices and annual survival rate estimates from MAPS are useful for predicting the driving mechanisms causing year-to-year population changes in landbirds at Denali National Park.

From 1992 through 1997, 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, followed by the same pattern of decreases and increases in numbers of adults captured the following year. 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. Large 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 1992-1997, but was disrupted at Denali during the 1998-2000 seasons, when all three parameters showed changes in the same direction (positive during the 1997-1998 comparison and negative during the 1998-1999 and 1999-2000 comparisons). Productivity in 1999 and 2000 (0.426 and 0.416, respectively) were the lowest recorded during the nine years of data (Table 8).

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 has 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 a near-significant, negative relationship between productivity at Denali and SOI (Figure 4A): productivity is 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 nine-year period (Figure 4B), caused productivity to be lower than expected (Table 8) and disrupted the density-dependent effect. It will be interesting to see what happens in 2001. If the La Niña moderates, as currently predicted, we might expect 2001 to be characterized by low breeding population sizes with relatively good productivity, and a return to the density-dependent dynamic until the next severe La Niña or El Niño event. In the future, by integrating this correlation into station-specific data, we will further understand how populations vary, both in response to year-to-year, density-dependent effects and, over longer time frames, to variation in the El Niño-Southern Oscillation cycles (e.g., due to global climate change).

Accounting for the significant positive increase in SOI with year during the nine-year study period, we found a negative correlation between expected productivity and year (Figure 4C). The predicted, annual percent decline (*APC*) in productivity (for all species pooled) based on this correlation, -1.0%, compares very favorably to the observed *APC* in productivity at Denali (Figure 2), -1.1%. Thus, it appears that the slight and general declines observed in both productivity and population size (because of the productivity/population correlation shown in Figure 3) may be largely explained by global climate patterns during the 1990's.

This may not be the case for all of the target species, however. To see what other parameters may be driving population trends of the eight target species at Denali National Park, we compared the six measures listed in Table 11, including productivity and survival as a function of body mass. Five of the eight species (Orange-crowned Warbler, Wilson's Warbler, American Tree Sparrow, White-crowned Sparrow, and Dark-eyed Junco) seemed to show relatively stable population dynamics at Denali, having non-significant population trends and expected or close-to-expected adult survival and productivity according to body mass (Table 11, Figures 2-5). For all five of these species the productivity/population correlation was positive (significantly positive in two cases) and $\Delta QAIC_C$ was quite high suggesting that there is relatively little interannual variation in survival and that interannual variation in population trends are driven primarily by interannual variation in productivity. The only parameter value of concern among these five species is the significant negative productivity trend in Wilson's Warbler. The productivity/population effect is also significant in this species, indicating that interannual variation in productivity strongly influences population size at Denali; thus, we might expect populations of this species to begin declining in upcoming years. The population dynamics of Wilson's Warbler, especially as it relates to productivity, bears watching.

For Arctic Warbler, populations have shown a substantial but non-significant decline, productivity trend was near-significantly positive, the productivity/population correlation was weak and not significant, $\Delta QAIC_C$ was low, and both adult survival and productivity were lower than expected based on body mass (Table 11). We believe that low survival in some years, combined with overall low productivity, may be driving the population declines in this species at Denali. The weak productivity/population correlation combined with the low $\Delta QAIC_C$ value suggests that interannual variation in survival rates may be influencing interannual variation in population trends as much as or more than interannual variation in productivity. Thus, although survival in most years is probably adequate to support the population, the low survival in other years (e.g., 1993-1994, 1996-1997, and 1998-1999) may be accounting for the population decline. According to body mass, expected productivity is also low, and low overall productivity may also be contributing to the population decline. This may be occurring despite the increasing productivity trend and the weak productivity/population correlation. The fact that this is the only Palearctic species among the target list and that it is at the edge of its breeding range may also affect its population dynamics. Arctic Warbler is another species at Denali to monitor closely.

For Swainson's Thrush, populations have shown a substantial and highly significant decline, productivity trend was near-significantly positive, the productivity/population correlation was positive and significant, $\Delta QAIC_C$ was high, and productivity was substantially lower than expected and adult survival was close to expected based on body mass (Table 11). We interpret these results as suggesting that poor productivity by Swainson's Thrushes may be the main contributor to the population decline of this species at Denali; if productivity were naturally low in this species we might expect survival to be higher than expected at Denali, which it is not. The significant productivity/population correlation and very high $\Delta QAIC_C$ indicates that interannual variation in productivity, rather than interannual variation in survival, is driving the interannual variation in population size. It may be encouraging that the productivity trend was near-significantly positive, suggesting that the rate of decline my lessen in the near future. However, the fact that the productivity trend was positive does not indicate that productivity is yet high enough to support a stable population. We recommend that factors affecting productivity of Swainson's Thrush at Denali be researched further in an attempt to identify causes and, if feasible, management actions that should be taken to increase the productivity of this species in the park.

For Yellow-rumped Warbler, populations have shown a substantial and significant increase, productivity trend was not significant, the productivity/population correlation was significant, $\Delta QAIC_C$ was very high, and adult survival was substantially higher than expected and productivity was lower than expected based on body mass (Table 11). We interpret these results as indicating that good over-winter survival by adult Yellow-rumped Warblers is the major cause of the population increase of this species at Denali, overcompensating for it's relatively low productivity. The significant productivity/population correlation indicates that interannual variation in productivity causes the observed interannual variation in population size, although the underlying increasing population trend seems to be driven by high and constant survival. The high over-winter adult survival may relate to recent population increases of this species in suburban neighborhoods of Central and Southern California, which contain increasing densities of the flowering and berry-producing trees in which Yellow-rumped Warblers feed.

Thus, we are able to identify likely proximate demographic causes of population trends in the three species showing the greatest nine-year population changes at Denali, and all three show differing combinations of parameters that appear to be affecting populations. For Arctic Warbler low survival in some years and low productivity overall appear to be causing a substantial but non-significant population decline; for Swainson's Thrush low productivity at Denali appears to contribute to a significant population decline; and for Yellow-rumped Warbler high (and constant) overwinter survival appears to be contributing to significant population increases at Denali.

A very interesting result of this report is the fact that productivity at Denali is much higher than that found in North America as a whole (Figure 7) whereas adult survival at Denali appears to be similar to that found in North America as a whole (Figure 6). In past reports we have postulated that productivity might be substantially higher at Denali than in the lower 48 states because of greater food resources and less brood parasitism and nest predation at higher latitudes, whereas survival rates generally might be lower at Denali than in the lower 48 United States because of longer, more difficult migrations. While our results continue to support the former hypothesis we now believe that variation in adult survival by latitude may not be as great as previously speculated.

The one population parameter that we have not been able to measure adequately is juvenile survival, i.e., 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. The results of Figures 6 and 7 lead us now to speculate that an inverse relationship between juvenile survival and latitude may be more pronounced than the relationship between adult survival and latitude; in other words, juveniles fledging from Denali may have a lower chance of returning to breed than juveniles fledging from the lower 48 states, whereas adult survival seems to be more similar between these two areas. In essence, therefore, populations at Denali appear to be more r-selected (producing more young with a lower chance of surviving to breed) compared to populations in the lower 48 states which appear to be more K-selected (producing fewer young with a greater chance of surviving to breed). This is as might be expected given the greater food resources during the summer at northern latitudes. In future analyses we will attempt to estimate juvenile survival through two methods: (1) by using data that separate captures of one-year-old birds (SYs) from older birds (ASYs), and (2) by modeling temporal symmetry in mark-recapture data (that is, by running survival analyses in reverse order) to estimate annual recruitment (and thus 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 good position to examine differences in adult and juvenal survival according to geographic location, climate, and habitat considerations.

Assimilating all of our results, interannual variation in productivity generally appears to be more of a factor in determining interannual variation in population trends at Denali than interannual variation in overwinter survival of adults. Evidence for this includes the positive productivity/ population correlation for eight of nine species, an effect which was significant for four species and all species pooled; the relatively small amount of time-dependence in adult survival; and the strong correlation between this and the productivity/population correlation. 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 few species with pronounced population changes, average overall values of adult survival rates (Arctic Warbler, Yellow-rumped Warbler) appear to affect overall population trends as often as do average overall values of productivity (Arctic Warbler, Swainson’s Thrush). If, indeed, juvenal survival has a greater influence than adult survival on bird populations at Denali, as we speculate above, then good productivity is needed to provide an adequate pool of juvenile birds. Management practices to protect or increase the reproductive potential of birds are thus of paramount importance in maintaining healthy bird populations in Denali.

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. As in previous years, the population dynamics at the Permafrost station seem to be somewhat different than at the other Denali stations. 2000 was no exception, with Permafrost showing the largest decrease from 1999 in adult population size and the largest increase in productivity. This sort of between-station variation begs further analysis and further underscores the need to maintain the quality of all habitats in Denali National Park and Preserve.

With nine years of data, reasonably precise estimates of adult survival probabilities using the transient model could be obtained for eight of nine target species breeding in Denali National Park. The mean precision of survival-rate estimates for the eight species using nine years of data (CV=17.9%; Table 10) was notably improved over that from eight (CV=23.8%), seven (CV=26.5%), and six years of data (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 accurate 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.

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 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, both overall and at the individual species level. In future analyses, we hope to include estimates of juvenile recruitment and survival in order to fully understand what parameters are most affecting population changes in each target 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 those involving body mass reported here, we have initiated two broad-scale analyses to help us further understand the population dynamics of landbirds and potential management actions to assist bird populations. 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. in press). 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 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 2000). This 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 12 years of data have been obtained, that is, after the 2003 field season.

CONCLUSIONS AND RECOMMENDATIONS

(1) In Denali National Park and Preserve, both population sizes and productivity tended to remain relatively constant for most species during the nine-year period 1992-2000, although some indications of population decline are being noted in both parameters; e.g., trends in both population and productivity were negative for six of nine target species and all species pooled, and productivity was lower in 2000 than in any of the previous eight years.

(2) Nine-year trends in adult population size were determined from constant-effort changes in indices of adult population size obtained from mist net capture data for nine target species. Swainson's Thrush continues to show significant population declines and Arctic Warbler shows substantial but non-significant population declines. By contrast, the population trend for

Yellow-rumped Warbler has been significantly positive. Trends in the populations of the other six species appear rather stable (although generally with a slightly decreasing tendency).

(3) Productivity trends were fairly stable for six of nine species as well as all species pooled. Productivity trends for two species (Arctic Warbler and Swainson's Thrush) showed substantial increases, which were nearly significant for both species, whereas Wilson's Warbler showed a substantial and significant decline in productivity trend.

(4) Eight of the nine species, as well as all species pooled, showed a positive "productivity/ population correlation", indicating that a change in productivity one year results in a corresponding change in population size the following year. This positive relationship was significant for four species and for all species pooled.

(5) We compared the strength of the productivity/population correlation (as measured by its correlation coefficient, *r*) with $\Delta QAIC_C$, a measure of interannual variability in survival, and found a strong and significant relationship among the eight species for which survival could be estimated. Thus, species with more interannual variation in survival showed weaker correlations between changes in productivity one year and changes in population size the next year. This significant relationship is very important as it validates that both annual productivity indices and annual survival rate estimates from MAPS are useful for predicting the driving mechanisms causing year-to-year population changes in landbirds at Denali National Park.

(6) From 1992 through 1997, 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, 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 1998-2000 seasons, when all three parameters showed changes in the same direction. Productivity in 1999 and 2000 (0.426 and 0.416, respectively) were the lowest recorded during the nine years of data collection.

(7) To examine the possibility that global climate patterns are affecting productivity at Denali we compared annual productivity values with mean monthly SOI values and found a near-significant 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 nine-year period, caused productivity to be lower than expected and disrupted the density-dependent effect. Accounting for a significant positive increase in SOI with year during the nine-year study period, the predicted, annual percent decline (*APC*) in productivity based on this correlation, -1.0%, compares very favorably with the observed *APC* in productivity trend at Denali, -1.1%. Thus, it appears that the slight and general declines observed in both productivity and population size (because of the significant productivity/population correlation) may be largely explained by global climate patterns during the 1990's.

(8) In order to investigate possible causes for population trends of individual target species at Denali, we examined trends in productivity, relationships between changes in productivity with changes in population the following year ("productivity/population correlation"), interannual variability in survival, and comparisons of adult survival and productivity values with those expected based on relationships of these parameters with body mass at Denali and across North America. Five of the eight target species for which survival could be estimated showed relatively stable population dynamics at Denali, having non-significant population trends and expected or close-to-expected adult survival rates and productivity indices according to body mass. For Arctic Warbler our data suggest that lower-than-expected adult survival in some years, along with generally low productivity, may be causing the substantial but non-significant population decline. For Yellow-rumped Warbler we believe that good over-winter survival by adults has contributed to a significant population increase at Denali. For Swainson's Thrush, we believe that poor productivity at Denali may be the main contributor to the highly significant population decline of this species there, and we recommend that factors affecting productivity of this species at Denali be researched further in attempt to identify causes. If feasible, management actions should then be undertaken to increase the productivity of this species in the park.

(9) We speculate that interannual variation in productivity is generally more of a factor in determining interannual variation in population trends at Denali than is interannual variation in overwinter survival of adults. Evidence for this includes the positive productivity/population effects for eight of nine species, the relatively small amount of time-dependence in adult survival, and the strong correlation between this and the productivity/population effect. For the few species with more pronounced population changes, however, it appears that overall values of adult survival rates drive overall population trends about as often as do overall values of productivity.

(10) A very interesting result of our analyses is that adult survival at Denali appears to be similar to that found in North America as a whole, whereas productivity at Denali is much higher than that found in North America as a whole, suggesting that juvenile survival (a parameter we have been unable to measure thus far) is much poorer than adult survival at Denali and is the factor counterbalancing the higher productivity in the park. If this is true then good productivity is needed to provide an adequate source pool of juvenile birds. Management practices to protect or increase the reproductive potential of birds are thus of paramount importance in maintaining healthy bird populations in Denali. In future analyses we will attempt to estimate juvenal survival with data that separates captures of one-year-old birds from older birds and by running survival analyses in reverse order to estimate annual recruitment (and thus index survival) of one-year-old birds.

(11) Reasonably precise estimates of annual adult survival and recapture probabilities and proportion of young among newly captured adults were obtained from modified Cormack-Jolly-Seber mark-recapture analyses (using the program SURVIV and the transient model) from nine years (1992-2000) of MAPS data for eight breeding species at Denali National Park. The precision of the estimates increased from 1999 to 2000 and should continue to increase for several more years as additional years of data accumulate. This will allow improved

analyses of the role of productivity and 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.

(12) 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 juvenal recruitment and indices of juvenile survival in order to fully understand which parameters are most affecting population changes in each target 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.

(13) Finally, we have initiated two additional types of 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 able to identify the proximate demographic causes of population decline within a 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 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 when 12 years of data have been obtained, that is, after the 2003 field season.

(14) 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.

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Table 1. Summary of the 2000 MAPS program in Denali National Park.

Station Name	Code	No.	Major Habitat Type	Latitude-longitude	Avg. Elev. (m)	2000 operation: Total number of net-hours[1]	No. of periods	Inclusive dates
Igloo Creek	IGCR	17705	Riparian willow scrub	63°35'40"N,149°36'30"W	945	306.5 (275.0)	6	6/15-8/01
Buhach Creek	BUCR	17730	Willow/tundra scrub	63°25'20"N,150°26'40"W	884	297.3 (248.2)	6	6/11-8/03
Strangler Hill	STHI	17731	Alder/birch scrub hillside	63°26'50"N,150°48'30"W	686	269.2 (241.2)	6	6/10-8/04
Mile Seven	MISE	17703	Spruce forest, spruce/birch scrub, wet willow scrub	63°43'00"N,149°04'50"W	838	328.0 (290.3)	6	6/17-7/31
Permafrost	PERM	17704	Mature spruce forest, riparian alder, wet willow scrub	63°42'50"N,149°01'10"W	716	343.0 (278.2)	6	6/13-7/30
Rock Creek	ROCR	17706	Mature spruce forest, riparian alder woodland	63°43'30"N,148°58'00"W	686	297.7 (262.8)	6	6/12-7/29
ALL STATIONS COMBINED						1841.7 (1595.7)	6	6/10-8/04

[1] Total net-hours in 2000. Net-hours in 2000 that could be compared in a constant-effort manner to 1999 are shown in parentheses.

Table 2. Capture summary for the six individual MAPS stations operated in Denali National Park in 2000.
N = Newly Banded, U = Unbanded, R = Recaptures of banded birds.

	Igloo Creek			Buhach Creek			Strangler Hill			Mile Seven			Permafrost			Rock Creek		
Species	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R
Three-toed Woodpecker													1					
Alder Flycatcher				1			7		2				1					
Unidentified Empidonax					1													
Black Phoebe				1														
Unidentified Flycatcher								1										
Gray Jay							1								1	2		
Black-capped Chickadee	1									1						1		
Boreal Chickadee										7	1		2		6		2	2
Ruby-crowned Kinglet										1			3					
Arctic Warbler	15	1	15	2														
Gray-cheeked Thrush				1			2		4							1		
Swainson's Thrush							3	2	3				5		2	4		
Hermit Thrush	2		1															
American Robin										2			1					
Varied Thrush													2			3		
Orange-crowned Warbler	9		3	11		4	5	3	6	5			1					
Yellow-rumped Warbler							3			10			2			9	2	2
Blackpoll Warbler							2			1	1	1						
Northern Waterthrush							1											
Wilson's Warbler	15	4	7	59	7	22	37	8	6	14	4	6	6		8	3		
American Tree Sparrow	5	1	2	14	2	3	1			9	1	1	12	2				
Savannah Sparrow				4			4	1										
Fox Sparrow	1		2	3			7	1	5					2				
Lincoln's Sparrow	1																	
White-crowned Sparrow	16		12	17	2	3	9	3	1	17		8	20	5	5	1		
Golden-crowned Sparrow										1	1							
Dark-eyed Junco							2	1		12		3	12		4	11	1	8
Common Redpoll	11	1		29	4	7	10	2	2	10	1		7		1			

Table 2. (cont.) Capture summary for the six individual MAPS stations operated in Denali National Park in 2000.
N = Newly Banded, U = Unbanded, R = Recaptures of banded birds.

	Igloo Creek			Buhach Creek			Strangler Hill			Mile Seven			Permafrost			Rock Creek		
Species	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R	N	U	R
Unidentified Bird								1										
ALL SPECIES POOLED	76	7	42	142	16	39	94	23	29	90	9	19	75	9	27	35	5	12
TOTAL NUMBER OF CAPTURES		125			197			146			118			111			52	
NUMBER OF SPECIES	10	4	7	11	4	5	15	8	8	13	6	5	14	3	7	9	3	3
TOTAL NUMBER OF SPECIES		10			11			15			13			16			10	

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 2000.

	Igloo Creek			Buhach Creek			Strangler Hill			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.
Three-toed Woodpecker													1.7	0.0	0.00			
Alder Flycatcher				2.0	0.0	0.00	15.6	0.0	0.00				1.7	0.0	0.00			
Gray Jay							0.0	2.2	1.00				1.7	0.0	0.00	4.0	0.0	0.00
Black-capped Chick.	2.0	0.0	0.00							0.0	1.8	1.00				0.0	2.0	1.00
Boreal Chickadee										9.1	3.7	0.29	5.2	1.7	0.25	4.0	0.0	0.00
Ruby-crowned Kinglet										0.0	1.8	1.00	5.2	0.0	0.00			
Arctic Warbler	27.4	13.7	0.33	4.0	0.0	0.00												
Gray-cheeked Thrush				0.0	2.0	1.00	8.9	2.2	0.20							2.0	0.0	0.00
Swainson's Thrush							4.5	4.5	0.50				10.5	0.0	0.00	2.0	6.0	0.75
Hermit Thrush	5.9	0.0	0.00															
American Robin										3.7	0.0	0.00	1.7	0.0	0.00			
Varied Thrush													3.5	0.0	0.00	4.0	2.0	0.33
Orange-crowned Warb.	7.8	11.7	0.60	20.2	4.0	0.17	15.6	0.0	0.00	1.8	5.5	0.75	0.0	1.7	1.00			
Yellow-rumped Warbler							4.5	2.2	0.33	7.3	11.0	0.60	3.5	0.0	0.00	14.1	8.1	0.36
Blackpoll Warbler							2.2	2.2	0.50	3.7	0.0	0.00						
Northern Waterthrush							0.0	2.2	1.00									
Wilson's Warbler	23.5	9.8	0.29	56.5	82.7	0.59	22.3	71.3	0.76	16.5	11.0	0.40	12.2	1.7	0.13	4.0	0.0	0.00
American Tree Sparrow	5.9	5.9	0.50	28.3	4.0	0.13	0.0	2.2	1.00	7.3	9.1	0.56	0.0	21.0	1.00			
Savannah Sparrow				6.1	2.0	0.25	8.9	2.2	0.20									
Fox Sparrow	2.0	2.0	0.50	6.1	0.0	0.00	15.6	6.7	0.30									
Lincoln's Sparrow	0.0	2.0	1.00															
White-crowned Sparrow	17.6	19.6	0.53	24.2	10.1	0.29	15.6	6.7	0.30	25.6	11.0	0.30	10.5	28.0	0.73	0.0	2.0	1.00
Golden-crowned Spar.										0.0	1.8	1.00						
Dark-eyed Junco							0.0	4.5	1.00	5.5	18.3	0.77	8.7	14.0	0.62	16.1	10.1	0.39
Common Redpoll	21.5	0.0	0.00	44.4	14.1	0.24	22.3	0.0	0.00	12.8	5.5	0.30	12.2	0.0	0.00			
ALL SPECIES POOLED	113.5	64.6	0.36	191.7	119.1	0.38	136.0	109.2	0.45	93.3	80.5	0.46	78.7	68.2	0.46	50.4	30.2	0.38

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 on Denali National Park in 2000.

	Igloo Creek			Buhach Creek			Strangler Hill			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.
NUMBER OF SPECIES	9	7		9	7		11	12		10	11		13	6		8	6	
TOTAL NUMBER OF SPECIES		10			10			15			13			15			10	

Table 4. Summary of results for all six Denali National Park MAPS stations combined in 2000.

Species	Birds captured: Newly banded	Un-banded	Recap-tured	Birds/600net-hours: Adults	Young	Prop. Young
Three-toed Woodpecker	1			0.3	0.0	0.00
Alder Flycatcher	9		2	2.9	0.0	0.00
Unidentified Empidonax		1				
Black Phoebe	1					
Unidentified Flycatcher		1				
Gray Jay	3		1	1.0	0.3	0.25
Black-capped Chickadee	3			0.3	0.7	0.67
Boreal Chickadee	9	3	8	3.3	1.0	0.23
Ruby-crowned Kinglet	4			1.0	0.3	0.25
Arctic Warbler	17	1	15	4.6	2.3	0.33
Gray-cheeked Thrush	4		4	1.6	0.7	0.29
Swainson's Thrush	12	2	5	2.9	1.6	0.36
Hermit Thrush	2		1	1.0	0.0	0.00
American Robin	3			1.0	0.0	0.00
Varied Thrush	5			1.0	0.3	0.25
Orange-crowned Warbler	31	3	13	7.2	3.9	0.35
Yellow-rumped Warbler	24	2	2	4.2	3.6	0.46
Blackpoll Warbler	3	1	1	0.7	0.3	0.33
Northern Waterthrush	1			0.0	0.3	1.00
Wilson's Warbler	134	23	49	19.2	27.7	0.59
American Tree Sparrow	41	6	6	5.9	7.5	0.56
Savannah Sparrow	8	1		2.0	0.7	0.25
Fox Sparrow	11	3	7	2.9	1.3	0.31
Lincoln's Sparrow	1			0.0	0.3	1.00
White-crowned Sparrow	80	10	29	12.7	13.4	0.51
Golden-crowned Sparrow	1	1		0.0	0.3	1.00
Dark-eyed Junco	37	2	15	4.6	8.1	0.64
Common Redpoll	67	8	10	16.0	3.3	0.17
Unidentified Bird		1				
ALL SPECIES POOLED	512	69	168	109.1	77.9	0.42
TOTAL NUMBER OF CAPTURES		749				
NUMBER OF SPECIES	26	14	16	22	21	
TOTAL NUMBER OF SPECIES		26			25	

Table 5. Percentage changes between 1999 and 2000 in the numbers of individual ADULT birds captured at six constant-effort MAPS stations in Denali National Park.

Species	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	n[1]	All six stations combined: No. adults 1999	No. adults 2000	% change	SE[2]
Three-toed Woodpecker					++++[3]		1	0	1	++++[3]	
Alder Flycatcher		-75.0	+133.3		++++		3	7	9	+28.6	92.6
Hammond's Flycatcher			-100.0				1	1	0	-100.0	
Gray Jay	-100.0			-100.0	0.0	++++[3]	4	4	3	-25.0	75.7
Black-capped Chickadee	-100.0					-100.0	2	3	0	-100.0	88.9
Boreal Chickadee				+400.0	-25.0	-33.3	3	8	10	+25.0	70.4
Ruby-crowned Kinglet					++++		1	0	3	++++	
Arctic Warbler	0.0	+100.0		-100.0			3	15	15	0.0	11.5
Gray-cheeked Thrush		-100.0	-42.9			++++	3	8	5	-37.5	18.9
Swainson's Thrush			++++[3]	-100.0	+20.0	-66.7	4	9	9	0.0	40.6
Hermit Thrush	+50.0						1	2	3	+50.0	
American Robin			-100.0	++++[3]	-50.0	-100.0	4	4	3	-25.0	66.9
Varied Thrush				-100.0	++++	++++	3	1	4	+300.0	600.0
Bohemian Waxwing		-100.0					1	1	0	-100.0	
Orange-crowned Warbler	-60.0	-25.0	-46.2	-66.7	-100.0		5	41	21	-48.8	9.5***
Yellow Warbler		-100.0					1	5	0	-100.0	
Yellow-rumped Warbler			-66.7	0.0	-60.0	+133.3	4	14	13	-7.1	43.6
Blackpoll Warbler			++++	+100.0	-100.0		3	2	3	+50.0	114.6
Northern Waterthrush			-100.0				1	1	0	-100.0	
Wilson's Warbler	-40.0	-47.9	-47.1	-52.9	-41.7	-33.3	6	117	63	-46.2	1.9***
American Tree Sparrow	-40.0	+100.0	-100.0	++++	-100.0		5	13	19	+46.2	60.4
Savannah Sparrow		-60.0	++++				2	5	5	0.0	120.0
Fox Sparrow	-66.7	++++[3]	+50.0				3	7	10	+42.9	78.0
Lincoln's Sparrow							0	0	0		
White-crowned Sparrow	+28.6	0.0	+16.7	+20.0	-57.1		5	48	45	-6.3	18.9
Golden-crowned Sparrow							0	0	0		
Dark-eyed Junco			-100.0	-66.7	-16.7	+60.0	4	21	16	-23.8	31.7
White-winged Crossbill				-100.0			1	5	0	-100.0	
Common Redpoll	+22.2	-36.7	-28.6	+50.0	-72.2		5	75	51	-32.0	14.1*
ALL SPECIES POOLED	-23.3	-32.3	-20.8	-19.3	-40.3	+31.6	6	417	311	-25.4	4.8***

Table 5.(cont.) Percentage changes between 1999 and 2000 in the numbers of individual ADULT birds captured at six constant-effort MAPS stations in Denali National Park.

Species	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	All six stations combined
No. species that increased[4]	3(0)	3(1)	6(3)	6(2)	5(4)	5(3)	9(2)
No. species that decreased[5]	6(2)	8(3)	10(5)	8(5)	10(3)	5(2)	15(6)
No. species remained same	1	1	0	1	1	0	3
TOTAL NUMBER OF SPECIES	10	12	16	15	16	10	27
Proportion of increasing (decreasing) species	(0.600)	(0.667)	(0.625)	(0.533)	(0.625)	0.500	(0.556)
Sig. of increase (decrease)[6]	(0.377)	(0.194)	(0.227)	(0.500)	(0.227)	0.623	(0.351)

[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 1999.
[4] No. of species for which adults were captured in 2000 but not in 1999 are in parentheses.
[5] No. of species for which adults were captured in 1999 but not in 2000 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 1999 and 2000 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	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	n[1]	1999	2000	% change	SE[2]
Three-toed Woodpecker							0	0	0		
Alder Flycatcher					-100.0		1	2	0	-100.0	
Hammond's Flycatcher							0	0	0		
Gray Jay	-100.0		++++[3]	-100.0		-100.0	4	4	1	-75.0	33.9
Black-capped Chickadee	-100.0			++++[3]	-100.0	++++[3]	4	3	2	-33.3	79.1
Boreal Chickadee			-100.0	++++	++++[3]		3	1	3	+200.0	458.3
Ruby-crowned Kinglet				++++			1	0	1	++++[3]	
Arctic Warbler	+40.0						1	5	7	+40.0	
Gray-cheeked Thrush		++++[3]	0.0				2	1	2	+100.0	200.0
Swainson's Thrush	-100.0		+100.0		-100.0	-25.0	4	10	5	-50.0	29.4
Hermit Thrush							0	0	0		
American Robin				-100.0			1	1	0	-100.0	
Varied Thrush						0.0	1	1	1	0.0	
Bohemian Waxwing							0	0	0		
Orange-crowned Warbler	+20.0	-50.0	-100.0	++++	-100.0		5	17	11	-35.3	36.8
Yellow Warbler		-100.0					1	5	0	-100.0	
Yellow-rumped Warbler			++++	+400.0		+300.0	3	2	10	+400.0	86.6**
Blackpoll Warbler			++++	-100.0			2	1	1	0.0	200.0
Northern Waterthrush			-100.0				1	2	0	-100.0	
Wilson's Warbler	-76.2	+25.9	+460.0	-50.0	-87.5	-100.0	6	73	73	0.0	45.3
American Tree Sparrow	-57.1	-100.0	-66.7	-33.3	++++	-100.0	6	31	20	-35.5	53.5
Savannah Sparrow		-100.0	0.0				2	11	1	-90.9	16.5
Fox Sparrow	0.0	-100.0	-62.5	-100.0		-100.0	5	12	4	-66.7	8.8***
Lincoln's Sparrow	++++[3]						1	0	1	++++	
White-crowned Sparrow	-37.5	-71.4	-40.0	-28.6	+433.3		5	45	38	-15.6	39.8
Golden-crowned Sparrow				++++			1	0	1	++++	
Dark-eyed Junco		-100.0	0.0	+500.0	+33.3	+33.3	5	13	20	+53.8	43.3
White-winged Crossbill			-100.0	-100.0	-100.0		3	3	0	-100.0	88.9
Common Redpoll	-100.0	-70.0	-100.0	++++	-100.0		5	44	9	-79.5	12.2***
ALL SPECIES POOLED	-49.2	-51.0	-6.4	+20.0	+11.8	-13.3	6	287	211	-26.5	13.4

Table 6.(cont.) Percentage changes between 1999 and 2000 in the numbers of individual YOUNG birds captured at six constant-effort MAPS stations in Denali National Park.

Species	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	All six stations combined
No. species that increased[4]	3(1)	2(1)	5(3)	8(6)	4(2)	3(1)	8(3)
No. species that decreased[5]	7(4)	8(5)	8(5)	8(5)	7(6)	5(4)	14(5)
No. species remained same	1	0	3	0	0	1	3
TOTAL NUMBER OF SPECIES	11	10	16	16	11	9	25
Proportion of increasing (decreasing) species	(0.636)	(0.800)	(0.500)	0.500	0.364	(0.556)	(0.560)
Sig. of increase (decrease)[6]	(0.274)	(0.055) *	(0.598)	0.598	0.887	(0.500)	(0.345)

[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 1999.
[4] No. of species for which young were captured in 2000 but not in 1999 are in parentheses.
[5] No. of species for which young were captured in 1999 but not in 2000 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 1999 and 2000 in the PROPORTION OF YOUNG in the catch at six constant-effort MAPS stations in Denali National Park.

								All six stations combined				
Species	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	n[1]	Prop. young 1999	Prop. young 2000	Absol. change	SE[2]	
Three-toed Woodpecker					+-+-+[3]		1	-----[4]	0.000	+-+-+[3]		
Alder Flycatcher		0.000	0.000		-1.000		3	0.222	0.000	-0.222	0.260	
Hammond's Flycatcher			+-+-+[3]				1	0.000	-----[4]	+-+-+		
Gray Jay	+-+-+[3]		+-+-+	+-+-+[3]	0.000	-1.000	5	0.500	0.250	-0.250	0.313	
Black-capped Chickadee	+-+-+			+-+-+	+-+-+	+1.000	4	0.500	1.000	+0.500	0.136	**
Boreal Chickadee			+-+-+	+0.286	+0.250	0.000	4	0.111	0.231	+0.120	0.146	
Ruby-crowned Kinglet				+-+-+	+-+-+		2	-----	0.250	+-+-+		
Arctic Warbler	+0.072	0.000		+-+-+			3	0.250	0.318	+0.068	0.063	
Gray-cheeked Thrush		+1.000	+0.075			+-+-+[3]	3	0.111	0.286	+0.175	0.156	
Swainson's Thrush	+-+-+		-0.500	+-+-+	-0.375	+0.179	5	0.526	0.357	-0.169	0.240	
Hermit Thrush	0.000						1	0.000	0.000	0.000		
American Robin			+-+-+	-1.000	0.000	+-+-+	4	0.200	0.000	-0.200	0.217	
Varied Thrush				+-+-+	+-+-+	-0.667	3	0.500	0.200	-0.300	0.455	
Bohemian Waxwing		+-+-+					1	0.000	-----	+-+-+		
Orange-crowned Warbler	+0.267	-0.068	-0.188	+0.750	+-+-+		5	0.293	0.344	+0.051	0.163	
Yellow Warbler		+-+-+					1	0.500	-----	+-+-+		
Yellow-rumped Warbler			+0.500	+0.375	0.000	+0.114	4	0.125	0.435	+0.310	0.121	
Blackpoll Warbler			+-+-+	-0.500	+-+-+		3	0.333	0.250	-0.083	0.290	
Northern Waterthrush			+-+-+				1	0.667	-----	+-+-+		
Wilson's Warbler	-0.218	+0.216	+0.530	+0.014	-0.275	-0.400	6	0.384	0.537	+0.153	0.091	
American Tree Sparrow	-0.083	-0.700	+0.250	-0.500	+1.000	+-+-+	6	0.705	0.513	-0.192	0.246	
Savannah Sparrow		-0.667	-0.750				2	0.688	0.167	-0.521	0.118	
Fox Sparrow	+0.250	-1.000	-0.333	+-+-+		+-+-+	5	0.632	0.286	-0.346	0.131	*
Lincoln's Sparrow	+-+-+						1	-----	1.000	+-+-+		
White-crowned Sparrow	-0.169	-0.293	-0.155	-0.118	+0.551		5	0.484	0.458	-0.026	0.135	
Golden-crowned Sparrow				+-+-+			1	-----	1.000	+-+-+		
Dark-eyed Junco		+-+-+	+0.333	+0.567	+0.115	-0.042	5	0.382	0.556	+0.173	0.145	
White-winged Crossbill			+-+-+	+-+-+	+-+-+		3	0.375	-----	+-+-+		
Common Redpoll	-0.357	-0.160	-0.500	+0.333	-0.217		5	0.370	0.150	-0.220	0.085	*
ALL SPECIES POOLED	-0.100	-0.078	+0.041	+0.094	+0.148	-0.099	6	0.408	0.404	-0.004	0.031	

Table 7.(cont.) Absolute changes between 1999 and 2000 in the PROPORTION OF YOUNG in the catch at six constant-effort MAPS stations in Denali National Park.

Species	Igloo Creek	Buhach Creek	Strang. Hill	Mile Seven	Perma-frost	Rock Creek	All six stations combined
No. species that increased	3	2	5	6	4	3	8
No. species that decreased	4	6	6	4	4	4	11
No. species remained same	1	2	1	0	3	1	1
TOTAL NUMBER OF SPECIES[5]	8	10	12	10	11	8	20
Proportion of increasing (decreasing) species	(0.500)	(0.600)	0.417	0.600	0.364	(0.500)	(0.550)
Sig. of increase (decrease)[6]	(0.637)	(0.377)	0.806	0.377	0.887	(0.637)	(0.412)

[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 8. Annual numbers of individuals captured (based on all captures) and year-to-year changes (based on constant-effort comparisons) of adults and young and of the proportion of young in the catch for all six stations combined for nine target species at Denali National Park from 1992-2000.

Adults[1]

Target species[2]	1992	%Chg.	1993	%Chg.	1994	%Chg.	1995	%Chg.	1996	%Chg.	1997	%Chg.	1998	%Chg.	1999	%Chg.	2000
Arctic Warbler	40	-31.8	19	+33.3	33	-28.1	27	+50.0	40	+18.9	55	-37.7	33	-54.5	15	0.0	16
Swainson's Thrush	19	+15.8	22	-33.3	14	-16.7	11	+44.4	14	-33.3	10	+40.0	14	-35.7	10	0.0	9
Orange-crowned Warb.	15	-71.4	4	+200.0	12	+109.1	23	-33.3	18	0.0	40	+56.4	67	-29.7	47	-48.8	22
Yellow-rumped Warbler	6	-50.0	4	+300.0	16	-6.7	15	+7.1	15	-21.4	11	+90.0	19	-11.1	16	-7.1	15
Wilson's Warbler	43	+50.0	59	-3.8	50	+8.0	55	+3.8	60	-34.5	126	+14.3	154	-13.3	127	-46.2	68
American Tree Spar.	13	0.0	15	+83.3	22	-59.1	9	+75.0	16	-6.7	30	-24.1	23	-28.6	15	+46.2	21
White-crowned Spar.	47	-6.5	45	+28.6	55	-49.1	28	+46.4	42	+2.5	65	+34.4	91	-42.9	50	-6.3	48
Dark-eyed Junco	14	-35.7	9	+88.9	17	-12.5	15	0.0	16	0.0	18	-5.6	18	+41.2	24	-23.8	16
Common Redpoll	25	+14.3	26	-20.8	27	-29.6	22	-10.5	17	+46.7	57	+12.7	71	+21.3	78	-32.0	57
ALL SPECIES POOLED	277	-7.4	238	+17.7	273	-16.6	237	+12.8	268	-7.1	485	+12.2	573	-16.2	455	-25.4	335

Young[1]

Target species[2]	1992	%Chg.	1993	%Chg.	1994	%Chg.	1995	%Chg.	1996	%Chg.	1997	%Chg.	1998	%Chg.	1999	%Chg.	2000
Arctic Warbler	23	-60.0	2	+50.0	11	-36.4	8	+275.0	17	-26.7	19	-61.1	7	0.0	5	+40.0	7
Swainson's Thrush	6	-60.0	3	0.0	3	+66.7	5	+20.0	6	-40.0	3	+133.3	9	+71.4	12	-50.0	5
Orange-crowned Warb.	22	0.0	4	+25.0	11	+27.3	15	+58.3	23	-15.8	18	+294.4	89	-74.3	19	-35.3	12
Yellow-rumped Warbler	2	+350.0	9	+122.2	20	-65.0	7	-33.3	4	0.0	3	+466.7	20	-82.4	3	+400.0	11
Wilson's Warbler	94	+30.0	91	-49.4	61	+38.6	87	-27.0	57	+11.1	121	+55.2	236	-55.9	85	0.0	85
American Tree Spar.	43	0.0	31	+16.7	34	-23.5	27	-45.0	12	+41.7	39	-5.1	55	-7.3	38	-35.5	23
White-crowned Spar.	60	+49.0	89	-64.8	25	+132.0	62	-10.5	51	+37.3	107	-36.5	86	-18.8	54	-15.6	41
Dark-eyed Junco	15	+100.0	32	-59.4	14	-15.4	11	+27.3	14	+164.3	41	-30.0	30	-50.0	15	+53.8	25
Common Redpoll	3	+300.0	7	+16.7	10	0.0	9	-22.2	7	-28.6	14	+21.4	22	+176.5	49	-79.5	10
ALL SPECIES POOLED	298	+33.7	291	-33.3	209	+20.7	265	-9.6	217	+23.3	420	+20.8	636	-35.5	337	-26.5	239

Table 8. (cont.) Annual numbers of individuals captured (based on all captures) and year-to-year changes (based on constant-effort comparisons) of adults and young and of the proportion of young in the catch for all six stations combined for nine target species at Denali National Park from 1992-2000.

	Proportion of young[1]																
Target species[2]	1992	Chg.	1993	Chg.	1994	Chg.	1995	Chg.	1996	Chg.	1997	Chg.	1998	Chg.	1999	Chg.	2000
Arctic Warbler	0.365	-0.068	0.095	+0.011	0.250	-0.022	0.229	+0.151	0.298	-0.088	0.257	-0.079	0.175	+0.118	0.250	+0.068	0.304
Swainson's Thrush	0.240	-0.125	0.120	+0.051	0.176	+0.133	0.313	-0.041	0.300	-0.021	0.231	+0.103	0.391	+0.238	0.545	-0.169	0.357
Orange-crowned Warb.	0.595	+0.252	0.500	-0.206	0.478	-0.122	0.395	+0.212	0.561	-0.043	0.310	+0.222	0.571	-0.237	0.288	+0.051	0.353
Yellow-rumped Warbler	0.250	+0.500	0.692	-0.137	0.556	-0.238	0.318	-0.089	0.211	+0.038	0.214	+0.241	0.513	-0.328	0.158	+0.310	0.423
Wilson's Warbler	0.686	-0.034	0.607	-0.159	0.550	+0.061	0.613	-0.087	0.487	+0.130	0.490	+0.076	0.605	-0.167	0.401	+0.153	0.556
American Tree Spar.	0.768	0.000	0.674	-0.107	0.607	+0.136	0.750	-0.274	0.429	+0.104	0.565	+0.054	0.705	+0.056	0.717	-0.192	0.523
White-crowned Spar.	0.561	+0.114	0.664	-0.302	0.313	+0.362	0.689	-0.116	0.548	+0.070	0.622	-0.185	0.486	+0.088	0.519	-0.026	0.461
Dark-eyed Junco	0.517	+0.252	0.780	-0.347	0.452	-0.008	0.423	+0.060	0.467	+0.231	0.695	-0.067	0.625	-0.254	0.385	+0.173	0.610
Common Redpoll	0.107	+0.097	0.212	+0.069	0.270	+0.071	0.290	-0.030	0.292	-0.133	0.197	+0.012	0.237	+0.170	0.386	-0.220	0.149
ALL SPECIES POOLED	0.518	+0.092	0.550	-0.140	0.434	+0.092	0.528	-0.055	0.447	+0.071	0.464	+0.018	0.526	-0.065	0.426	-0.003	0.416

[1] Annual numbers are based on all adult or young individuals captured at all six stations pooled in a given year (only 1997-2000 values and changes include data from Strangler Hill and Buhach Creek). Year-to-year changes in the number of adults or young captured or proportion of young are from analyses of constant-effort data only. They do not reflect exactly the percentage changes in annual numbers. The two sets of data are presented for efficiency, and because constant-effort totals for a given year (e.g., 1994) will differ for comparisons with previous (1993) vs. subsequent (1995) years.

[2] Target species are those for which an average of at least seven individual adult birds (pooled from stations where the species was classified as either a breeder or transient) were recorded per year over the nine years 1992-2000 (63 year unique records) .

** Note: Values for a given year may differ from previous reports as corrections are occasionally made to previously collected data using information provided by captures in the current year.

Table 9. Summary statistics for survival analyses with temporally-variable survival and recapture probabilities in transient models using nine years (1992-2000) of mark-recapture data from four MAPS stations at Denali National Park (data from Buhach Creek and Strangler Hill are not included). $QAIC_C$[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]
Arctic Warbler	86.8*	90.2	93.6	96.0	96.5	100.1	104.6	106.1	3.4
	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	
Swainson's Thrush	74.3*	86.6	84.0	84.8	92.8	100.5	98.6	105.5	12.3
	(0.999)	(0.998)	(0.999)	(0.999)	(1.000)	(0.998)	(0.999)	(1.000)	
Orange-crowned Warbler	61.2*	69.2	64.6	71.9	75.0	81.8	77.3	88.2	8.0
	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	
Yellow-rumped Warbler	48.8*	63.0	58.2	60.9	70.7	76.5	70.0	83.3	14.2
	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	
Wilson's Warbler	95.0*	105.7	106.5	104.2	116.8	110.4	113.9	119.9	10.7
	(1.000)	(1.000)	(0.999)	(1.000)	(0.999)	(1.000)	(1.000)	(1.000)	
American Tree Sparrow	62.7*	71.9	73.9	69.2	81.4	81.9	83.3	90.4	9.2
	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	(1.000)	
White-crowned Sparrow	119.3*	129.8	122.3	126.0	131.2	134.0	128.8	138.0	10.5
	(0.979)	(0.968)	(0.997)	(0.988)	(0.997)	(0.995)	(1.000)	(0.999)	
Dark-eyed Junco	70.9*	82.0	83.2	80.6	94.3	93.2	95.1	104.0	11.1
	(0.997)	(0.996)	(0.994)	(0.998)	(0.994)	(0.998)	(0.996)	(0.998)	

[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.

Table 9. (cont.) Summary statistics for survival analyses with temporally-variable survival and recapture probabilities in transient models using nine years (1992-2000) of mark-recapture data from four MAPS stations in Denali National Park (data from Buhach Creek and Strangler Hill are not included). $QAIC_C$[1] and (GOF)[2] are presented for all models.

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[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 10. Estimates of adult survival and recapture probabilities and proportion of residents using both temporally-variable and -constant models for eight species breeding at four MAPS stations in Denali National Park obtained from nine years (1992-2000) 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]
Arctic Warbler	1	220	388	44	φPτ	86.8	0.353 (0.058)	16.4	0.632 (0.112)	0.551 (0.149)
Swainson's Thrush	2	86	135	23	φPτ	74.3	0.529 (0.084)	15.9	0.407 (0.114)	0.612 (0.221)
Orange-crowned Warbler	2	111	177	17	φPτ	61.2	0.491 (0.110)	22.4	0.343 (0.130)	0.467 (0.208)
Yellow-rumped Warbler	3	98	125	10	φPτ	48.8	0.599 (0.147)	24.5	0.215 (0.116)	0.368 (0.219)
Wilson's Warbler	4	424	687	47	φPτ	95.0	0.381 (0.059)	15.5	0.402 (0.093)	0.367 (0.101)
American Tree Sparrow	2	86	183	24	φPτ	62.7	0.466 (0.079)	17.0	0.657 (0.129)	0.382 (0.147)
White-crowned Sparrow	3	305	541	68	φPτ	119.3	0.447 (0.051)	11.4	0.392 (0.072)	0.769 (0.168)
Dark-eyed Junco	3	125	207	19	φPτ	70.9	0.471 (0.096)	20.4	0.381 (0.129)	0.444 (0.186)

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

Table 11. Summary of population trends and primary demographic parameters for eight target species at Denali National Park. See methods and cited Figures and Tables for derivation of these values.

Species	PT (Figure 1)	PrT (Figure 2)	Productivity/ population correlation (Figure 3)	$\Delta QAIC_C$ (Table 9)	Comparison with body mass: Survivorship (Figure 6)	Comparison with body mass: Productivity (Figure 7)
Arctic Warbler	-0.058	+0.038*	+0.225	3.4	lower	lower
Swainson's Thrush	-0.080***	+0.023*	+0.840**	12.3	expected	lower
Orange-crowned Warbler	+0.018	-0.006	+0.555	8.0	expected	expected
Yellow-rumped Warbler	+0.167**	+0.004	+0.787**	14.2	higher	lower
Wilson's Warbler	-0.014	-0.037**	+0.759**	10.7	expected	expected
American Tree Sparrow	-0.054	-0.007	+0.457	9.2	expected	expected
White-crowned Sparrow	-0.026	-0.007	+0.795**	10.5	expected	expected
Dark-eyed Junco	+0.022	-0.007	+0.488	11.1	expected	expected

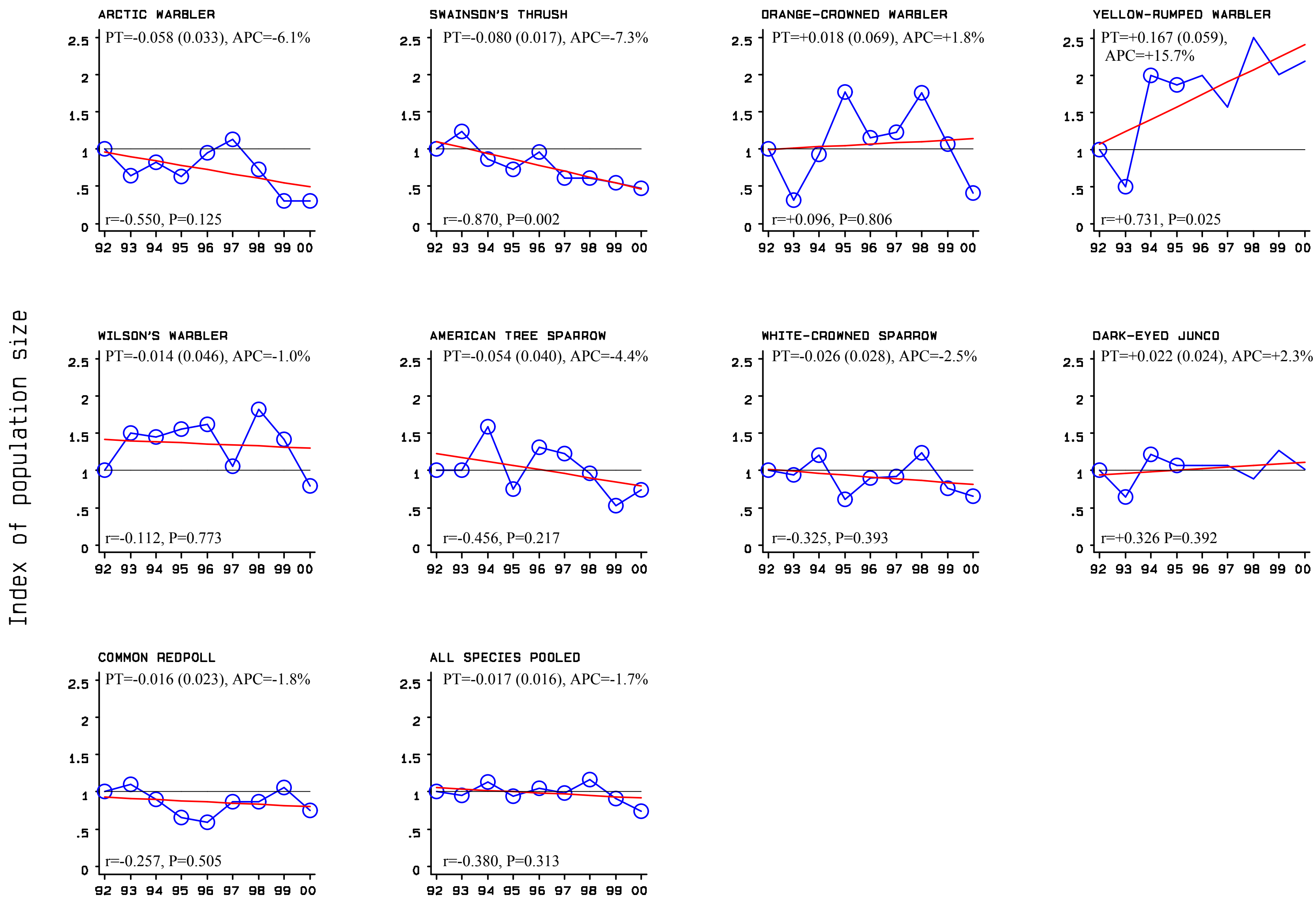

Figure 1. Population trends for nine species and all species pooled in Denali National Park over the nine years 1992-2000. The index of population size was arbitrarily defined as 1.0 in 1992. Indices for subsequent years were determined from constant-effort between-year changes in the number of adult birds captured from stations where the species was a regular or usual breeder and summer resident. Data from Buhach Creek and Strangler Hill from 1997-2000 were not included. The slope of the regression line for annual change in the index of adult population size was used as the measure of the population trend (*PT*), and it and the standard error of the slope (in parentheses) are presented on each graph. The annual percentage change (*APC*), and the correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

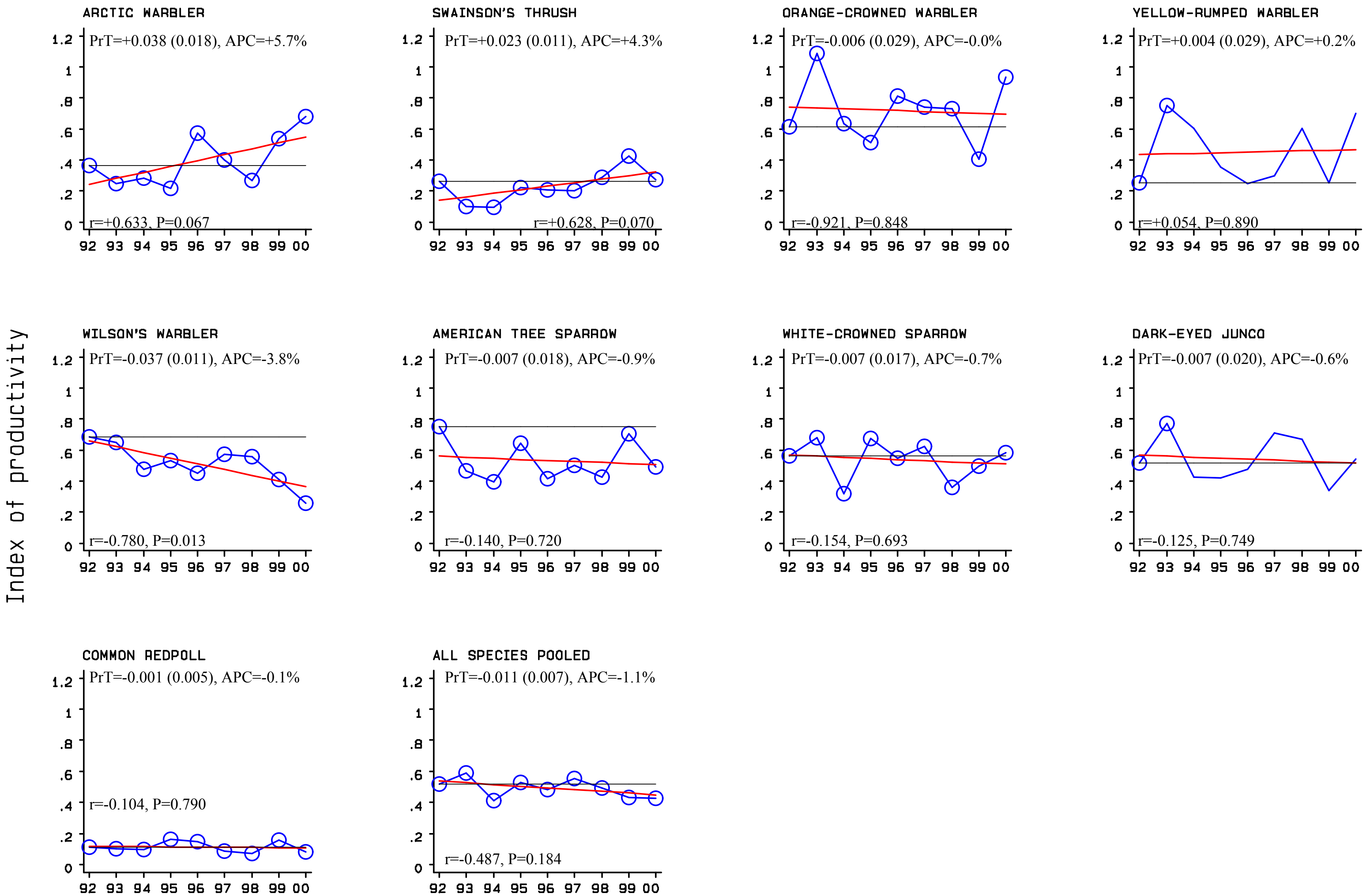

Figure 2. Trend in productivity for nine species and all species pooled in Denali National Park over the nine years 1992-2000. The productivity index was defined as the actual productivity value in 1992. Indices for subsequent years were determined from constant-effort between-year changes in proportion of young in the catch from stations where the species was a regular or usual breeder and summer resident. Data from Buhach Creek and Strangler Hill from 1997-2000 were not included. 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 annual percentage change (*APC*), and the correlation coefficient (*r*) and significance of the correlation coefficient (*P*) are also shown on each graph.

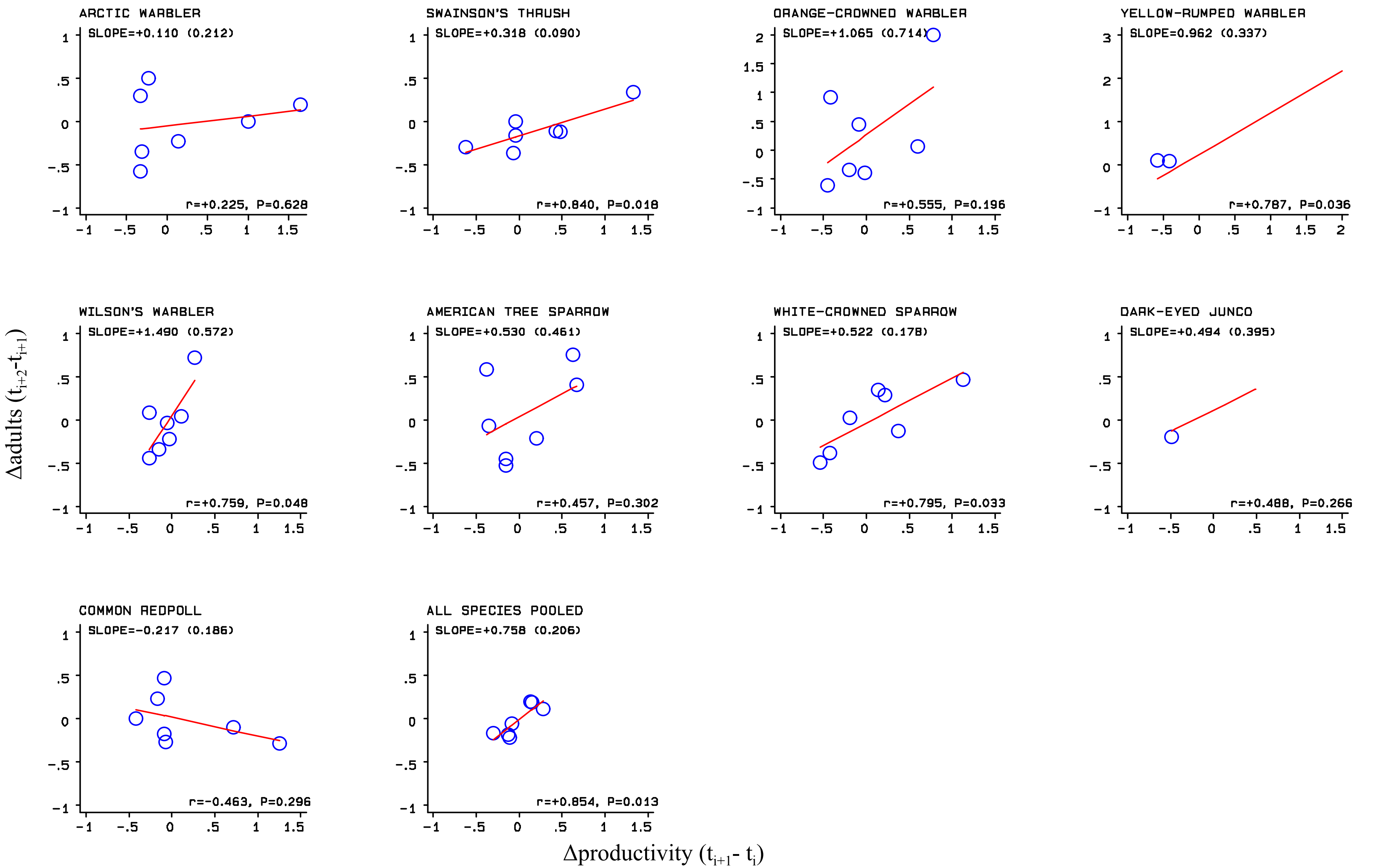

Figure 3. The regression of the percent change in the number of adults between year i+2 and year i+1 on the percent change in productivity between year i+1 and year i ("productivity/population correlation") for nine species and all species pooled in Denali National Park. The constant-effort between-year 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.

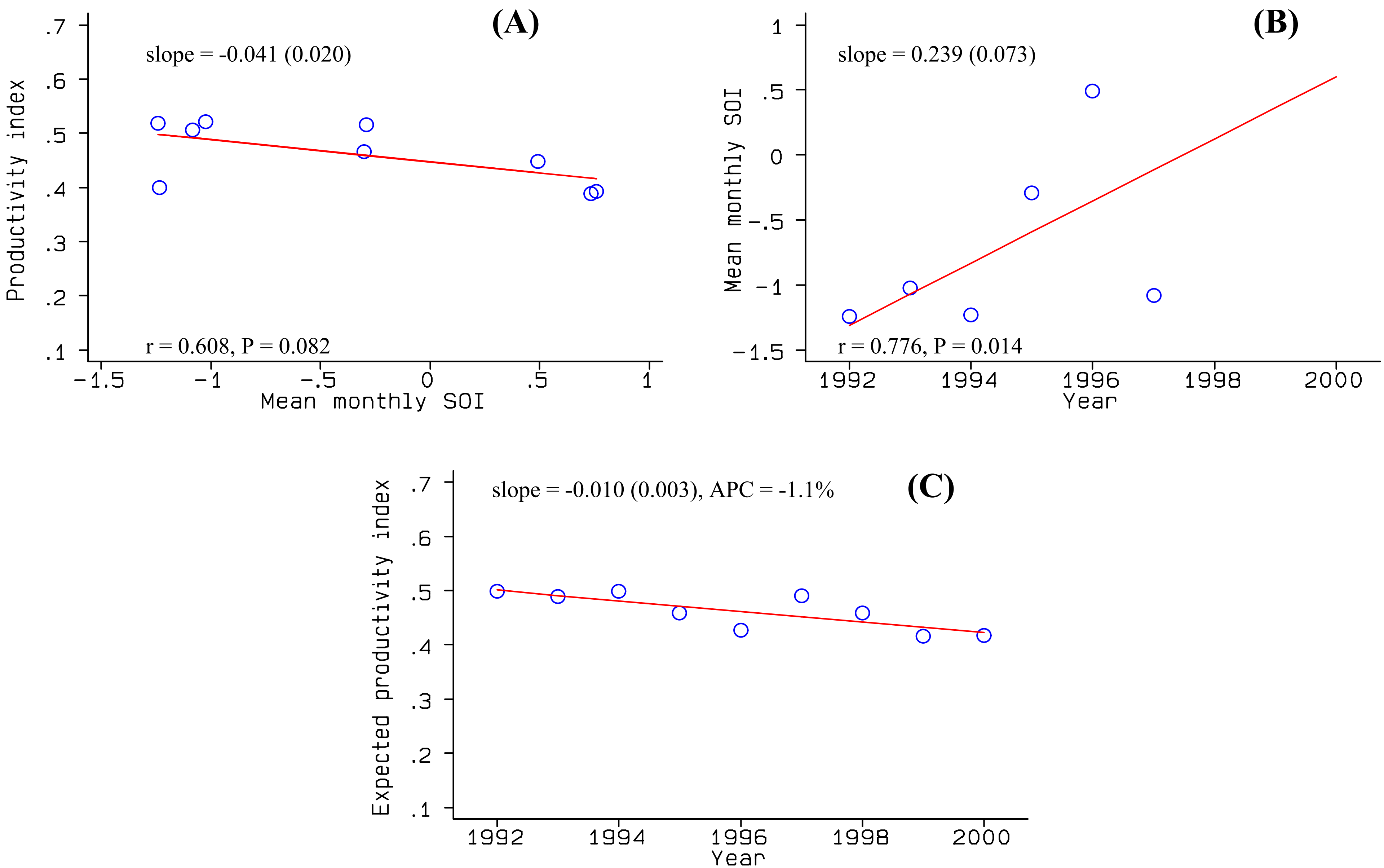

Figure 4. Effects of El Nino/Southern Oscillation (ENSO) on productivity at Denali National Park. (A) Annual productivity indices (for all species at the four long-running stations pooled) as a function of mean monthly Southern Oscillation Index (SOI; see text); (B) Mean monthly SOI as a function of year; (C) Expected annual productivity indices (based on relationships shown in A and B) as a function of year.

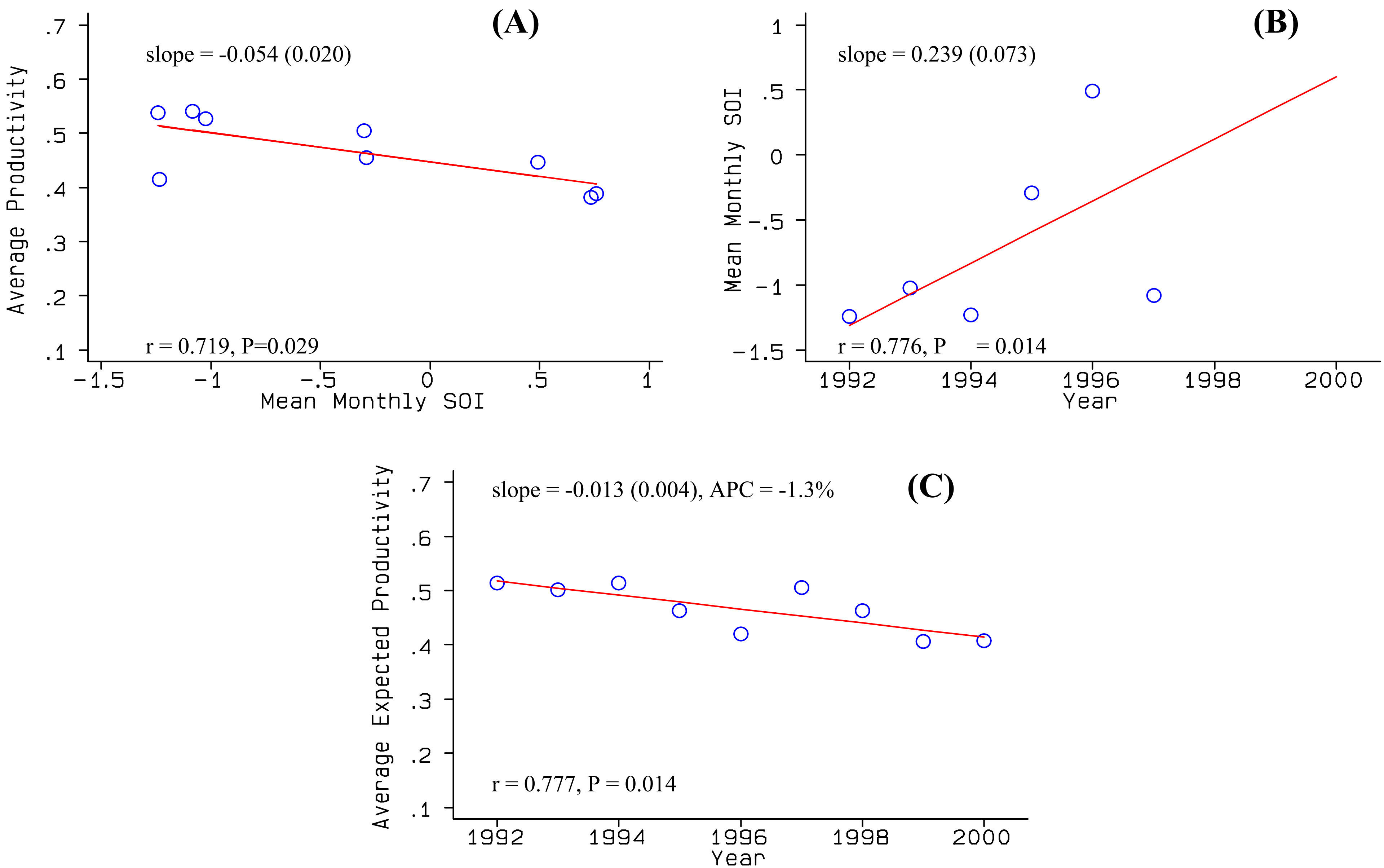

Figure 4. Productivity as correlated with Southern Oscillation Index in Denali National Park. A) The relationship of productivity to the mean monthly SOI; B) The correlation of mean monthly SOI and year; C) Expected productivity by year calculated using the relationship described in A and B.

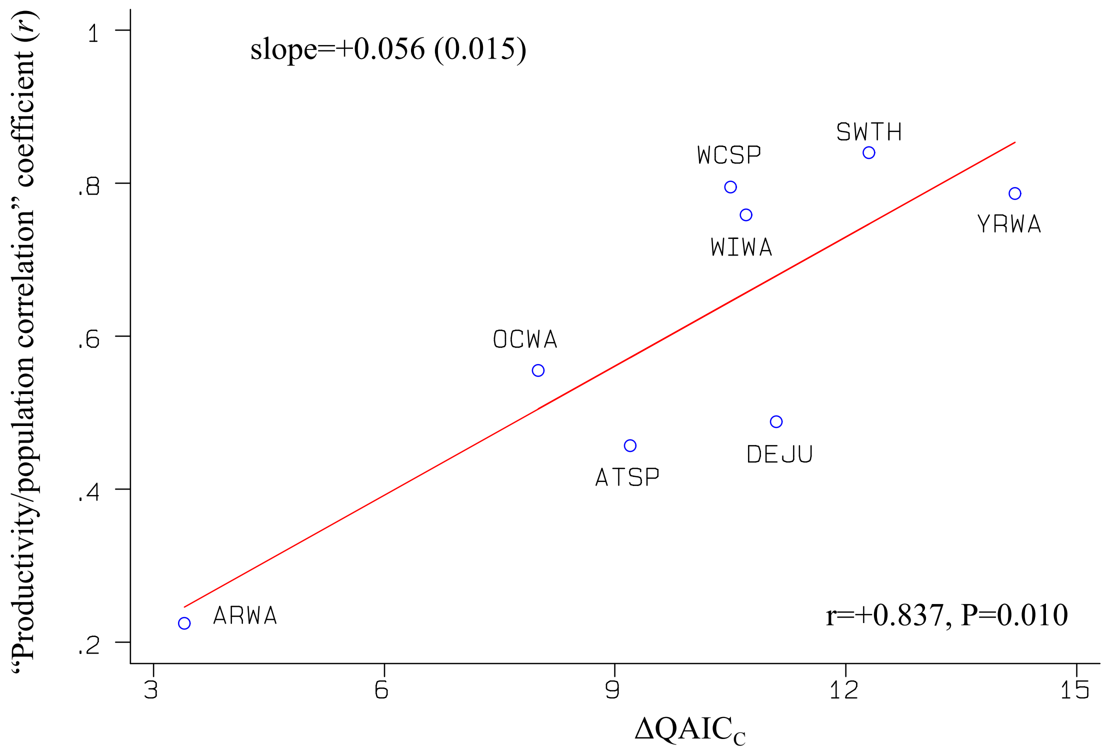

Figure 5. The "productivity/population correlation" (Figure 3; strength of the effect represented by the *r*-value) as a function of $\Delta QAIC_C$ (Table 9; a measure of the degree of interannual variation in survival), for eight target species at Denali National Park (see text).

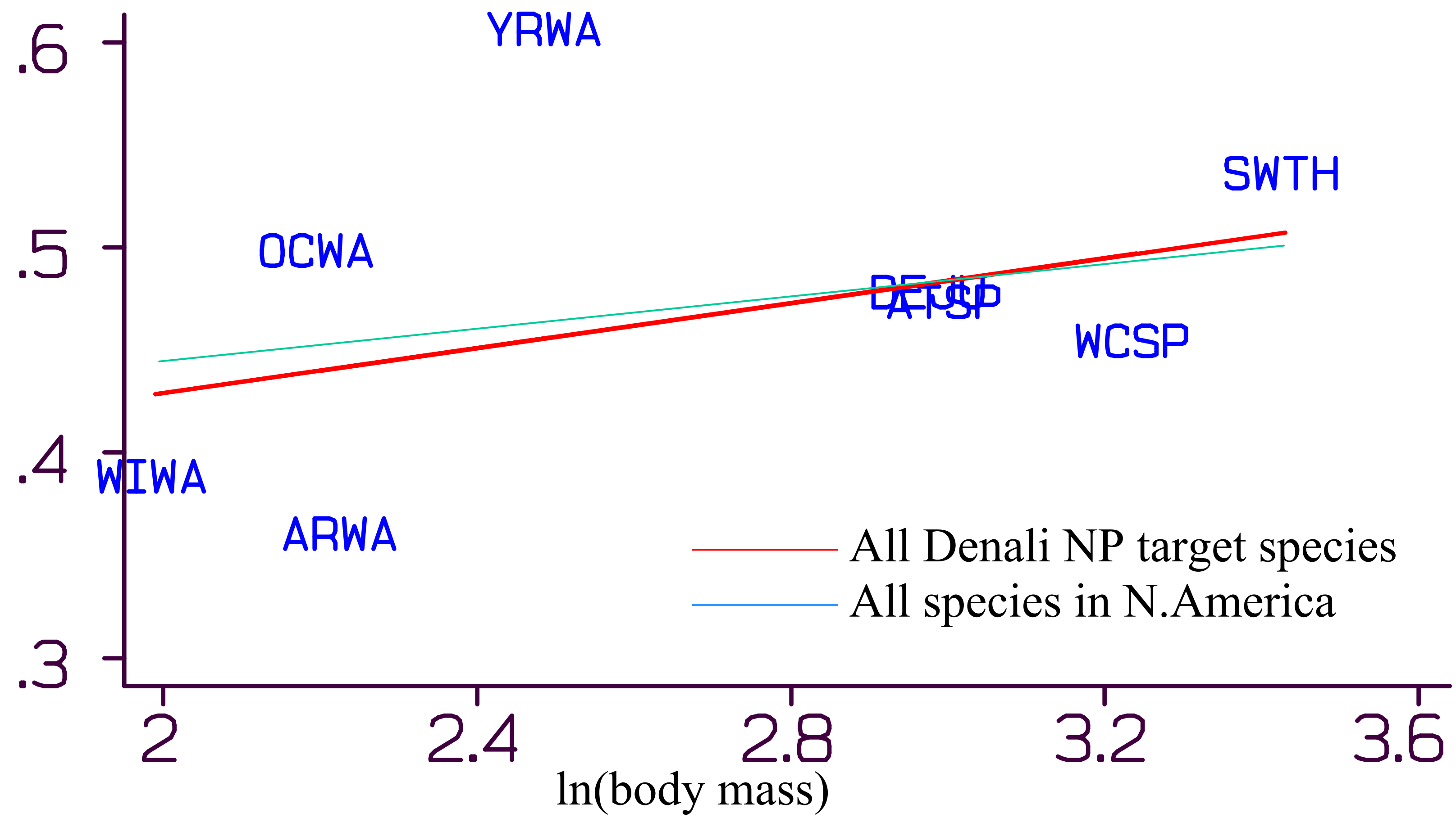

Figure 6. The correlation between adult survival rates at Denali National Park and the natural log of the body mass for the eight target species for which survivorship estimates could be calculated for the nine years 1992-2000, and for all species throughout all of North America.

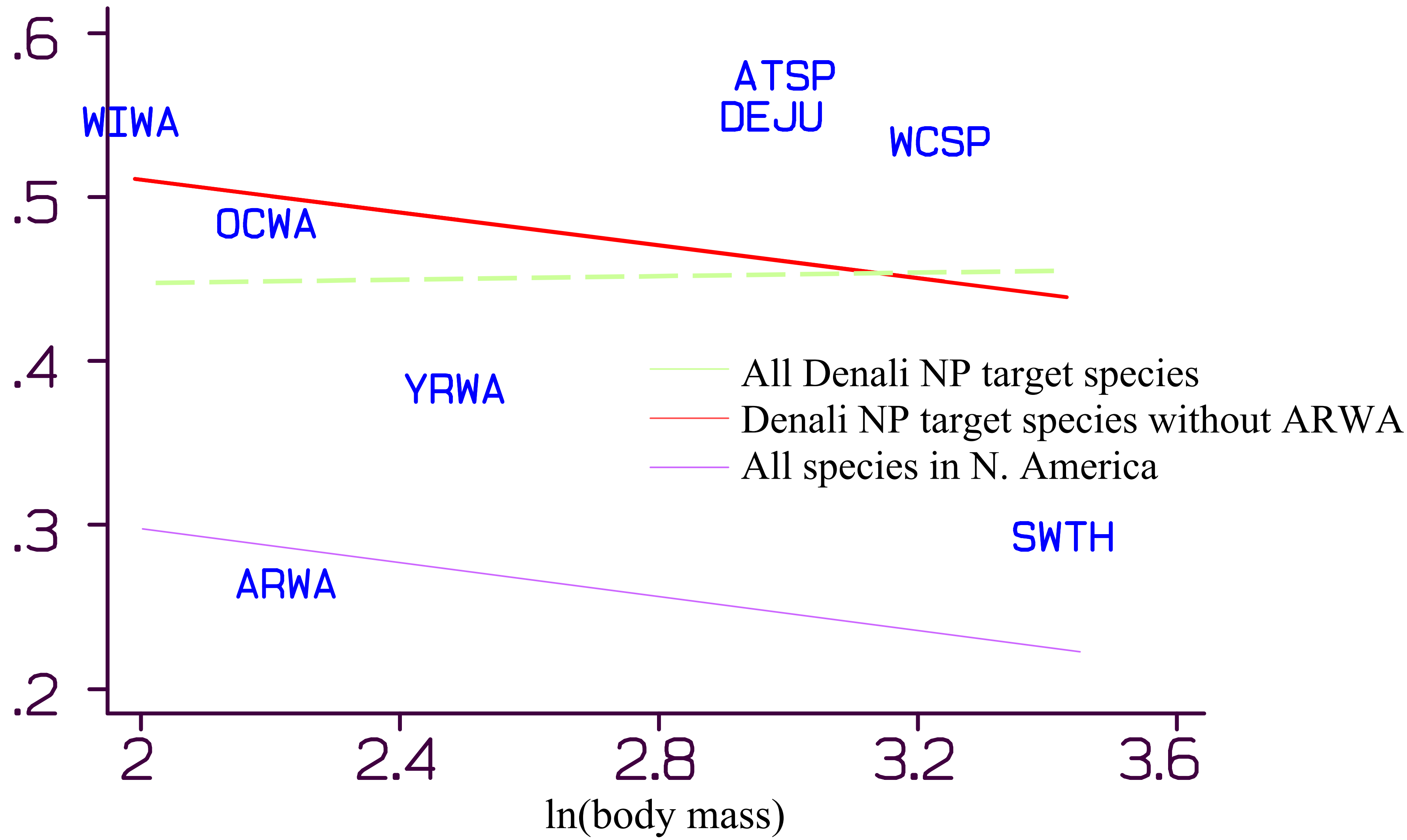

Figure 7. The correlation between productivity index at Denali National Park and the natural log of the body mass for the eight target species for which survivorship estimates could be calculated for the nine years 1992-2000, and for all species throughout all of North America.