

## METHODOLOGICAL CONSIDERATIONS OF THE MONITORING AVIAN PRODUCTIVITY AND SURVIVORSHIP (MAPS) PROGRAM

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*Abstract.* The Monitoring Avian Productivity and Survivorship (MAPS) Program is a cooperative program to generate annual indices of adult population size, post-fledging productivity, and estimates of adult survivorship for landbirds at multiple spatial scales. The program consists of a network of constant effort mist-netting and banding stations spread across North America. We use MAPS data collected from 1989 through 1993 (1995 for one analysis) to investigate methods of data collection and analysis, focusing on the following critical areas: density of nets, starting and ending dates each year, number of days of operation per 10-day period, verification of data, pooling of data for between-year comparisons, comparison of indices of adult population size from mist netting and point counts, and the use and interpretation of mark-recapture analyses. Results provide justification for current recommended MAPS methodology: operation of about ten 12-m, 30-mm-mesh mist nets over an area of about 8 ha, for six morning hours per day, for one day per 10-day period, and for six to ten 10-day periods (depending on latitude), with operations beginning after and ending before most of the migrant individuals have passed through the local area.

*Key Words:* constant-effort mist netting, MAPS, methods, population size, productivity, survivorship.

The Monitoring Avian Productivity and Survivorship (MAPS) Program is a North America-wide constant effort mist-netting program that was established to collect large-scale, long-term demographic data on landbirds. Its primary purposes are to (1) help identify causal factors driving population trends documented by other North American avian monitoring programs, such as the Breeding Bird Survey (BBS), Breeding Bird Census, Winter Bird Population Study, and Christmas Bird Count; (2) help formulate management actions to reverse population declines and maintain stable or increasing populations; and (3) help evaluate and enhance the effectiveness of implemented management actions (DeSante 1991a, 1992; DeSante et al. 1993a,b, 1995, 2001). BBS and other monitoring programs have supplied convincing evidence for recent declines in many landbird species, including many that winter in the Neotropics (Robbins et al. 1989, Terborgh 1989), and those findings were the major impetus leading to the establishment of the Neotropical Migratory Bird Conservation Program, "Partners in Flight." By themselves, however, the monitoring programs listed above provide little direction on management needed to reverse population declines. They provide no information on primary demographic parameters (productivity and survivorship), and thus fail to distinguish problems caused by birth-rate effects on the breeding grounds from problems caused by death-rate effects that may operate primarily on the wintering grounds or migration routes (Temple and

Wiens 1989, DeSante 1992). MAPS is designed to fill this information gap.

MAPS is a cooperative effort among public agencies, private organizations, and individual bird banders. It was established in 1989 by The Institute for Bird Populations and was patterned to a large extent after the Constant Effort Sites (CES) Scheme, operated by the British Trust for Ornithology (BTO) since 1981 (Baillie et al. 1986, Peach et al. *this volume*). MAPS has grown continuously since 1989 to over 500 stations operated continent-wide during 2002.

In this paper we discuss some of the reasoning and testing behind the methods chosen for the MAPS protocol, and the ramifications of both field and analytical methods on the accuracy and precision of results. We also identify some unresolved methodological and analytical difficulties regarding the interpretation of MAPS data, and indicate where additional work is needed to resolve these issues.

### METHODS

The following terminology is used in this paper. Post-fledging "productivity" is an index of the relative number of hatch-year birds that attain independence from their parents and begin post-juvenile dispersal, and is represented by proportion of young in the catch. Adult "survivorship" is a measure of death rate and is estimated by mark-recapture analyses as the apparent annual survival probability of adults; that is, the probability of an adult bird surviving and returning in year  $i+1$  to the location where it was marked

in year  $i$ . Survivorship thus includes components of actual survival and site fidelity. "Recapture probability" is the conditional probability of recapturing a marked bird in year  $i+1$ , given that it survived from year  $i$  to  $i+1$  and returned in year  $i+1$  to the location where it was marked in year  $i$ . "First capture" refers to the first capture of a bird in year  $i$ , regardless of whether or not it had been captured in a previous year. Effort "saturation" is said to have occurred in a closed population when rate of first captures declines due to most birds already having been captured once. "Net avoidance" refers to lowered recapture probability of individual birds that have been captured (or, perhaps, hit a net and bounced out), as a result of learning to avoid nets or specific net sites.

The overall design of the MAPS Program and methods used to establish and operate MAPS stations have been described in detail in DeSante et al. (1993a,b, 2002). Analysis methods are detailed in DeSante et al. (1993b, 1995, 1996), DeSante and Burton (1994), and Nott and DeSante (2002), and are only briefly outlined here. Indices of annual population size are calculated as the numbers of first captures of adult birds of each species (and of all species pooled) in each year, pooled over all stations of interest (e.g., grouped by geographic region, habitat characteristics, or population trends of a target species) that lie within the breeding range of each species. Similar calculations are completed for first captures of young birds, and indices of productivity are then calculated for each species (and for all species pooled) as the proportion of young in the total catch. Following Baillie et al. (1986), the significance of annual changes is inferred statistically from confidence intervals calculated from the standard errors of the mean percent changes (Baillie et al. 1986, DeSante et al. 1993a, DeSante and Burton 1994). Peach et al. (1996) give revised formulae that take into account between-station heterogeneity in capture trends. We infer the statistical significance of regional between-year changes in adult population size and productivity by means of binomial tests on the proportion of target species that increased in each region. Annual adult survival rates and adult recapture probabilities are estimated from modified Cormack-Jolly-Seber (CJS) mark-recapture models (Clobert et al. 1987, Pollock et al. 1990, Lebreton et al. 1992).

Miscellaneous analyses were conducted in support of the results and discussion to follow. For purposes of clarity, we include details related to each analysis along with the relevant results. Results are given as means  $\pm$ SE unless stated otherwise.

## RESULTS AND DISCUSSION

### FIELD METHODS

#### *Net characteristics*

Number and density of nets can have important effects on the precision of mark-recapture estimates of adult population size and adult survivorship. Spreading nets as widely as possible will tend to

increase the number of territories intersected, and thus the population size sampled, but will tend to decrease recapture probability for the birds on any single territory, and vice versa. There should exist some intermediate net density that will simultaneously optimize both the number of different individual adults captured and the recapture probability of these adults, although this optimal net density is likely to differ among species and among habitat types.

Figure 1 presents a plot of total capture rate (including recaptures) of adult birds (all species pooled), as a function of net density. Data were collected in 1990 from 25 MAPS stations located in forest or forest-edge habitats, all using 12-m nets, and all operated for one or two days per 10-day period. (Stations that were operated for more than two days per 10-day period were excluded from this analysis because of potential saturation and net-avoidance problems; see Burton and DeSante *this volume* and below). Highest capture rates appeared to occur at net densities between about 0.6 and 1.7 nets per ha, although variance was high. As a rule of thumb, therefore, we suggest that MAPS stations operate 12-m nets at net densities between about 1.0 and 1.5 nets per ha, and recommend that 10 nets be operated in an 8-ha netting area (1.25 nets per ha). The upper limit on the number of nets that can be used at any station, and the lower limit on net density, should be set by the number of people available to operate a station. Operators must be able to visit all net locations within 10–15 min if no birds are caught (Ralph et al. 1993). We suggest that the 8-ha netting area be centrally located in a 20-ha study area of similar habitat that defines the MAPS station and its boundaries.

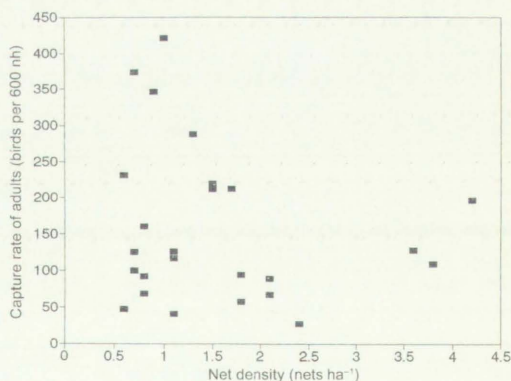


FIGURE 1. Capture rate of adult birds (all species pooled) at varying net densities. Data are from 25 MAPS stations operated in forest or forest-edge habitats for one or two days per 10-day period in 1990.

To provide optimal coverage, nets should be placed relatively uniformly throughout the netting area. Within this general constraint, however, nets should be placed opportunistically at locations where birds can be captured most efficiently, such as brushy portions of wooded areas, forest breaks, and near water. This is because larger sample sizes and higher recapture probabilities contribute to stronger inference in analyses (as well as being more interesting for station operators).

To promote similarity of species' catchability among stations, we recommend that all stations use the same type of net. For maximum captures of small birds (most target species weigh less than about 30–35 g), and for ease of extraction of birds of all sizes, we suggest the use of 30-mm mesh, four-tier, tethered, black nylon mist nets (Heimerdinger and Leberman 1966, Pardieck and Waide 1992). All nets should be 12 m in length, for uniformity and ease of handling. If nets of other lengths must be used, netting effort should be calculated accordingly (e.g., the use of a 6-m net for one hour should be counted as 1/2 net-h).

#### *Schedule of operation*

*Start and end times.*—The breeding season is divided into 12 equal 10-day periods between May 1 and August 28 (although some stations in extreme southern United States may start earlier). It is important that the first netting session take place after the vast majority of spring migrant individuals of the target species have moved through the study area. This is because inclusion of migrating adult individuals in the data will negatively bias both productivity indices and survivorship estimates, since low (or zero) recapture rates of migrants can be mistaken as high mortality in adults.

For example, we estimated adult survival probabilities (all species pooled) from three years of mark-recapture data for each of eight stations operated in 1989–1991. Four of these eight stations were also migration-banding stations, and submitted data to the MAPS Program that were collected during the latter part of the migration season. Annual survival estimates for various species from these eight stations ranged from 0.05 to 0.38 (mean =  $0.27 \pm 0.04$ ), and were only 50–60% of the generally expected values for temperate-zone passerines (Loery et al. 1987, Karr et al. 1990a, Pollock et al. 1990, Peach 1993). Moreover, data from these early netting sessions cannot simply be dropped from analysis, because this could introduce another negative bias in survival

estimates if locally-resident birds that are captured during these early netting sessions display net avoidance and are not captured during subsequent netting sessions (Burton and DeSante *this volume*).

Even though mark-recapture analysis models have recently been developed to account for the presence of transient individuals (Peach et al. 1990, Peach 1993, Pradel et al. 1997, Nott and DeSante 2002; also see DeSante et al. 1995 and below), it is likely that these models will perform better with data free from large numbers of migrant individuals. To avoid operating MAPS stations while large numbers of spring migrants are still passing through, we have established a tiered schedule for beginning the operation of MAPS stations (Fig. 2) that ranges from Period 1 (May 1–10) in the extreme southern parts of the United States through Period 5 (June 10–19) over most of Canada and Alaska. We strongly discourage netting at MAPS stations prior to the appropriate time for beginning operation of the station.

At the other end of the season, we originally recommended that all MAPS stations be operated through Period 12 (August 19–28), even though fall migration of target species may already be underway. We reasoned that data from later periods (e.g., Periods 11 and 12) could be eliminated prior to analysis if desired, especially as very few adults breeding at MAPS stations are captured for the first time late in the season. Moreover, excluding late netting sessions from British CES analysis did not significantly change regional productivity indices, but tended to increase precision of the estimates (Baillie et al. 1986, Peach et al. *this volume*). This led to recommendations in the CES Scheme to operate each station, if possible, for all twelve 10-day periods.

Similar analyses of MAPS precision have not yet been conducted. However, using data from six stations in each of three regions, we compared productivity indices based on data collected over all or only part of the 1992 season. In all three cases, we found highly significant correlation between the productivity indices from the two time periods (Fig. 3), although this might have been expected because data from the truncated period were included in the data from the entire time period. At Shenandoah (Fig. 3A), where only one netting session was run after August 8, the slope of the regression was not significantly different from 1.0 ( $P = 0.30$ ). At Wenatchee (Fig. 3B) and Flathead (Fig. 3C), which each had two netting sessions after August 8, the slopes were significantly or near significantly different from 1.0 ( $P = 0.03$  for Wenatchee and  $P = 0.07$  for Flathead). In all three locations, data from the longer time period

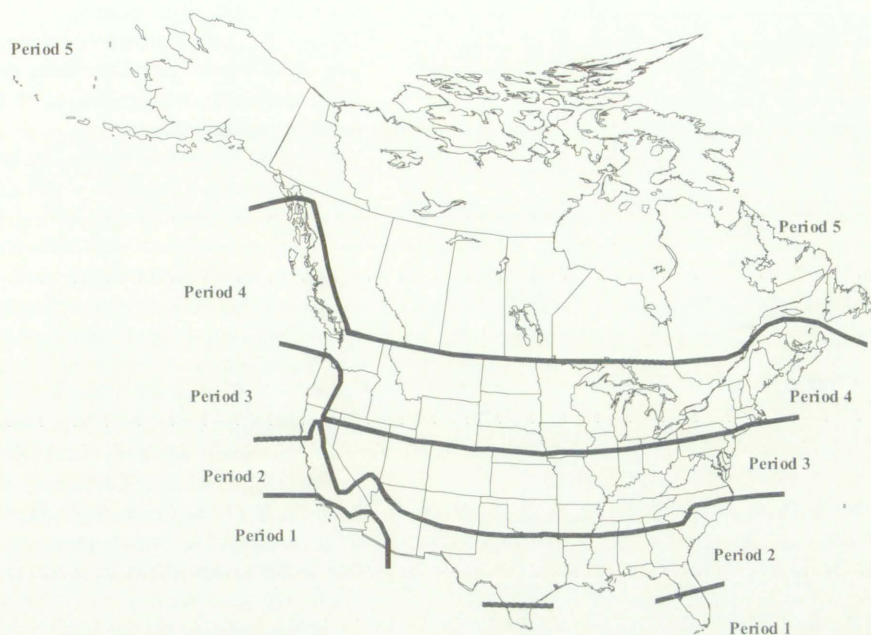


FIGURE 2. Recommended starting periods for MAPS stations in five geographic regions. Period 1 = May 1–10; Period 2 = May 11–20; Period 3 = May 21–30; Period 4 = May 31–June 9; Period 5 = June 10–19.

gave higher productivity indices. Differences, however, were small between productivity indices calculated from the truncated period and those calculated from the entire period (averaged over species for which at least 10 aged individuals were captured during the entire period):  $0.03 \pm 0.02$  ( $N = 11$  species) at Shenandoah,  $0.09 \pm 0.02$  ( $N = 24$ ) at Wenatchee, and  $0.08 \pm 0.02$  ( $N = 20$ ) at Flathead. Results for individual species were similar; most showed higher productivity indices when these were calculated over the longer period, and in most of the relatively common species these increases were small ( $<0.10$ , including ten of the 11 species studied at Shenandoah, 15 of 24 at Wenatchee, and 14 of 20 at Flathead). Despite the small magnitude of difference, the lower productivity indices calculated without data from the last two netting periods may provide a more representative index of local productivity, rather than being confounded by an influx of migrating individuals from further north.

To gauge the extent to which migrating individuals might be occurring at MAPS stations and to assess the timing of their occurrences, we analyzed levels of subcutaneous fat found on birds captured at MAPS stations during 1992–1995 as a function of geographical region and 10-day period (Fig. 4). Throughout the breeding season (June through early August), substantial numbers of birds (10–30% de-

pending on region) had very light fat deposits (fat classes 1 or 2). Few birds (generally  $<5\%$ ) had light-moderate fat deposits (fat class 3) and very few (generally  $<1\%$ ) had moderate-heavy or heavy fat deposits (fat class 4 or greater). In sharp contrast, during Periods 1–3 (May 1–30, although the total numbers of captures were low during these periods because most stations delayed initiating station operation according to the schedule presented in Fig. 2) and Periods 11–12 (August 9–28), substantial numbers of birds (generally  $>10\%$ ) had moderate to high fat deposits (fat classes  $\geq 3$ ).

These data suggest that substantial numbers of migrating individual birds are being captured at MAPS stations in all geographic regions during Periods 11 and 12, and that the operation of MAPS stations should be curtailed after Period 10 (July 30–August 8). This will likely have a negligible effect on recapture probabilities of locally resident adults, because few such birds are captured during Periods 11–12 that were not already captured earlier in the season. It will, however, provide productivity indices more representative of the local area in which the station is located, and will reduce the time commitment and expense of operating MAPS stations by 17%–25%, depending on the starting date of the station. This recommendation was included in standardized MAPS protocol beginning in 1997.

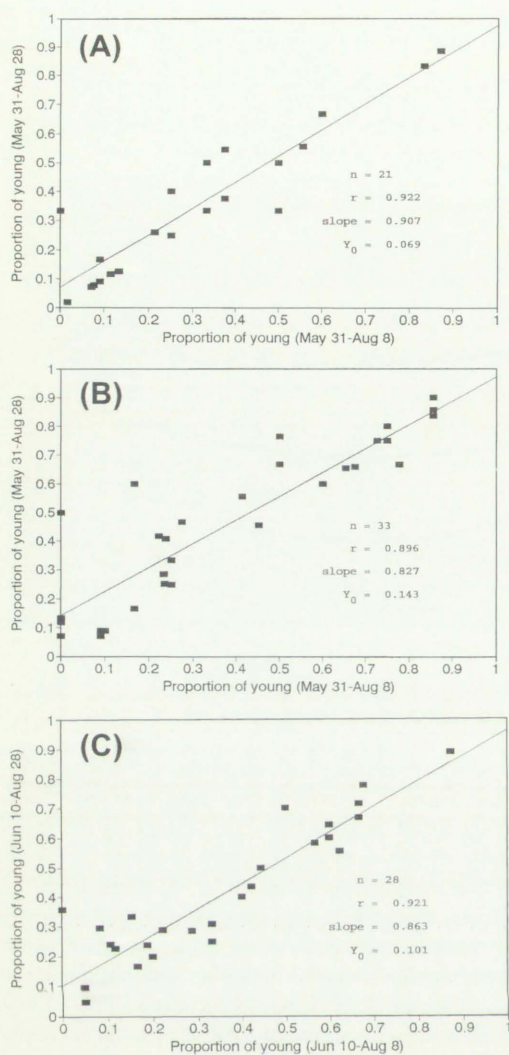


FIGURE 3. Regression of the proportion of young caught during all 10-day periods vs. the proportion of young caught in all but the last two 10-day periods during 1992 for all stations (N) at three stations.

The difference between North America and Britain is apparently that huge numbers of long-distance migrant landbirds from farther north pass through North American MAPS stations during mid-late August, whereas relatively few such migrants from north of Britain pass through British CES stations during that time.

*Netting frequency.*—Increasing the number of days of operation per 10-day period will, of course, increase the number of birds captured. However, there is also likely to be a rapid fall-off in captures after two or three days of operation because of

saturation and net-avoidance effects (Burton and DeSante *this volume*). Another potential problem of netting too often is that disturbance to captured birds might contribute to nest failures or to birds moving out of the netting area.

Surprisingly little is known about the extent and role of saturation and net avoidance in affecting the results of mist-netting studies. Kaiser (1993b) showed that migrating birds may sometimes avoid specific capture locations after first capture, but do not recognize nets in other locations as something to be avoided. How long avoidance of capture location may last is poorly known. MAPS data collected during the breeding season showed that some adult individuals of certain species (e.g., Swainson's Thrush [scientific names in tables], MacGillivray's Warbler, Lincoln's Sparrow) are often recaptured later in the season in the same net in which they were first captured (Institute for Bird Populations, unpubl. data). The actual extent of net avoidance probably varies among species, possibly differs between the breeding season (when birds are faithful to a nest site) and non-breeding seasons, and may even differ among individuals within a species. Recent advances in mark-recapture software (RELEASE) provide goodness-of-fit tests that can detect net-avoidance effects (Pradel 1993). However, such tests have not yet been applied to MAPS data.

Burton and DeSante (*this volume*) suggested that both saturation and net-avoidance effects seemed to occur in adults but not in young birds, and appeared to increase with increasing frequency of operation. We tested this by establishing two adjacent MAPS stations in a single habitat type at the Patuxent River Naval Air Station and operating one for one day per 10-day period and the other for two days per 10-day period (usually consecutive days), over two years (1992 and 1993). In both years, the rate of first captures for young birds (all species pooled) was roughly the same between stations; i.e., about twice as many individual young birds were captured at the two-day station as at the one-day station (Table 1). This was expected, because there was constant turnover of young birds through dispersal, such that net avoidance should not have been a serious problem. By contrast, the rate of first captures for adult birds (all species pooled) was lower at the two-day station than at the one-day station by 22.2% in 1992 and by 35.7% in 1993. As a result, the productivity index was 9% higher at the two-day station in 1992 and 42% higher in 1993. Clearly, increasing the frequency of operation at a station tends to bias productivity indices positively.

TABLE 1. NUMBERS OF INDIVIDUAL ADULT AND YOUNG BIRDS CAPTURED PER 600 NET-HOURS AND THE PROPORTIONS OF YOUNG IN THE CATCH AT TWO ADJACENT MAPS STATIONS

Species	1992							1993							
	One-day station			Two-day station				Difference <sup>a</sup>	One-day station			Two-day station			
	Adult	Young	Proportion young	Adult	Young	Proportion young	Adult		Young	Proportion young	Adult	Young	Proportion young	Difference	
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	—	—	—	0.0	0.6	1.00		0.9	0.0	0.00	0.5	0.0	0.00		
Red-bellied Woodpecker ( <i>Melanerpes carolinus</i> )	—	—	—	1.2	0.0	0.00		1.8	0.0	0.00	—	—	—		
Downy Woodpecker ( <i>Picoides pubescens</i> )	1.2	—	0.00	0.6	0.0	0.00		—	—	—	0.0	0.5	1.00		
Northern Flicker ( <i>Colaptes auratus</i> )	1.2	—	0.00	—	—	—		—	—	—	—	—	—		
Eastern Wood-Pewee ( <i>Contopus virens</i> )	—	—	—	0.6	0.0	0.00		1.0	0.0	0.00	—	—	—		
Acadian Flycatcher ( <i>Empidonax virens</i> )	2.5	0.0	0.00	2.3	1.2	0.33	+0.33	7.0	1.0	0.12	4.6	1.8	0.29	+0.17	
Great Crested Flycatcher ( <i>Myiarchus crinitus</i> )	1.2	0.0	0.00	—	—	—		0.9	0.0	0.00	—	—	—		
White-eyed Vireo ( <i>Vireo griseus</i> )	3.8	0.0	0.00	2.9	0.0	0.00		2.8	1.8	0.40	1.0	1.0	0.50	+0.10	
Yellow-throated Vireo ( <i>V. flavifrons</i> )	—	—	—	0.6	0.0	0.00		—	—	—	—	—	—		
Red-eyed Vireo ( <i>V. olivaceus</i> )	13.8	1.2	0.08	8.8	1.8	0.17	+0.09	11.0	0.0	0.00	5.1	1.0	0.17	+0.17	
Blue Jay ( <i>Cyanocitta cristata</i> )	—	—	—	—	—	—		—	—	—	1.5	0.5	0.25		
Carolina Chickadee ( <i>Poecile carolinensis</i> )	1.2	0.0	0.00	1.8	0.6	0.25	+0.25	2.0	0.0	0.00	3.7	0.9	0.20	+0.20	
Tufted Titmouse ( <i>Baeolophus bicolor</i> )	3.8	5.0	0.57	2.9	2.9	0.50	-0.07	1.8	3.7	0.67	3.1	4.1	0.57	-0.10	
Carolina Wren ( <i>Thryothorus ludovicianus</i> )	5.0	3.8	0.43	3.5	5.3	0.60	+0.17	1.8	3.7	0.67	3.1	6.1	0.67	0.00	
Veery ( <i>Catharus fuscescens</i> )	1.2	0.0	0.00	—	—	—		—	—	—	0.5	0.0	0.00		
Wood Thrush ( <i>Hylocichla mustelina</i> )	2.5	2.5	0.50	3.5	1.8	0.33	-0.17	5.5	0.9	0.14	5.6	1.5	0.21	+0.07	
American Robin ( <i>Turdus migratorius</i> )	—	—	—	—	—	—		0.9	0.0	0.00	—	—	—		
Gray Catbird ( <i>Dumetella carolinensis</i> )	1.2	0.0	0.00	0.6	0.0	0.00		—	—	—	1.0	0.0	0.00		
Brown Thrasher ( <i>Toxostoma rufum</i> )	—	—	—	0.6	0.6	0.50		—	—	—	0.5	0.0	0.00		
Pine Warbler ( <i>Dendroica pinus</i> )	—	—	—	0.6	0.0	0.00		—	—	—	0.5	0.5	0.50		
Black-and-white Warbler ( <i>Mniotilta varia</i> )	—	—	—	0.0	0.6	1.00		0.0	2.8	1.00	0.5	2.5	0.83	-0.17	
American Redstart ( <i>Setophaga ruticilla</i> )	—	—	—	1.2	0.0	0.00		—	—	—	—	—	—		
Prothonotary Warbler ( <i>Protonotaria citrea</i> )	—	—	—	—	—	—		0.9	0.0	0.00	—	—	—		
Worm-eating Warbler ( <i>Helmitheros vermivorus</i> )	2.5	0.0	0.00	—	—	—		0.9	0.9	0.50	0.5	1.0	0.67	+0.17	
Ovenbird ( <i>Seiurus aurocapillus</i> )	5.0	1.3	0.20	1.8	1.8	0.50	+0.30	5.5	2.8	0.33	3.1	2.5	0.46	+0.13	
Louisiana Waterthrush ( <i>S. motacilla</i> )	—	—	—	—	—	—		1.8	0.9	0.33	0.0	1.0	1.00	+0.77	
Kentucky Warbler ( <i>Oporornis formosus</i> )	8.8	5.0	0.36	2.9	0.0	0.00	-0.36	5.5	2.8	0.33	5.1	3.1	0.38	+0.05	
Common Yellowthroat ( <i>Geothlypis trichas</i> )	—	—	—	—	—	—		0.9	0.0	0.00	1.0	0.0	0.00		
Hooded Warbler ( <i>Wilsonia citrina</i> )	3.8	0.0	0.00	5.3	0.0	0.00		12.0	1.8	0.13	3.6	1.0	0.22	+0.09	
Yellow-breasted Chat ( <i>Icteria virens</i> )	—	—	—	—	—	—		—	—	—	0.5	0.0	0.00		
Summer Tanager ( <i>Piranga rubra</i> )	—	—	—	—	—	—		0.9	0.0	0.00	1.5	0.0	0.00		
Scarlet Tanager ( <i>P. olivacea</i> )	—	—	—	1.2	0.0	0.00		—	—	—	0.5	0.0	0.00		

TABLE 1. CONTINUED

Species	1992						1993					
	One-day station			Two-day station			One-day station			Two-day station		
	Adult	Young	Proportion young	Adult	Young	Proportion young	Adult	Young	Proportion young	Adult	Young	Proportion young
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	2.5	0.0	0.00	4.7	0.6	0.11	4.6	0.9	0.17	2.0	0.5	0.20
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	—	—	—	—	—	—	0.9	0.0	0.00	0.5	0.0	0.00
Swamp Sparrow ( <i>Melospiza georgiana</i> )	—	—	—	0.6	0.0	0.00	—	—	—	—	—	—
Common Grackle ( <i>Quisculus quiscula</i> )	—	—	—	0.6	0.0	0.00	3.7	0.0	0.00	1.0	0.0	0.00
Brown-headed Cowbird ( <i>Molothrus ater</i> )	1.2	0.0	0.00	0.0	0.6	1.00	—	—	—	—	—	—
All species pooled	62.5	18.8	0.23	53.3	18.1	0.25	73.7	25.8	0.26	47.4	27.5	0.37
Number of species	18	6		22	12		22	13		25	16	
Total number of species	18			25			23			27		

Notes: Data were from stations operated at the Patuxent Naval Air Station.

\* Difference in proportion of young between 2-day and 1-day stations; shown only for cases when at least one station had a non-zero value.

We found similar results in 1990 and 1991 data obtained from the Palomarin MAPS station operated by the Point Reyes Bird Observatory (Table 2). This station is typically operated every day from May 1 through August 28. We compared productivity indices obtained from all 10 days of operation per 10-day period (the all-days method) with those obtained from only the first complete day of operation in each 10-day period (the first-day method). Analyses were conducted for all species pooled, and for 16 target species in which at least 10 first captures of adult birds were recorded during all days of operation in either year. In 1990, the all-days method showed 9.8% higher productivity for all species pooled, and 13.8% higher for the 16 target species. In 1991, the all-days method increased productivity for all species pooled by 7.2%, and for the target species by 15.1%. However, the two methods detected similar differences in productivity between 1990 and 1991. For all species pooled, productivity decreased 9.8% according to the all-days method and 7.6% according to the first-day method. For the 16 target species, the decreases were 9% and 10%, respectively, for the all-day and first-day methods. These results suggest that net avoidance may not affect the estimation of annual changes in productivity. However, this will only be true if the number of netting days in each netting session remains constant across all netting sessions at the station, both within and between seasons.

Another important conclusion is that a single day of operation per 10-day period is sufficient to provide accurate information on between-year changes in productivity indices, at least for the more common species. Because adding more stations will improve precision of regional productivity estimates more than will adding days of effort at a single station (Burton and DeSante *this volume*), we recommend that the best use of excess manpower would be to establish several (or larger) MAPS stations that operate for one day per 10-day period, rather than operate for additional days at a single station.

In accordance with the CES protocol (Baillie et al. 1986) and the data presented above, we strongly recommend that MAPS stations be operated for only one day in each 10-day period, with visits in adjacent periods being at least six days apart. Beginning in 1992, virtually all MAPS stations have used this recommendation for implementing the MAPS protocol.

*Daily timing.*—MAPS protocol recommends operating the entire array of nets for at least 4 h and, preferably, for 6 h per day beginning at local sunrise. This covers the period of the day when birds are

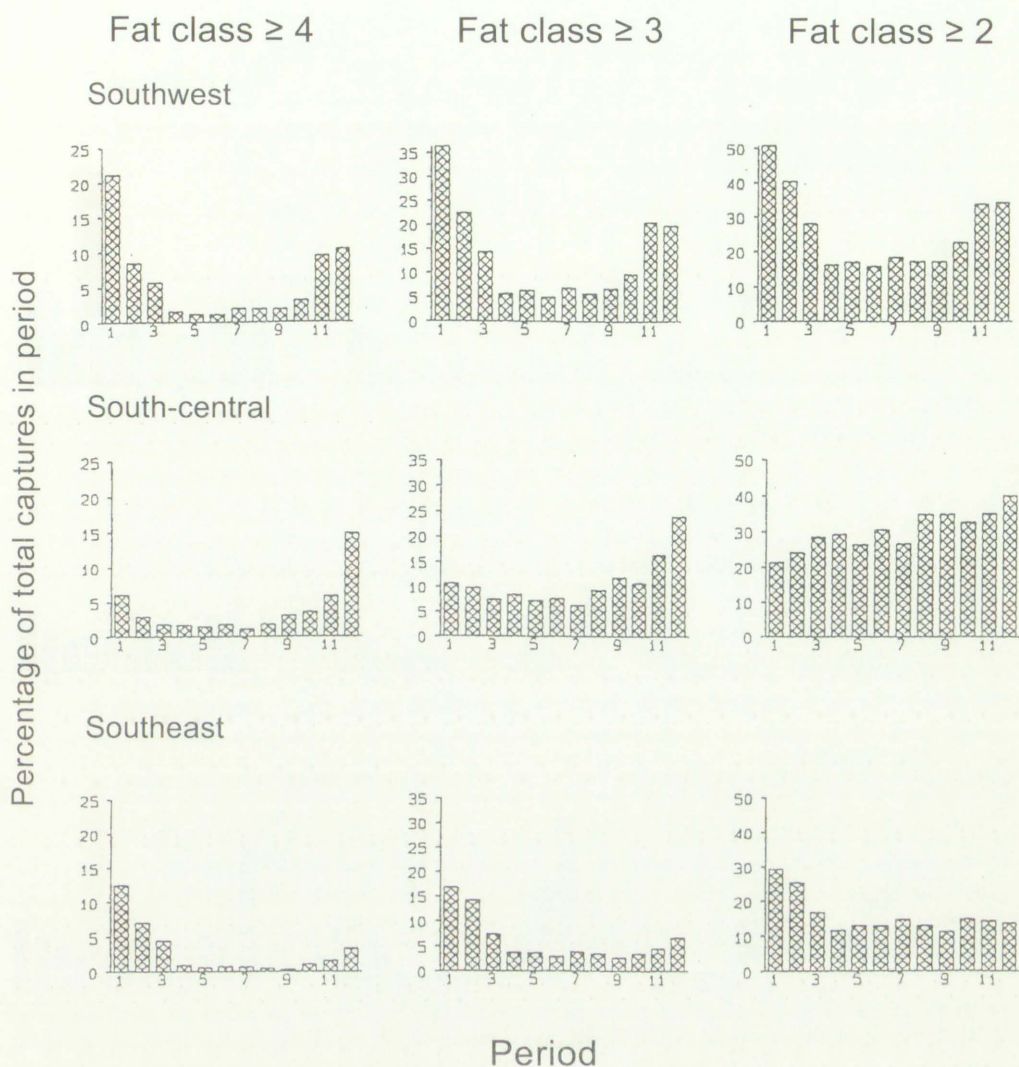


FIGURE 4. Frequency distributions of classes of subcutaneous fat carried by birds captured in the MAP Program as a function of 10-day period for three southern regions. Periods: 1 = May 1–10; 2 = May 11–20; 3 = May 21–30; 4 = May 31–Jun 9; 5 = Jun 10–19; 6 = Jun 20–29; 7 = Jun 30–Jul 9; 8 = Jul 10–19; 9 = Jul 20–29; 10 = Jul 30–Aug 8; 11 = Aug 9–18; 12 = Aug 19–28. (Continued on next page.)

most active. We recommend that nets not be operated if the average wind speed exceeds 10 knots (or gusts exceed 20 knots) or if other weather variables (i.e., precipitation or extreme heat or cold) are likely to endanger captured birds. If nets are closed early or opened late due to inclement weather or other unforeseen circumstances, we recommend that the missing hours be made up with netting in the equivalent time period on another day within the same 10-day period (or early in the next period). However, we only recommend making up lost effort if half or more of a normal day's operation is missed.

#### Standardization

All aspects of station operation must be kept constant through all years of operation. Otherwise, changes in numbers of birds captured could reflect changes in netting protocol, rather than changes in population characteristics. This is the reason for specifying the MAPS protocol in such detail. There may be large differences between stations in the numbers and ages of birds captured, but this should not affect regional estimates of annual change in productivity as long as the protocol at each station



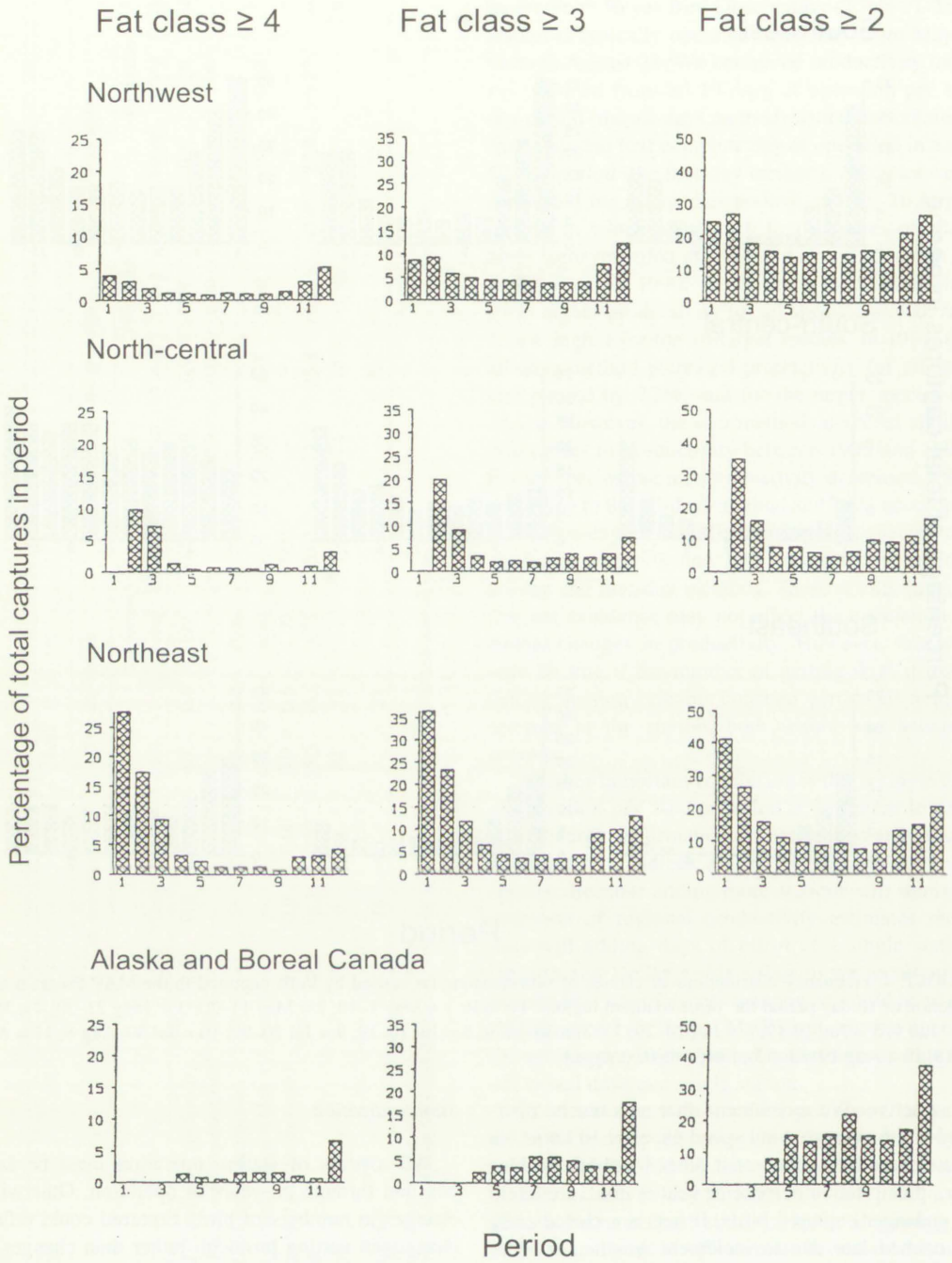


FIGURE 4. Continued. Four northern regions.

TABLE 2. PRODUCTIVITY INDICES (PROPORTION OF YOUNG IN THE CATCH) CALCULATED BY TWO METHODS FROM DATA COLLECTED AT A MAPS STATION OPERATED DAILY

Species	1990				1991				Difference: 1991-1990		
	N <sup>a</sup>	All days <sup>b</sup>	First day <sup>c</sup>	Difference <sup>d</sup>	N	All days	First day	Difference	All days	First day	Difference
Pacific-slope Flycatcher ( <i>Empidonax difficilis</i> )	16	0.91	0.85	+0.06	35	0.73	0.53	+0.20	-0.18	-0.31	+0.14
Warbling Vireo ( <i>Vireo gilvus</i> )	23	0.23	0.33	-0.10	9	0.18	0.00	+0.18	-0.05	-0.33	+0.28
Tree Swallow ( <i>Tachycineta bicolor</i> )	12	0.00	0.00	0.00	12	0.00	0.00	0.00	0.00	0.00	0.00
Barn Swallow ( <i>Hirundo rustica</i> )	14	0.65	0.57	+0.08	9	0.44	0.00	+0.44	-0.21	-0.57	+0.36
Chestnut-backed Chickadee ( <i>Poecile rufescens</i> )	12	0.80	0.75	+0.05	12	0.79	0.81	-0.02	-0.01	+0.06	-0.07
Bushtit ( <i>Psaltriparus minimus</i> )	7	0.67	0.00	+0.67	10	0.66	0.83	-0.18	-0.01	+0.83	-0.85
Bewick's Wren ( <i>Thryomanes bewickii</i> )	12	0.73	0.67	+0.07	13	0.63	0.56	+0.07	-0.11	-0.11	+0.01
Swainson's Thrush ( <i>Catharus ustulatus</i> )	45	0.39	0.25	+0.14	54	0.34	0.31	+0.03	-0.05	+0.06	-0.11
Wrentit ( <i>Chamaea fasciata</i> )	12	0.78	0.56	+0.23	19	0.80	0.83	-0.04	+0.01	+0.28	-0.26
Orange-crowned Warbler ( <i>Vermivora celata</i> )	51	0.45	0.50	-0.05	40	0.48	0.20	+0.28	+0.04	-0.30	+0.34
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	40	0.75	0.65	+0.11	45	0.63	0.47	+0.17	-0.12	-0.18	+0.06
Song Sparrow ( <i>Melospiza melodia</i> )	25	0.67	0.83	-0.17	15	0.78	0.88	-0.10	+0.11	+0.04	+0.07
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	7	0.76	1.00	-0.24	13	0.80	1.00	-0.20	+0.04	0.00	+0.04
Purple Finch ( <i>Carpodacus purpureus</i> )	48	0.44	0.45	-0.02	54	0.29	0.21	+0.08	-0.14	-0.24	+0.10
Pine Siskin ( <i>Carduelis pinus</i> )	14	0.39	0.25	+0.14	29	0.15	0.00	+0.15	-0.24	-0.25	+0.01
American Goldfinch ( <i>C. tristis</i> )	9	0.10	0.00	+0.10	20	0.23	0.25	-0.02	+0.13	+0.25	-0.12
All species pooled	415	0.66	0.60	+0.06	472	0.60	0.56	+0.04	-0.06	-0.05	-0.02
Mean of 16 species		0.55	0.48	+0.07		0.50	0.43	+0.07	-0.05	-0.05	-0.00
SE of the mean		±0.07	±0.08	±0.05		±0.07	±0.09	±0.04	±0.03	±0.08	±0.07
Prop. species increase <sup>e</sup>				0.63				0.56	0.31	0.38	0.63

Notes: Data were from the Palomarin Field Station, operated by the Point Reyes Bird Observatory. Results are shown for species with at least ten first captures of adult birds in either year, and for all species pooled.

<sup>a</sup> Number of first captures of adult birds during all days of operation.

<sup>b</sup> Calculated using data from all days of operation each 10-day period.

<sup>c</sup> Calculated using data from only the first complete day of operation each 10-day period.

<sup>d</sup> Difference in proportion of young (or difference between the 1990-1991 difference in proportion of young) calculated by the two methods (presented as all-days method minus first-day method).

<sup>e</sup> Proportion of species for which the increase was positive.

remains constant from year to year. Consistency is needed in the numbers and design of nets used, their placement, and schedule of operation (time of starting and ending each day, number of days/10-day period, start and end date in the season). Finally, nets should be opened, checked, and closed in the same order, and that sequence should remain constant for all days and years of operation.

#### COLLECTION OF DATA AT A MAPS STATION

The following data are required for all birds captured in the MAPS Program, including recaptures, because they are required by the banding offices or are needed for calculation of productivity indices and survivorship estimates: station code, net number, date, time of capture (net-run time), band number, capture code (newly banded, recaptured, band changed, unbanded), status code (whether or not released back into the population), species, age, how aged, sex, and how sexed. In contrast, the following data are considered supplemental and are used in verification programs designed to identify questionable or contradictory species, age, and sex determinations: degree of skull pneumatization, extent of cloacal protuberance or brood patch, extent of body molt, type of flight-feather molt, extent of juvenal plumage, extent of primary-feather wear, wing chord, body mass, fat class, and bander's name. We strongly encourage all MAPS cooperators to collect these supplemental data, for without them there is no way of verifying the accuracy of the species, age, and sex determinations (see also Ralph et al. 1993). All other data that might be collected on mist-netted birds (e.g., tier of the net in which it was captured, direction bird entered the net, etc.) are not needed for the MAPS Program, although we accept any notes cooperators wish to add regarding any capture record. We require that all MAPS data be submitted using standardized metrics and codes provided by the MAPS Program.

We also require MAPS cooperators to provide detailed data on mist-netting effort, including station code, date, times of opening and closing each net array (or individual nets, if some are opened or closed earlier or later), and, if possible, starting times for all net runs. All times are rounded to the nearest 10-min (0700, 0710, 0720, etc.). These effort data are necessary for standardizing the effort at each station from year-to-year, for selecting data to be used in each year-to-year comparison (see below), and for estimating the effects of missed effort.

#### ANALYTICAL METHODS

##### *Data verification*

Each year, about 1/3 of all MAPS stations were operated by field biologist interns trained and supervised by biologists from The Institute for Bird Populations. Because these interns frequently had relatively little prior experience with mist netting and banding, we began their work periods with an intensive three-week training program. In addition, we developed data checks designed to catch errors during data entry and to provide a pre-analysis verification of the data. Verification procedures included four types: (1) checks that assured that entered codes were valid and that data fell within accepted ranges; (2) comparisons of species, age, and sex determinations against the supplemental data used to make those determinations (i.e., degree of skull pneumatization; presence of cloacal protuberances, brood patches, or juvenal plumage; and extent of body and flight-feather molt and primary-feather wear) that flagged discrepancies or suspicious data; (3) checks that identified unusual band numbers or band sizes for each species; and (4) checks that screened original banding and recapture data from all years of station operation for inconsistencies in species, age, and sex determinations for each band number.

An analysis of intern-collected data for 1993 showed that these four verification procedures flagged 4.7% of 16,790 capture records (Table 3). Although the majority of flagged records involved contradictions within a given capture record, a substantial proportion involved inconsistencies among different capture records. Of these, many were not errors at all, but cases in which recaptures provided additional information that allowed resolution of "unknown" codes in the earlier records.

The most frequent corrections to the data set were for sex determination (3.2% of total records). Most of these involved changing an unknown to a known sex upon recapture or, to a lesser extent, vice versa. The latter cases often involved birds questionably or erroneously sexed by small cloacal protuberances or light brood patches early in the season. Changes in age determination were less frequent (1.7% of total records) and usually involved questionable or erroneous skull determinations, often caused by confusion between a fully pneumatized (adult) and a nearly completely non-pneumatized (young) skull, with errors being detected upon recapture. Questionable sex determinations often led to questionable age determinations and vice-versa; both age

TABLE 3. RESULTS OF MAPS DATA VERIFICATION PROCEDURES FOR ALL 1993 DATA VERIFIED AGAINST 1992 OR OTHER PREVIOUS YEARS, SHOWING NUMBER (N) AND PERCENT OF RECORDS REQUIRING A CHANGE IN THE DATABASE

	Data collected by					
	Institute interns		Independent station operators		Both groups combined	
Datum needing alteration	N	Percent	N	Percent	N	Percent
Sex	533	3.2	1,104	3.6	1,637	3.5
Age	284	1.7	643	2.1	927	2.0
Species or band number	78	0.5	22	0.1	100	0.2
All changes combined	781	4.7	1,658	5.4	2,439	5.1
Total records	16,790		30,696		47,486	

and sex were changed in 0.6% of records. Species (or band number) was by far the least often changed determination (0.5% of total records). Most changes in species determinations were caused by misread bands on recaptured birds (which sometimes resulted in age or sex changes as well). These findings suggest that, after verification and correction, errors remaining in intern-collected data were essentially negligible for species determinations, well below 1% for age determinations, and less than about 1% for sex determinations.

After data verification, only 21 (0.1%) of the 29,299 intern-collected capture records during both 1992 and 1993 were given unknown species determinations, 407 (1.4%) were given unknown age determinations and 14,152 (48.3%) were given unknown sex determinations. Of the 16,486 intern-collected capture records of adult birds during both 1992 and 1993, only 17.9% (mostly of sexually monomorphic species) were given unknown sex after data verification, thereby indicating that most of the unsexed birds in the total sample were young birds.

Verification procedures were also applied to the approximately 2/3 of the total data that were submitted from independent stations (i.e., stations not operated by IBP trained and supervised interns). We detected a slightly higher proportion of "errors" in species, age, or sex determinations (5.4% of 30,696 records) than in intern-collected data, although the relative frequency among the error types was similar (Table 3). We were surprised by this error rate, because most independent stations were operated by experienced banders with Master banding permits (although some data may have been collected by sub-permittees). Our results suggest either that the quality of our intern training was exceptionally good, or that the training of licensed banders in North America could stand improvement. Data collected by Dale (*this volume*) support the second conclusion. As a result of these studies, the Institute for Bird Populations in 1995 spearheaded the creation of

the North American Banding Council that, by 2002, had developed standardized training materials and certification programs for banders. Such programs previously existed in a number of European countries, including Finland and the United Kingdom, and most CES Scheme ringers (banders) were known to be highly experienced or were observed in action by BTO staff on ringing courses. Thus, the quality of ringing data collected there is assumed to be higher than in North America, and ringing data submitted to the CES Scheme are analyzed without any verification.

#### *Pooling data from different stations*

Analysis methods require pooling of data from multiple stations. Although MAPS protocol recommends one day of netting per 10-day sample period, a few stations net more frequently; this was especially true in the early years of MAPS. Using data from one MAPS region, we analyzed the effect of pooling data from stations using different netting schedules on between-year changes for 1990–1991 and for 1991–1992 (Table 4). Data were pooled in four ways for analysis. Using data from all days of operation in each 10-day period, we calculated one index uncorrected for effort, and another corrected to birds/600 net-h. We also calculated unadjusted and effort-adjusted totals using data only from the first complete day of operation in each netting period. The all-days, unadjusted index method tends to weight the data from each station roughly according to effort expended at the station. (Because of saturation and net-avoidance effects, however, a station operated on a daily basis will generally not capture 10× as many birds, especially adults, as a station operated only one day per 10-day period.) In contrast, the all-days, effort-adjusted index method tends to weight each station equally. (Again, however, because of saturation and net-avoidance effects, stations operated on multiple days in each 10-day period will generally be relatively under-weighted relative

TABLE 4. CHANGES IN THE NUMBERS OF ADULT AND YOUNG BIRDS AND THE PROPORTION OF YOUNG FROM 1990 TO 1991 AND FROM 1991 TO 1992

Species	Percent change in numbers of adults					Percent change in numbers of young					Change in proportion of young				
	N <sup>c</sup>	All days <sup>a</sup>		One day <sup>b</sup>		N	All days		One day		N	All days		One day	
		Birds/	600 nh <sup>e</sup>	Birds/	600 nh		Birds/	600 nh	Birds/	600 nh		Birds/	600 nh	Birds/	600 nh
<i>Changes between 1990 and 1991</i>															
Dusky Flycatcher ( <i>Empidonax oberholseri</i> )	2	+19	+144	+33	+15	1	-76	-78	-91	-92	1	-0.26	-0.26	-0.34	-0.34
"Western" Flycatcher ( <i>E. difficilis</i> or <i>occidentalis</i> )	4	+58*	+33**	+38	+26	4	-37**	-38*	-6	-26	4	-0.18	-0.19	-0.09	-0.13
Swainson's Thrush	6	+7	+49	-10	+22	6	+17	+16	+26*	+12	6	+0.02	-0.06	+0.07	-0.03
American Robin	6	+31	+19	+36	+37	2	+100	-95	-100	-100	5	+0.02	-0.14	-0.07	-0.13
Warbling Vireo	5	-8	-10	+4	-6	4	-33*	-13	-35	-29	4	-0.06	-0.02	-0.09	-0.06
Orange-crowned Warbler	5	+3	+30	+88	+37	4	-16*	-18	+21*	+9	4	-0.04	-0.07	-0.08	-0.03
Yellow Warbler ( <i>Dendroica petechia</i> )	5	-23	+5	+8	+18	5	+8	+53	0	+3	5	+0.08	+0.08	+0.02	-0.02
MacGillivray's Warbler ( <i>Oporornis tolmiei</i> )	4	+20	-18	+22	-1	4	-12	-1	-22	-21	4	-0.08	+0.02	-0.12	-0.08
Wilson's Warbler	4	+40	+43	+59	+55	4	-23	+55	+25	+74	4	-0.14	+0.02	-0.02	+0.06
Song Sparrow	5	-15	-20	-7	-10	5	+53	+30	+91	+47	5	+0.12	+0.10	+0.15	+0.11
Lincoln's Sparrow ( <i>Melospiza lincolnii</i> )	2	+14	+54	+56	+53	2	0	+50	+500	+525	2	-0.03	-0.01	+0.20	+0.20
Dark-eyed Junco ( <i>Junco hyemalis</i> )	5	+70*	+45*	+82	+63	4	+5	-44*	-16	-36*	4	-0.10	-0.22**	-0.22**	-0.22**
All species pooled	6	+23*	+22	+29*	+24	6	+4	+1	+32	+3	6	-0.04	-0.05	+0.00	-0.05
Proportion increasing <sup>f</sup>		0.75	0.75	0.83*	0.75		0.42	0.42	0.42	0.50		0.33	0.33	0.33	0.25
<i>Changes between 1991 and 1992</i>															
Dusky Flycatcher	6	-10	-12	-31*	-32*	6	+85	+2	+550**	+750*	2	+0.09	+0.08	+0.22	+0.22
"Western" Flycatcher	10	-13	+1	+13	+8	9	+86**	+105*	+125*	147*	8	+0.16	+0.10	+0.15	+0.09
Swainson's Thrush	9	-5	-2	-3	-6	4	+141**	+180**	+191**	+206**	6	+0.23*	+0.26	+0.28*	+0.29
American Robin	10	-23	-19	-34	-33	7	+20	+15	+67	+63	8	+0.07	+0.06	+0.09	+0.08
Warbling Vireo	10	-28*	-18	-11	-13	8	+133*	+46	+86	+55	8	+0.25**	+0.13	+0.16	+0.12
Orange-crowned Warbler	9	+105	+161	+86	+155	10	+204**	+237*	+261**	+238*	9	+0.06	+0.02	+0.03	-0.01
Yellow Warbler	7	-17	-17*	-25*	-26*	7	+48	+38	+80**	+68*	7	+0.12	+0.08	+0.12	+0.11
MacGillivray's Warbler	10	-3	-8	-13	-14	11	+71**	+62	+82*	+70*	9	+0.14	+0.14	+0.18	+0.17
Wilson's Warbler	11	-1	+46	-1	+27	11	+167**	+135*	+178*	+152*	11	+0.26	+0.12	+0.25	+0.17
Song Sparrow	9	-14	-22	-17	-20	10	+14	+14	+6	+12	8	+0.05	+0.09	+0.05	+0.08
Lincoln's Sparrow	4	-20	-22*	-42**	-42**	5	+41*	+28	+39	+33	4	+0.13	+0.08	+0.18**	+0.16*
Dark-eyed Junco	10	-3	+1	+8	+7	9	+120	+229*	+215*	+214*	9	+0.20*	+0.29**	+0.27*	+0.27*
All species pooled	11	-11*	-1	-7	-2	11	+93**	+136**	+113**	+137**	11	+0.19**	+0.21**	+0.20**	+0.22**
Proportion increasing <sup>f</sup>		0.08**	0.33	0.25	0.33		1.00**	1.00**	1.00**	1.00**		1.00**	1.00**	1.00**	0.92**

Notes: Data from the Northwest MAPS region, pooled in four different ways (see text).

<sup>a</sup> Calculated using data from all days of operation during each 10-day period.

<sup>b</sup> Calculated using data from only the first complete day of operation during each 10-day period.

<sup>c</sup> The number of stations from which data were pooled. At least one bird of the relevant age had to have been captured in one or the other of the two years being compared. For calculating change in proportion of young, at least one bird (any age) had to have been captured in each of the years being compared.

<sup>d</sup> Total number of first captures.

<sup>e</sup> Total number of first captures/600 net-h.

<sup>f</sup> Proportion of the 12 target species for which increases were recorded. Significance is from a one-sided binomial test showing whether the proportion of increasing species differs from 0.50.

\* denotes  $0.05 \leq P < 0.10$ , \*\* denotes  $0.01 \leq P < 0.05$ , \*\*\* denotes  $P < 0.01$ , \*\*\*\* denotes  $0.0001 \leq P < 0.001$ .

to stations operated only one day per 10-day period.) The one-day, unadjusted index method weights each station according to the number of nets used and the length of time they are operated each day, whereas the one-day effort-adjusted index method weights each station equally.

The four methods often produced substantially different regional between-year changes in the numbers of first captures of adults and young, and substantial, but perhaps smaller, differences in regional changes in proportion of young (Table 4). Differences among the four methods were generally less for all species pooled than for individual species. Note particularly the differences among the four methods in the 1990–1991 between-year changes in numbers of adult Swainson's Thrushes, numbers of young Orange-crowned and Wilson's warblers, and proportion of young Wilson's Warblers.

Data for Swainson's Thrush show the effect that particular stations can have on these results, depending on which pooling method is used (Table 5). Station 103 (which comprised over 50% of first captures) drove the 1990–1991 comparison in the all-days unadjusted index method, because this station was weighted as if it were 10 stations. If between-year changes in adult numbers are not homogeneous across an entire region, then regional changes produced by this method will be severely biased toward the stations that are operated most often. The opposite bias occurred when data were standardized to first captures/600 net-h. This was true whether all days per 10-day period were used or only the first day per 10-day period. In both of these cases, Station

105, which had the smallest total effort, drove the regional increases in adult capture rates.

Finally, it should be noted that differences in results from the four methods were more pronounced for 1990–1991 than for 1991–1992. This was not only a result of differing effort among stations included in each comparison, but also because the underlying changes between 1990 and 1991 may in fact have differed between coastal lowland and interior montane stations (DeSante et al. 1993a). Pooling data over stations where bird populations may be subject to different demographic stressors, such as critical weather factors, can mask important differences in population and demographic changes and, thus, may be inappropriate. This caution, of course, applies to all large-scale monitoring programs, including the Breeding Bird Survey, that pool data from multiple stations or routes to provide regional indices.

The pooling method we have adopted is to use only one day of data from each 10-day period for all stations (thus converting all stations to one-day stations). Next, we adjust each station's numbers to ensure equal effort (at each station but not among stations) in the two years being compared. For each netting period, the time during which each individual net was open is compared between years. Any bird captured at a time when that net was not open during the comparison year is excluded from the comparison. We then use the total number of first captures (rather than first captures/600 net-h) from those single days in each period, such that stations are weighted according to the number of birds that they contribute to the regional total.

TABLE 5. STATION-SPECIFIC INDICES AND CHANGES BETWEEN 1990 AND 1991 IN REGIONAL INDICES OF ADULT POPULATION SIZE FOR SWAINSON'S THRUSH

Station number	1990						1991					
	All days per period <sup>a</sup>			One day per period <sup>b</sup>			All days per period			One day per period		
	Total net-h	Birds <sup>c</sup>	Birds/600 nh <sup>d</sup>	Total net-h	Birds	Birds/600 nh	Total net-h	Birds	Birds/600 nh	Total net-h	Birds	Birds/600 nh
101	360.00	3	5.0	360.00	3	5.0	360.00	2	3.3	360.00	2	3.3
102	324.00	1	1.9	324.00	1	1.9	324.00	2	3.7	324.00	2	3.7
103	13518.50	45	2.0	1440.00	9	3.8	12399.00	54	2.6	1440.00	9	3.8
105	216.00	0	0.0	216.00	0	0.0	216.00	4	11.1	216.00	4	11.1
106	2007.70	36	10.8	1039.60	25	14.4	1987.60	29	8.8	1041.60	18	10.4
107	1222.75	1	0.5	437.83	1	1.4	1345.67	1	0.4	518.92	0	0.0
Total		86	20.1		39	26.4		92	30.0		35	32.3
Percent changes between 1990 and 1991 in number of adults captured							+7%	+49%			-10%	+22%

Notes: Data from the Northwest MAPS region, analyzed with four different methods (see text).

<sup>a</sup> Using data from all days each period that the station was run.

<sup>b</sup> Using data from only the first complete day each period that the station was run.

<sup>c</sup> Using the total number of first captures of adults.

<sup>d</sup> Using the number of first captures of adults/600 net-h.

### Validation of MAPS population size indices

MAPS indices of adult population size were compared to independently derived indices of abundance, to determine whether different sources of data would give similar results. For each of 36 Washington and Oregon MAPS stations operated in 1992, we established nine point-count locations, 150 m apart, generally in a 3 × 3 array. We replicated 10-min counts at these nine points three times, once in each of the first three 10-day periods that each station was operated. Most of these 36 stations were located at the edge between a mixed coniferous forest and a montane meadow or riparian corridor. All point counts at a given station were conducted by the same observer, but different observers conducted point counts at different stations. For each station, we ran correlation analyses between species-specific indices of relative abundance derived from mist nets (total number of first captures of adult birds during the entire season) and analogous indices derived from point counts (total number of individual adult birds detected at all distances from the points, excluding flyovers, from all three replicates combined). Data were included from each species detected by at least one of the count methods.

Indices of adult population size from the two methods for the various species were significantly ( $P < 0.05$ ) correlated at 33 of the 36 stations; highly significant ( $P < 0.001$ ) correlations were obtained for 25 stations (Table 6; mean over 36 stations:  $r = 0.61 \pm 0.06$ , range = 0.09–0.94). Lack of correlation at the other three stations resulted from capture or counting of large flocks of apparently non-breeding adult birds (usually Pine Siskins or Evening Grosbeaks [*Coccythraustes vespertinus*]). These results suggest that constant effort mist netting according to MAPS protocol effectively sampled adult birds in proportion to their relative abundance as determined by point counts. Kaiser and Bauer (1994) also found significant correlation between first captures of adult birds and numbers of adult birds detected on point counts ( $r = 0.83$ ,  $N = 29$ ,  $P < 0.001$ ).

### Cormack-Jolly-Seber analyses of mark-recapture data

One of the important goals of MAPS is to detect differences and changes in annual adult survival, using CJS mark-recapture analyses. These analyses do not require constant effort data, as the estimation

TABLE 6. CORRELATION BETWEEN INDICES OF ADULT POPULATION SIZE DERIVED FROM MIST-NETTING DATA AND ANALOGOUS INDICES DERIVED FROM POINT-COUNT DATA

Station	N <sup>a</sup>	r	Station	N <sup>a</sup>	r
<i>Mount Baker NF</i>			<i>Siuslaw NF</i>		
Frog Lake	25	0.74 ***	Mary's Peak	26	0.89 ***
Murphy Creek	19	0.80 ***	Nettle Creek	28	0.68 ***
Beaver Lake	27	0.80 ***	Beaver Ridge	26	0.88 ***
Copper Creek	15	0.52 *	Homestead	26	0.94 ***
Perry Creek	23	0.52 *	Cougar Creek	30	0.69 ***
Monte Cristo Lake	33	0.59 ***	Crab Creek	26	0.76 ***
<i>Wenatchee NF</i>			<i>Willamette NF</i>		
Timothy Meadow	44	0.48 ***	Ikenik	46	0.69 ***
Quartz Creek	30	0.39 *	Fingerboard Prairie	40	0.39 *
Two Point	45	0.32 *	Strube Flat	28	0.34 +
Pleasant Valley	37	0.63 ***	Clear Cut	38	0.71 ***
Rattlesnake Spring	42	0.16	Major Prairie	31	0.45 **
Deep Creek	30	0.09	Brock Creek	40	0.59 ***
<i>Umatilla NF</i>			<i>Fremont NF</i>		
Buzzard Creek	36	0.82 ***	Sycan River	46	0.57 ***
Brock Meadow	37	0.42 **	Deadhorse	49	0.48 ***
Fry Meadow	38	0.61 ***	Cold Creek	38	0.82 ***
Coyote Ridge	44	0.37 *	Augur Creek	46	0.50 ***
Buck Mt. Meadow	38	0.84 ***	Island	45	0.68 ***
Phillips Creek	45	0.62 ***	Swamp Creek	29	0.86 ***

Notes: Data collected in 1992, from 36 MAPS stations in six National Forests in Oregon and Washington. Mist-netting data were the total number of first captures of adult birds during the entire season. Point-count data were the total number of detections (excluding flyovers) during nine unlimited-distance point counts replicated three times, once during each of the first three 10-day periods the station was operated.

<sup>a</sup> Number of species for which adults were detected by either mist netting or point counts.

+ denotes  $0.05 \leq P < 0.10$ , \* denotes  $0.01 \leq P < 0.05$ , \*\* denotes  $0.001 \leq P < 0.01$ , \*\*\* denotes  $0.0001 \leq P < 0.001$ .

of recapture probability takes into account differences in effort between years. However, estimating regional survivorship precisely requires pooling of data among stations, and recapture probabilities are likely to differ among stations because of variation in habitat and operation (number, density, and location of nets). Although Carothers (1973, 1979) showed that bias in survival estimates produced by heterogeneous recapture probabilities was frequently small, Peach (1993) suggested that effects of among-station heterogeneity in recapture probability should be checked before pooling data among stations. Current analyses of MAPS data from Alaska and western boreal Canada indicate that MAPS recapture probabilities are generally best modeled as a function of sex but not as a function of geographic area or habitat type (Institute for Bird Populations, unpubl. data).

Using the computer program SURGE4, and pooling three years (1990–1992) of mark-recapture data from each of 27 stations east of the Rocky Mountains, we calculated maximum-likelihood estimates for annual adult survival and recapture probabilities for 13 individual target species; for all permanent resident,

short-distance migrant, and long-distance migrant species pooled; and for all species pooled (Table 7). In the following discussion, we assume that heterogeneity in recapture probability was small or, if not small, did not seriously bias estimates of survival and recapture probability.

Estimates of survival and recapture probability for the 13 target species (Table 7) generally compared favorably to those from the longer-term British CES Scheme. For example, Peach (1993) found that the estimated average annual adult survival rate (1983–1991), based on pooled mark-recapture data from multiple CES ringing stations for six target species in Britain, was 0.44 (range 0.32–0.57). Our mean estimated adult survival rate was 0.42 (range 0.19–0.85). The precision of survival estimates from MAPS, however, was lower than those from the CES, probably because of the lower sample sizes resulting from just three years of MAPS data compared to eight years of CES data. Recapture probabilities from MAPS for the 13 target species ranged from 0.03–0.66, averaged to 0.35, and were again roughly similar to estimates from the CES Program.

In contrast, estimates of annual adult survival

TABLE 7. MODIFIED CORMACK-JOLLY-SEBER CAPTURE-RECAPTURE ANALYSES FOR SELECTED TARGET SPECIES DERIVED FROM THE CAPTURE HISTORIES OF ADULT BIRDS

Species	Number of			Survival probability <sup>a</sup>		Recapture probability <sup>b</sup>	
	Stations <sup>c</sup>	Individuals <sup>d</sup>	Captures <sup>e</sup>	Estimate ± SE	CV	Estimate ± SE	CV
Black-capped Chickadee	21	253	346	0.55 ± 0.29	51.8	0.16 ± 0.10	58.0
Veery	12	245	449	0.39 ± 0.08	20.4	0.63 ± 0.13	20.4
Wood Thrush	17	302	427	0.19 ± 0.07	38.4	0.65 ± 0.24	36.7
Gray Catbird	21	1,260	1,953	0.29 ± 0.04	14.1	0.66 ± 0.09	13.7
Red-eyed Vireo	21	311	397	0.24 ± 0.10	41.4	0.61 ± 0.25	40.8
Yellow Warbler	16	450	608	0.46 ± 0.20	43.2	0.22 ± 0.11	49.7
American Redstart	15	204	249	0.44 ± 0.30	68.3	0.17 ± 0.13	76.6
Ovenbird	20	329	421	0.24 ± 0.13	56.4	0.47 ± 0.27	57.9
Common Yellowthroat	25	643	878	0.35 ± 0.13	35.6	0.23 ± 0.09	39.2
Northern Cardinal	21	359	459	0.55 ± 0.20	36.3	0.24 ± 0.10	41.2
Indigo Bunting ( <i>Passerina cyanea</i> )	14	202	269	0.85 ± 0.73	85.6	0.12 ± 0.11	90.4
Song Sparrow	22	653	1,133	0.47 ± 0.18	38.2	0.33 ± 0.14	41.2
American Goldfinch	21	686	784	0.48 ± 0.30	62.5	0.03 ± 0.02	78.9
<i>Group means for</i>							
Target Species	19	454	644	0.42 ± 0.21	45.6	0.35 ± 0.14	49.5
All Resident species	27	1,490	1,858	0.45 ± 0.09	21.0	0.21 ± 0.05	23.4
All short-distant migrant species	25	3,317	4,252	0.33 ± 0.06	19.6	0.21 ± 0.04	21.2
All long-distant migrant species	27	4,918	6,865	0.31 ± 0.03	10.6	0.42 ± 0.05	11.1
All species	79	9,725	12,975	0.33 ± 0.03	8.7	0.31 ± 0.03	9.3

Notes: Calculated using the computer program SURGE4, for species for which more than 200 capture histories were available from a total of more than ten stations where the species was known to be breeding.

<sup>a</sup> Defined as the probability of an adult bird surviving and returning in 1991 to the area where it was captured in 1990.

<sup>b</sup> Defined as the conditional probability of recapturing an adult bird in 1991, given that it did survive and return in 1991 to the same area where it was captured in 1990.

<sup>c</sup> Number of stations operated for three consecutive years (1990–1992) where the species was known to be breeding.

<sup>d</sup> Number of individual adult birds captured during the three years (1990–1992) at stations where the species was breeding; thus, the number of capture histories.

<sup>e</sup> Total number of captures (including recaptures) during the three years (1990–1992) at stations where the species was breeding.



rates of temperate-zone passerines from other studies, which used traps at nest sites or food-baited traps during the winter, were often somewhat higher than estimates from MAPS or CES. For example, the average annual survival rate of ten Maryland-wintering species was  $0.54 \pm 0.03$  (Karr et al. 1990a), that for Black-capped Chickadee (*Poecile atricapilla*) in Connecticut was  $0.59 \pm 0.02$  (Loery et al. 1987, Pollock et al. 1990), and that for European Dipper (*Cinclus cinclus*) in France was  $0.57 \pm 0.08$  (Lebreton et al. 1992). A likely reason for lower survival estimates from MAPS (and CES) is the inclusion in the sample of captured birds of transient individuals that are unlikely to be recaptured in subsequent years. Such transients can include late spring migrants, floaters, individuals breeding just outside the study area, post-breeding dispersing adults, and early fall migrants. Despite protocols that generally exclude late spring and early fall migrants from MAPS data (see section on netting schedules), substantial numbers of transient individuals are still likely to be included in the data.

Results of pooling species having various migration strategies illustrate a possible effect of including transients in mark-recapture analyses (Table 7). The survival probability of all permanent resident species pooled was higher than that for both short- and long-distance migrant species pooled, each of which might be expected to have more transients in the captured sample than would permanent resident species. On the other hand, the differences in survival between resident and migrant species might be real if migration causes enhanced mortality. Until the effects of transient birds can reliably be excluded from analyses, it will be difficult to interpret the biological significance of survival estimates.

Major advances in reducing the effects of transient individuals on survival estimates have been obtained in recent years (Peach et al. 1990, Peach 1993, Pradel et al. 1997, Nott and DeSante 2002, Kendall et al. *this volume*). Pradel et al. (1997) essentially uses an ad hoc approach that consists of ignoring the first observation of each individual bird and then proceeding as usual with the left-truncated capture histories. This method effectively permits estimation of an unbiased survival rate for resident birds and estimation of the proportion of transients among newly marked birds. DeSante et al. (1995) tested this model on four years of mark-recapture data from MAPS (1990–1993). Using this model, estimates of survival probability increased for eight species by 51%, from an average of 0.40 to 0.61, and estimates of recapture probability likewise in-

creased by 60%, from an average of 0.32 to 0.51. The precision of the estimates was also increased for both survival (by 11%) and recapture probability (by 24%). In addition, the estimated proportion of transients was high, about 65%. More recently, Nott and DeSante (2002) included Pradel et al.'s (1997) suggestion for a within-year length-of-stay addition to the transient model. The inclusion of the length-of-stay model further increased the precision of the survival estimates for resident individuals by an average of 16% for 10 species without substantially affecting the survival estimates themselves (survival estimates increased for 5 species and decreased for 5 species; Nott and DeSante 2002).

It must be emphasized, however, that regardless of whether or not a transient model is employed, survival rate estimates derived from CJS mark-recapture analyses are apparent survival rate estimates in which mortality and permanent emigration are confounded; low apparent survival could be caused either by high mortality or by high permanent emigration rates. The low survival for Wood Thrush (Table 7), for example, could result either from high mortality, presumably during the non-breeding season, or from a high emigration rate (caused perhaps by high rate of nest predation, or by breeding habitat alteration). In the latter case, management for Wood Thrush should be focused on the temperate breeding grounds, whereas low survival during the non-breeding season would call for management directed at the migration routes or tropical wintering grounds.

Thus, there exists a pressing need to design studies to distinguish the effects of permanent emigration from mortality. This will be difficult, because rigorous separation of their effects requires extensive networks of nearby stations to identify movements of birds between them. Effects of movements could then be separated from mortality using multi-state models, such as those described by Hestbeck et al. (1991). Nichols (in DeSante 1995) suggested another technique that calls for the establishment of nested study areas of increasing size and the estimation of survival rates over each area. Peach (1993) and, more recently, Cilimburg et al. (2002) investigated the effects of sampling area on survival rates and found that, in some cases, survival rates could be increased by as much as 23% by increasing the sampling area so as to include individuals that emigrated from the smaller-sized study area. Despite the fact that CJS mark-recapture models applied to data from small study areas, such as the 20-ha areas (with nets placed within the central 8 ha) used by MAPS, provide only estimates of apparent survival, it seems likely that

geographic or habitat variation in apparent survival within a given species could provide important management information, regardless of whether the low apparent survival rates are caused by high mortality or high emigration rates.

Finally, CJS mark-recapture methods can also be used to provide estimates of actual adult population size, complete with standard errors; that is, they can provide essentially unbiased abundance estimators. Such estimates can be compared with indices of abundance derived from constant effort mist netting (or from point counts or other methods of indexing relative abundance), to identify and estimate the magnitude of biases in those indices. These data can then be used to determine whether bias in the various indices remains constant among species, locations, or years, a constancy that is often assumed in analyses but which may not hold true (Sauer and Link *this volume*). Such analyses have not yet been conducted using MAPS data.

#### PEER REVIEW

A detailed evaluation of the statistical properties of MAPS data collected during the 1992–1995 MAPS pilot study (Rosenberg 1997), and an evaluation of the appropriateness and efficacy of the field and analytical methods being used by the MAPS Program (DeSante 1997), was completed in 1996. These evaluations were subjected to peer review by a panel of experts in mark-recapture modeling and population dynamics analyses at USGS/BRD Patuxent Wildlife Research Center (Geissler 1997), which concluded that “MAPS is technically sound and is based on the best available biological and statistical methods. The pilot substantially exceeded expectations in rapidly expanding the number of sites supported by independent agencies and organizations. MAPS complements other land bird monitoring programs such as the BBS by providing useful information on land bird demographics that is not available elsewhere. MAPS is the most important project in the nongame bird monitoring arena since the creation of the BBS.” Results of this review and evaluation have been published in several papers (DeSante et al. 1999; DeSante 2000; Rosenberg et al. 1999, 2000).

#### CONCLUSION

Initial analyses of the first five years of MAPS data (1989–1993) suggest that the field and analytical techniques currently in use can provide important

information regarding between-year changes, as well as longer-term trends and spatial differences, in annual indices of productivity and estimates of survivorship. The accuracy and precision of these indices and estimates, however, and thus their ultimate usefulness, depend on assumptions regarding age-, species-, and station-specific differences in dispersal characteristics, numbers of transients in the populations being sampled, and heterogeneity of recapture probabilities, as well as upon the basic statistical properties of the data, including the numbers and distributions of individuals that can be sampled at the various stations. The validity of several, but not all, of the assumptions underlying the field and analytical techniques has recently been verified and these results (e.g., DeSante 2000; DeSante et al. 1999, 2001; Nott and DeSante 2002; Nott et al. 2002) have further supported the usefulness of MAPS data. Two important questions that still need further investigation are (1) the degree that young concentrate in various habitats, and the effect of that on productivity indices; and (2) an assessment of the actual effect of permanent emigration on adult survival estimates. Also currently lacking is information on the sensitivity of results to violations of the assumptions, and on the sampling effort necessary to attain targeted levels of precision, although studies on the latter question are currently underway.

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