MONITORING BIRD POPULATIONS USING MIST NETS

C. JOHN RALPH AND ERICA H. DUNN, EDITORS

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Cover illustration: the life cycle of a Western Tanager (*Piranga ludoviciana*) shown through capture and banding. Original by Keith Hanson, redrawn by Gary Bloomfield.

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PREFACE

Mist nets were introduced to North America about mid-way through the 20th century. In the decades since then, they have become a widely adopted and indispensable bird-capturing tool for the scientific study of birds. At first, mist nets were an inventory tool, allowing in-hand comparison of species previously scrutinized only over the barrel of a shotgun, but in the early 1970s, netting began to be used for monitoring population trends and demographic composition. Early users had to develop protocols for mist netting based on their own experience. Some 30 years later, there has still been relatively little evaluation to determine the effect of different mist netting methods (or of extrinsic factors) on the numbers and kinds of birds that are captured, and the degree to which demography of captured birds represents true population characteristics.

Recognizing the need for greater evaluation of mist-netting and the need for standards on the use of this technique, a workshop was held in October 1993 entitled "The use of mist nets to monitor bird populations." The workshop took place at the Marconi Conference Center on the shores of Tomales Bay, California, and was sponsored by the Point Reyes Bird Observatory, U.S. Forest Service, U.S. Fish and Wildlife Service, Canadian Wildlife Service, and the Institute for Bird Populations.

The objectives of the workshop were to examine the strengths and weaknesses of mist-netting for a variety of population monitoring purposes, with a primary focus on passerines, and to develop recommendations on the best methods for using mist nets as a population monitoring tool. The conference attracted 40 participants from Canada, Costa Rica, Germany, Great Britain, and France, as well as from all across the United States. The majority of papers presented at the workshop are included in this volume, as well as several prepared as follow-up. During intensive breakout sessions, all participants reached consensus on recommended standards, reflected in the final chapter of this volume, "Recommendations for the use of mist nets for inventory and monitoring of bird populations." All manuscripts underwent extensive peer review as well as review by editors. During this process, delays made it possible for a reevaluation of all the manuscripts. All the authors enthusiastically participated in this process, and as a result many new data were brought forward, and updated analyses were incorporated into manuscripts during 2001–2003. As well, several new manuscripts were submitted that were not presented at the workshop. The co-editors completed the final editing in late 2003.

Both the manuscripts and the recommended standards for mist netting were greatly improved by comments from authors of all the papers in this volume, as well as from Bob Altman, Doug Barnum, Jeffrey Brawn, Deanna Dawson, Sam Droege, Joseph Engler, Denise Hardesty, Daniel Hernandez, Jane Hicks, Stephanie Jones, Joe Kaplan, James Karr, Martin McNicholl, Bill McShea, Rhonda Millikin, Nicolle Mode, Bert Murray, Glenn Olsen, Peter Pyle, John Rappole, Dan Reinking, W. John Richardson, Christian Vansteenwegen, Dennis Vroman, George Wallace, and Richard Weisbrod. The editors are also indebted to Linda Long for her dedicated and extensive work as editorial assistant, to John Rotenberry for his help in finalizing this volume, and to Keith Hanson for the very topical artwork that appears on its cover (redrawn by Gary Bloomfield). Finally, we thank the Canadian Wildlife Service, Institute for Bird Populations, Point Reyes Bird Observatory, U.S. Fish and Wildlife Service, and U.S. Forest Service for their contributions to the costs of the workshop and publication.

C. John Ralph
Erica H. Dunn

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USE OF MIST NETS AS A TOOL FOR BIRD POPULATION MONITORING

ERICA H. DUNN AND C. JOHN RALPH

Abstract. Mist nets are an important tool for population monitoring, here defined as assessment of species composition, relative abundance, population size, and demography. We review the strengths and limitations of mist netting for monitoring purposes, based on papers in this volume and other literature. Advantages of using mist nets over aural or visual count methods include ease of standardized sampling, low observer bias, ability to detect species that are often missed using other count methods, and opportunity to examine birds in the hand (providing information on condition, age, sex, and capture history). The primary limitation of mist netting, in common with most other survey methods, is from potential bias in sampling. However, there are many approaches to reducing or adjusting for bias, including standardization of netting methods, combining mist-net sampling with other survey types, and using mark–recapture techniques. Mist netting is an essential tool for species inventory, provides useful indices of relative abundance, and can be used to track temporal trends in abundance. It is also one of the most efficient methods of capture for mark–recapture studies.

Key Words: mark–recapture, mist net, population monitoring, sampling bias.

Mist netting is an important technique for population monitoring, helping to assess species composition, relative abundance, population size, and demography (productivity and survival). Whereas mist netting is time intensive and requires specialized training, it has certain advantages over visual and aural population monitoring techniques. Mist nets can sample species that are poorly detected by other means, counts are not subject to observer bias, netting effort is easily standardized, and each bird counted can also be examined in the hand. Capture allows birds to be aged, sexed, and marked to allow individual identification in future encounters. In addition, extra data can be collected that also contribute to population studies, such as breeding status or sub-species identification. Data can be collected for other research purposes at the same time (e.g., physiological state, molt, parasite loads, DNA sampling). Because mist netting is one of the most efficient means of capturing many bird species, especially those that are insectivorous, the technique is often used in mark–recapture studies.

In this paper, we discuss the strengths and limitations of mist netting for population monitoring applications, and summarize the literature in which population parameters based on mist-net captures were evaluated by comparing them with data from independent data sources. In addition, we review the main sources of potential bias in population indices based on numbers of birds captured, and discuss some ways to address such bias. Ralph et al. (*this volume a*) should be regarded as a companion paper to this one, because it recommends best practices in mist netting, accompanied by the reasons why recommended procedures will improve monitoring capability.

SPECIES COMPOSITION

Mist netting is often used as a tool to determine what species are present in a study area. The technique is a valuable component of species inventory because it detects more cryptic, ground-foraging, and non-singing birds than aural or visual surveys (Blake and Loiselle 2001, Rappole et al. 1993, 1998, Wallace et al. 1996, Whitman et al. 1997). Further, results are relatively unaffected by the bird identification skills of observers (Karr 1981a; although misidentification may still occur, Dale *this volume*). However, netting is often a less efficient means of species inventory than censuses such as point counts, in terms of species detected per unit effort (Ralph et al. 1995, Gram and Faaborg 1997, Whitman et al. 1997). Moreover, netting is known to under-sample or completely miss some species (such as aerial foraging swallows, or raptors), regardless of season (Wang and Finch 2002). As a result, most authors have recommended that mist netting be used as a supplement to visual or aural surveys when a species inventory is being prepared, rather than as a sole source of data (Faaborg et al. *this volume*, Whitman *this volume*). Kendall et al. (*this volume*) provide information on using mark–recapture techniques to estimate the total species present, even though only a proportion has been detected.

RELATIVE ABUNDANCE AND TRENDS

Mist-netting studies are commonly used to document differences in abundance indices among species, locations, years, or age classes (see next section), and to detect trends in population indices over the long term. No matter what count methods are used to obtain abundance indices, the proportion of the true population that is counted will likely vary over time and space, introducing bias, which we discuss below. Nonetheless, evaluation studies have shown that abundance indices derived from mist-net sampling often compare well to independent data on the parameters of interest.

For example, species rankings based on relative abundance in breeding season mist-net samples were usually correlated with abundance rankings based on point counts at the same locations (Table 1), although individual species' rankings sometimes differed markedly between count types (DeSante et al. *this volume*, Kaiser and Berthold *this volume*). Similar studies in wintering areas gave mixed results, in that agreement of species' rankings between methods was quite good for some data sets (e.g., Wallace et al. 1996 *this volume*), but very poor in others (Blake and Loiselle 2001). Faaborg et al. (*this volume*) found good correspondence for year-round residents but very little for wintering species, and Lynch (1989) found that level of correspondence differed among habitats. In the migration season, birds are perhaps less selective of specific habitat types (Moore et al. 1995). For example, Wang and Finch (2002) found good correspondence between mist-net and point-count abundance rankings of species during migration in all habitats studied.

Within species, annual abundance indices have been shown to fluctuate in parallel with indices based on other data sources (Table 1). Repeated mist netting throughout the breeding season gave indices that paralleled abundance data derived from spot mapping, in 3 of 4 species studied by Silkey et al. (1999, from a single netting station) and in 9 of 21 species studied by Peach et al. (*this volume*, pooling data from many locations). No comparable studies have been conducted during the wintering season. For the migration season, Dunn et al. (*this volume a*) showed that annual abundance indices based on daily mist-net samples were strongly correlated with indices based on a standardized daily census in 73% of 64 species.

Several comparisons have been made between long-term trends in abundance indices based on netting data and trends from independent sources (Table 1). Pooled data from constant-effort mist netting at many locations during the breeding season corresponded with regional population trends based on spot mapping in 15 of 21 species (Peach et al. 1998, *this volume*). Trends in numbers of migrants captured were often correlated with Breeding Bird Survey trends from regions to the north where the migrants were assumed to have originated (Hagan et al. 1992, Dunn and Hussell 1995, Dunn et al. 1997, Francis and Hussell 1998, Berthold *this volume*, Rimmer et al. *this volume*). Correlations were strongest when statistical techniques were used that compensated for variation in daily bird numbers caused by weather and date in the season, and precision of long-term trends has been shown to improve when netting at a single station is more frequent (Thomas et al. *this volume*). However, as noted by Rimmer et al. (*this volume*), birds from diverse portions of the breeding range are typically sampled at a single location, making direct comparisons between mist-net capture rates and Breeding Bird Survey trends difficult.

DEMOGRAPHIC MONITORING

Monitoring of productivity is a special case of abundance monitoring, in which abundance of adult and young birds is assessed separately. Because capture probabilities differ between age classes (Ballard et al. *this volume*, Burton and DeSante *this volume*, Nur et al. *this volume*), the relative proportions of young to adults cannot be regarded as absolute measures of the number of young produced per adult, but rather are indices of productivity (Bart et al. 1999).
Productivity indices from constant-effort mist netting in the breeding season have been compared to the numbers of nestlings found during intensive nest monitoring (Table 1). In some, but not all species, these estimates fluctuated in parallel between years (Nur and Geupel 1993b, du Feu and McMeeking *this volume*). Discrepancies may have resulted from post-fledging dispersal of young (e.g., Anders et al. 1998, Vega Rivera et al. 1998), so that mist-net samples represented local productivity in some species and regional productivity in others. Differences in mist-net based productivity indices among stations within a region (as found by Ralph et al. *this volume b*) could therefore result from true differences in local productivity, or from post-fledging redistribution of birds. Therefore, unless pilot work has demonstrated that productivity indices from mist netting accurately reflect local productivity in the target species, site-specific indices of productivity based on mist netting should at least be augmented by intensive nest monitoring (e.g., Gates and Gysel 1978, Roth and Johnson 1993).

In contrast, it has been demonstrated that collecting data from multiple netting stations is a good means of tracking regional productivity (Bart et al. 1999; Table 1). Cooperative programs that pool data from constant-effort sampling at many mist-net stations in a region include MAPS (Monitoring Avian Productivity and Survivorship; DeSante et al. *this volume*), the British Trust for Ornithology's

TABLE 1. COMPARISON OF POPULATION DATA COLLECTED BY MIST NETTING WITH DATA FROM INDEPENDENT SOURCES

Parameter	Season	Source of data for comparison	Correspondence of parameter between data sets	Source
Relative abundance of species	Breeding	Point counts	Correlated at 34 of 37 locations	DeSante et al. *this volume*, Kaiser and Berthold *this volume*
	Winter	Point counts	Roughly correlated in some data sets; not in others	Lynch 1989, Wallace et al. 1996, Blake and Loiselle 2001, Faaborg et al. *this volume*
	Migration	Point counts	Correlated in all habitats	Wang and Finch 2002
Annual abundance indices for individual species	Breeding	Spot mapping	Often correlated, but not in all species	Silkey et al. 1999, Peach et al. *this volume*
	Migration	Transect	Correlated in 73% of 64 species	Dunn et al. *this volume a*
Daily abundance indices	Migration	Point counts	Corresponded only roughly	Simons et al. *this volume*
	Migration	Radar	Corresponded only roughly	Simons et al. *this volume*
Population trends	Breeding	Spot mapping	Corresponded in 15 of 21 species	Peach et al. 1998, *this volume*
	Migration	Spot mapping	Often corresponded	Berthold *this volume*
	Migration	Breeding Bird Survey	Often corresponded	Hagan et al. 1992, Dunn and Hussell 1995, Dunn et al. 1997, Francis and Hussell 1998, Rimmer et al. *this volume*
Local productivity	Breeding	Nest monitoring	Corresponded in 4 of 4 species	du Feu and McMeeking *this volume*
	Breeding	Nest monitoring	Corresponded in 1 of 2 species	Nur and Geupel 1993b
Regional productivity	Breeding	Nest monitoring	Corresponded in 1 of 2 species	Nur and Geupel 1993b
	Breeding	Population model[a]	Corresponded (1 species studied)	Bart et al. 1999
Survivorship	Breeding	Resighting	Corresponded (1 species studied)	Nur et al. *this volume*
	Breeding	Band recoveries	Corresponded roughly (5 species studied)	Peach and Baillie *this volume*
	Breeding	Correlation with causal factor	Several examples	Peach et al. 1991, 1999
Sex ratio		Shooting	No correspondence (2 species)	Mawson 2000
Capture rate	Breeding	Other trap types	Does not always correspond	Bauchau and Van Noordwijk 1995, Collister and Fisher 1995

[a] A model containing results from annual range-wide counts and annual survival rates was used to estimate range-wide productivity in Kirtland's Warbler (*Dendroica kirtlandii*).

CES Scheme (Constant Effort Sites; Peach et al. *this volume*), the German MRI Program (Mettnau-Reit-Illmitz-Program; Kaiser and Berthold *this volume*), and the STOC program in France (Suivi Temporel du niveau d'abundance des populations d'Oiseaux terrestres Communs; Vansteenwegen et al. 1990). An evaluation of CES productivity indices (Peach et al. 1996) showed that although there was variation in capture rates and age proportions among locations, annual changes in age proportions at individual stations were similar in direction and magnitude across habitats and regions (Peach et al. 1996). Productivity indices based on pooled data also were similar among a cluster of stations in California (Ralph et al. *this volume b*), and pooled data from CES stations had acceptably low standard errors (Peach et al. *this volume*).

Migration data also may be useful for tracking regional productivity, as represented by the proportion of young birds in fall mist-net samples. However, this hypothesis has been little tested (Hussell *this volume*). It will be difficult to validate productivity indices that are based on capture of fall migrants, because independent productivity data from the breeding grounds will rarely be available (because breeding locations are unknown or unstudied). Nonetheless, some approaches to evaluation have been suggested for future research (Dunn et al. *this volume b*).

MAPS, CES, and the other cooperative demographic monitoring programs mentioned above are designed to collect information not only on productivity, but also on apparent survival rates. Whereas survival rates could be estimated for any season in which birds are site faithful and relatively sedentary, these cooperative studies estimate annual survival between breeding seasons. Average survival can also be estimated for individual netting stations, although sample sizes are usually too low to document annual differences (Faaborg and Arendt 1995, Hilton and Miller 2003).

There are fewer validation studies of survivorship estimates than of productivity indices, because independent estimates of survivorship are harder to obtain. Nur et al. (*this volume*) showed that survivorship of one species estimated from mist-net recaptures was similar to estimates based on resighting of marked individuals. Peach and Baillie (*this volume*) found that across five species, there was an overall (but non-significant) relationship between survivorship estimates based on CES and those based on band recoveries. Survival rates from CES were lower, probably because birds that emigrate from a station cannot be distinguished from birds that die, but the authors presented cogent arguments supporting the usefulness of CES estimates as indices of survival. There have also been several studies showing that change in annual survival rates was correlated with events likely to have had a strong effect on mortality (Peach et al. 1991, 1999).

POTENTIAL BIAS IN MIST-NET SAMPLES

As with bird counts obtained through visual and aural surveys, the numbers of birds captured in mist nets are indices of abundance, rather than total counts. Use of standardized, constant effort protocols will reduce variation in capture rates caused by uneven effort or net avoidance (Ralph et al. *this volume a*). However, even completely standardized operations capture only a proportion of all birds present, and that proportion will vary with species, habitat, weather, and other factors unrelated to true population size. Sauer and Link (*this volume*) showed that capturing different proportions of the true population could lead to false conclusions in comparison of samples, so it is important to investigate the potential for bias and to estimate its magnitude.

Capture rates at all seasons are affected by a multitude of factors, including distribution of nets with respect to territory size (Remsen and Good 1996, Ballard et al. *this volume*, Nur et al. *this volume*), mesh size of nets (Heimerdinger and Leberman 1966, Pardieck and Waide 1992, Jenni et al. 1996), season (Pagen et al. 2002), species (Jenni et al. 1996, Wang and Finch 2002), age class (Ballard et al. *this volume*, Burton and DeSante *this volume*, Nur et al. *this volume*), factors affecting movement rates (e.g., whether birds are incubating or molting), activity height (Remsen and Good 1996), and vegetation and habitat structure (Pagen et al. 2002, Ballard et al. *this volume*, Kaiser and Berthold *this volume*, Mallory et al. *this volume*, Whitman *this volume*).

Capture rates of migrants are also affected by most of these factors. Weather has a particularly strong effect on migrant numbers, because it influences rate of daily influx and departure from a location, and weather effects may be especially marked at stations near the edges of migration routes (Simons et al. *this volume*). In addition, during migration there will be daily variation in the proportion of birds migrating past the study site that actually stop there (Dunn and Hussell 1995). Migrating birds may be less selective of habitat during migration than are breeding birds, however, so habitat biases may be lower during migration than in other seasons.

After a review of sources of bias in mist-net captures, Remsen and Good (1996) concluded that unadjusted capture rates should not be used in quantitative comparisons of relative abundance, either among species, or within species among habitats. On the other hand, there is much evidence that a strong signal can be obtained from standardized index counts (Table 1). Whereas descriptive, non-qualitative results alone can be useful for land managers (e.g., Humple and Geupel 2002), information on relative abundance can add a great deal of value, particularly when conclusions are tempered by explicit discussion of the potential for bias and its possible magnitude. Moreover, long-term trend monitoring will not be compromised by the fact that numbers captured are only a proportion of true population size, as long as there are no temporal trends in the capture proportions themselves. In most studies such stability is assumed rather than directly tested, but Dugger et al. (2000) found that capture proportions in a neotropical study area remained relatively stable over time within species and locations. However, relatively small changes in a species' mean peak of activity can have a large effect on capture rates (Remsen and Good 1996). Long-term habitat change is the most likely source of systematic bias in long-term trends based on mist netting (Ralph et al. *this volume a*), and such change may be difficult to prevent even with regular management of the vegetation (Kaiser and Berthold *this volume*).

Mark–recapture methods can help to reduce the potential for bias caused by variation in capture proportions among mist-net samples (Sauer and Link *this volume*). Mark–recapture modeling estimates the proportion of all birds that is actually captured, which can then be used to estimate total population size (e.g., Kaiser and Bauer 1994, Kaiser and Berthold *this volume*). Peach and Baillie (*this volume*) and Kendall et al. (*this volume*) provided background on the uses of mark–recapture for this purpose, as well as for estimating adult survival, recruitment, and proportion of transients in a sample. The technique may have more limited value for migration studies, because the high rate of turnover in the birds present at a study location precludes using recapture rates to estimate population size. It should be noted that capture–recapture estimates of population size and capture probability are model-based, and the assumptions associated with any model must be considered when interpreting results.

Another means of addressing biases that may exist in mist-net samples is to adjust numbers of birds captured according to independent data on abundance. Although no count methods are completely problem-free, a few techniques have been developed that produce relatively unbiased estimates of density (Buckland et al. 2001, Bart and Earnst 2002, Thompson 2002). These methods can be used in combination with mist-netting studies to evaluate the presence and potential magnitude of bias in the mist-net samples. Once capture proportions have been quantified, the density estimation data can be used to adjust the mist-net samples during analysis.

FUTURE RESEARCH

The strengths and limitations of mist netting for population monitoring have received considerable attention in recent decades, but much remains to be learned. We suggest the following topics as priorities for research:

- The factors affecting the proportion of the true population captured need to be better quantified in a wider variety of species. In particular, more work is needed on effects of vegetation structure, habitat, and net avoidance.
- For programs that pool data from many stations, more work is needed on the most appropriate number and distribution of stations to ensure representative sampling at chosen geographic scales, the effects on results of frequency of operation, and on effects of station turnover.
- Additional validation studies are needed on abundance and demographic indices based on mist netting (including fall age ratios in migrating birds), and on population trends of temperate migrants sampled in their wintering areas.
- There is little information on age- or sex-specific differences in dispersal and habitat preference, or on degree of annual variation in these factors. Such knowledge is important for interpreting spatial and temporal differences in productivity indices.
- Mark–recapture methods are improving rapidly, but better models are needed to address dispersal of juveniles or previous breeders, and for pooling of data from multiple stations (especially when there is turnover in the sample of stations). Use of mark–recapture for migration studies also needs further investigation.

CONCLUSIONS

Mist netting as an extremely valuable tool for many kinds of population monitoring, not only for detecting the presence of species and counting individuals, but as an efficient means of capture to age individuals and mark them for future identification. It is almost unique among methods in providing demographic estimates in all seasons, for many species of birds. Although mist netting is especially effective as a monitoring technique when used in mark–recapture studies, it can also provide valuable indices of relative abundance. In addition, mist-net samples can be used to track long-term trends in abundance and productivity.

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EFFECTS OF MIST-NETTING FREQUENCY ON CAPTURE RATES AT MONITORING AVIAN PRODUCTIVITY AND SURVIVORSHIP (MAPS) STATIONS

KENNETH M. BURTON AND DAVID F. DESANTE

Abstract. Data from the Monitoring Avian Productivity and Survivorship (MAPS) Program were analyzed to evaluate the effect of frequency of operation (number of days per 10-day period) of mist nets at MAPS stations on capture rates of adult and young birds. A negative relationship existed between netting frequency and the number of captures of adult birds per unit effort. This suggests that net avoidance by adult birds can be an important consideration at higher frequencies. There also was a negative relationship between netting frequency and the rate of capture of individual adults; this demonstrates saturation of effort. With regard to young birds, however, netting frequency had no effect on either type of capture rate. These results indicate that data from stations run at high frequencies will produce inflated productivity indices by lowering capture rates of adults but not of young. Thus, when pooling data from stations operated at differing frequencies for large-scale demographic monitoring, the data must be adjusted to control for netting frequency. We interpret these findings and suggest more rigorous approaches to the study of these phenomena.

Key Words: capture rate, MAPS, mist net, net avoidance, netting frequency, productivity.

Constant-effort mist netting has been shown recently to be a viable method of monitoring demographic parameters of landbird populations (Baillie 1990; Baillie et al. 1986; Butcher et al. 1993; DeSante 1992; DeSante et al. 1993a,b; Nur and Geupel 1993a,b; Peach et al. 1991, Ralph et al. 1993). However, many questions remain regarding the optimal design of monitoring programs using mist netting, not least of which concerns the frequency at which mist nets should be operated (Nur and Geupel 1993b, Ballard et al. *this volume*). The question of how often to operate mist nets is not merely academic. Mist netting, although providing information not readily obtainable by other methods, such as point counting, is relatively labor intensive. Managers and researchers need to know what sampling effort is required to produce accurate and precise estimates of the target parameters (e.g., population size, productivity, survivorship, recruitment) in the most efficient manner possible. Furthermore, to avoid undue disturbance to the birds themselves, netting should not be conducted at a frequency higher than that necessary to obtain the desired information.

From a bird's point of view, there is no reward associated with being captured in a mist net. Common sense and anecdotal evidence suggest that after such an experience (particularly if repeated), birds are likely to stay away from the net for some time. This phenomenon is known as "net avoidance" or "net shyness," although it is debatable whether birds are avoiding the nets themselves, the net sites, both, or neither. The existence, magnitude, and duration of net avoidance undoubtedly vary among species and probably among individuals, and are likely to increase with repeated capture. At the population level, different age classes are likely to show different degrees of net avoidance due to behavioral differences and degree of naiveté. The degree of net-site avoidance undoubtedly depends to some extent on the site's proximity to a bird's nest in the breeding season, and on its proximity to food, shelter, or other resources, and thus net-site avoidance may vary seasonally.

Net avoidance is generally assumed to exist in mist-netting studies, but few studies have been conducted to examine its magnitude and effects on indices and estimates of population parameters. Stamm et al. (1960) documented steady declines, which they attributed to net shyness, in capture rates of all species combined immediately before and after spring migration in Maryland. As further evidence, they found a marked increase in capture rate, followed by another decline, after relocating their nets (an indication that birds learned to avoid the site of capture, rather than recognizing the nets *per se*). Swinebroad (1964), however, was unable to demonstrate net avoidance in a New Jersey Wood Thrush (*Hylocichla mustelina*) population and in fact had a higher-than-expected proportion of recaptures (based on population estimates from spot mapping); he concluded that placement of nets in areas of high activity within actively defended thrush territories resulted in a disproportionately high rate of repeat captures.

The variation in the results of these studies is further evidence that the intensity of net avoidance varies according to species, season, and perhaps even to population. However, Stamm et al. and Swinebroad banded at highly irregular intervals ranging from 1 to 21 days, making meaningful interpretation and comparison of their results difficult.

Because of territoriality, there is a limited pool of adult birds available at a given site. After these birds have been captured in a given year, an increase in effort will not increase the number of resident individuals captured, although non-breeding birds will continue to be captured. Thus, in a closed population, the capture rate of new individuals (i.e., first captures) is likely to decline as effort is increased, a phenomenon known as "saturation of effort." The length of time taken to reach saturation is dependent on population size, capture probability, and net density, in addition to sampling frequency.

Ballard et al. (*this volume*) found that nets operated five days a week (about 7 days out of 10) captured 50% more locally produced hatch-year Wrentits *(Chamaea fasciata*) than did nets run in the same study plot either once every ten days or twice a week (about three days out of ten). However, the number of locally breeding adult Wrentits captured did not differ significantly among the various regimes. These results suggest that saturation is a more significant issue with adult birds than with young; this is what one would expect, since adults tend to be more sedentary than young birds during the breeding season.

Monitoring Avian Productivity and Survivorship (MAPS) Program protocol (DeSante 1992; DeSante et al. 1993b, 2002) is for nets to be operated on one day per 10-day period. This recommendation was made to increase the number of stations by making them easier to operate, decrease the variability among stations, and minimize disturbance to the birds. Nur and Geupel (1993a,b), however, recommend that nets be operated as frequently as possible to increase annual capture probabilities, and to distinguish between residents and transients, based on multiple captures of the former, so as to be able to exclude the latter from survivorship estimations. Nur et al. (*this volume*) found that locally breeding Wrentits were captured repeatedly at their study site, while non-breeders were not. Furthermore, Sauer and Link (*this volume*) suggest that estimation of the degree of bias in population-parameter indices is possible by estimating capture probability, the reliability of which will be improved by increasing the number of samples. On the other hand, Pradel et al. (1997) suggest that sufficiently spaced capture sessions nearly always will preclude multiple captures of transients, making them easier to identify and exclude from survivorship analyses.

Obviously, no single netting regime is optimal for all purposes. Our contention has been that, for demographic-monitoring purposes, operation of nets once per 10-day period over at least six periods will provide sufficient within- and between-year recaptures to discriminate effectively between residents and transients, and that if additional effort is possible, more information would be provided by the establishment of additional stations than by increased effort at existing stations.

Some MAPS stations (mostly stations operated by bird observatories and other avian research centers and established prior to the inception of the MAPS Program) operate their nets more frequently than once per 10-day period. Thus, data from MAPS stations provide an excellent opportunity to examine the effects of netting frequency on capture rates across a wide spectrum of sites.

METHODS

MAPS mist-netting protocol is described in DeSante (1992) and DeSante et al. (1993b, 2002). At the end of each breeding season, banding data (including species, age, sex, and band number) are submitted to the Institute for Bird Populations (IBP) for analysis, along with detailed information on mist-netting effort (date, number of nets, opening and closing times, total net hours). Baseline descriptions of each station, including primary habitat type, are kept on file at IBP.

We used 1992 MAPS banding data to assess the relationship between netting frequency (number of days of operation of mist nets per 10-day period) and total capture rates (numbers of all captures, including repeats, per unit effort) as a measure of net avoidance. We also examined the relationship between netting frequency and rate of first capture (numbers of newly captured individuals, excluding repeats, per unit effort) as a measure of saturation. We used 600 net-h as the unit of effort; this represents one season's effort at a station consisting of ten 12-m nets operated for 6 h/day at a frequency of 1 day/period for 10 periods.

Stations were grouped into four primary habitat types: "forest," "woodland," "scrub," and "meadow." We first conducted ANOVAs using netting frequency and habitat and their interaction as main effects. Habitat had highly significant effects on both total and first capture rates (all age classes pooled; $F_{3,166} = 18.61$, $P < 0.001$). Forest and meadow habitats were underrepresented at netting frequencies higher than 1 day/period, so we excluded from further analysis stations in these two habitats. Capture-rate data from woodland and scrub habitats were log transformed prior to further analysis in order to meet the assumptions of the models used; frequency data did not require transformation.

Mean values ±1 SE are reported. Gallinaceous birds and hummingbirds were excluded from analysis because most MAPS operators do not have permits to band them.

RESULTS

Data from 76 MAPS stations in woodland and scrub habitats were available for analysis. Netting frequency at these stations ranged from 0.8 to 5.2 day/period (day/p) with a mean of 1.4 ± 0.10 day/p over an average of 9 ± 0.26 periods. Total capture rate of adults ranged from 23.2 to 357.6/600 net-h (mean = 139.6 ± 9.21); total capture rate of young ranged from 7.4 to 818.9/600 net-h (mean = 98.8 ± 13.46). Rate of first capture ranged from 16.6 to 343.5/600 net-h for adults (mean = 113.9 ± 7.62) and from 7.4 to 786.7/600 net-h for young (mean = 92.0 ± 12.83).

The effect of netting frequency on capture rates did not differ between the two habitats analyzed (woodland and scrub) for either adults or young (frequency × habitat effect, $F_{1,73} = 0.7$, $P = 0.42$).

Combining habitats, increasing netting frequency significantly reduced total capture rate of adults ($F_{1,73} = 6.9$, $P = 0.01$); however, it did not affect total capture rate of young ($F_{1,73} = 0.4$, $P = 0.51$). Netting frequency also affected first capture rate of adults ($F_{1,73} = 9.3$, $P < 0.01$) but not of young ($F_{1,73} = 1.3$, $P = 0.26$). Figures 1–4 illustrate, using non-transformed data, the trends for each of the two habitats. The slopes were negative in all cases, regardless of statistical significance. However, the r values were all less than 0.3, indicating that netting frequency did not explain much of the variance in capture rates, even for adults.

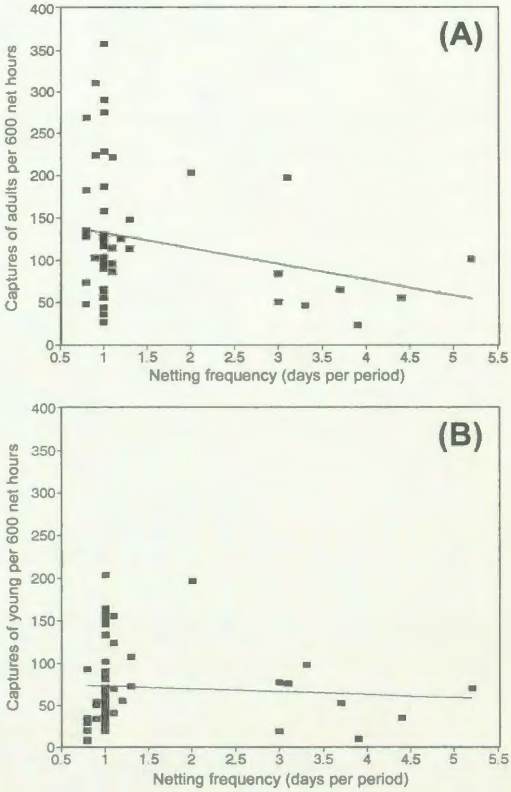

FIGURE 1. Total capture rates of (A) adults and (B) young vs. netting frequency at 54 MAPS stations in woodland habitats in 1992. (A) r = 0.25, slope = –18.7; (B) r = 0.07, slope = –3.6.

DISCUSSION

We found that net (or net-site) avoidance (as measured by decline in total capture rate) and effort saturation (as measured by decline in rate of first captures) can be significant in constant-effort mist-netting operations. Net avoidance and effort saturation during the breeding season appear to operate primarily on adults (presumably territorial, breeding individuals). The difference between adults and young is likely due to the higher degree of mobility among young during the breeding season.

Net avoidance and saturation, although distinct phenomena, have a similar effect on bird population studies: they result in inflated indices of productivity by lowering the capture rates of adults, but not of young. Statistics developed by Baillie et al. (1986) for the Constant Effort Sites Scheme, and adopted in the MAPS Program, use the number of individuals captured, rather than capture rates, in population size and productivity analyses. Stations are almost certain to capture more individuals by increasing their netting frequency and thus would contribute more data to these analyses, but, at least in regard to adults, this increase is not proportional to the increase in effort. Due to saturation, one cannot simply divide the number of individuals by the frequency of effort, as this would underestimate adult-population size and overestimate productivity. This is documented by DeSante et al. (*this volume*) in the case of a single station operated nearly daily. One solution might be to select data from a single day of operation from each period, either randomly or by some other criterion, for use in these analyses. DeSante et al. (*this volume*) demonstrate that this technique produces valid results. Another approach might be to calculate the total number of individuals captured using only the first day in each period, then only the second, and

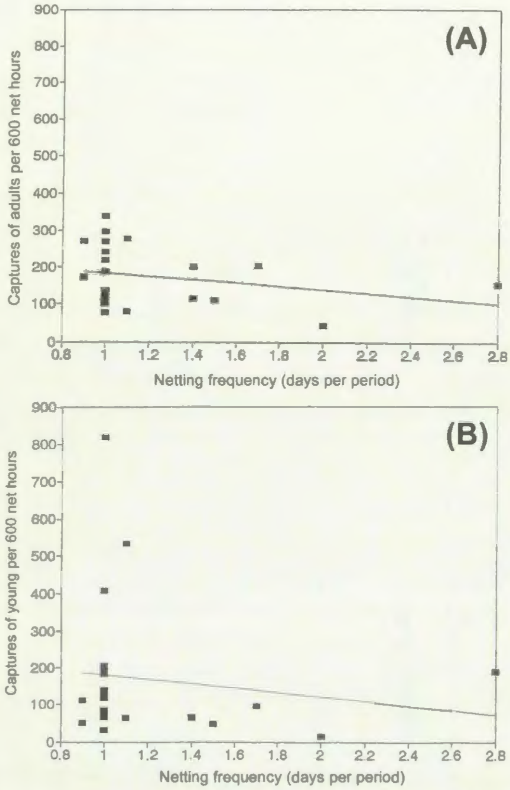

FIGURE 2. Total capture rates of (A) adults and (B) young vs. netting frequency at 22 MAPS stations in scrub habitats in 1992. (A) $r = 0.25$, slope $= -46.1$; (B) $r = 0.14$, slope $= -59.32$.

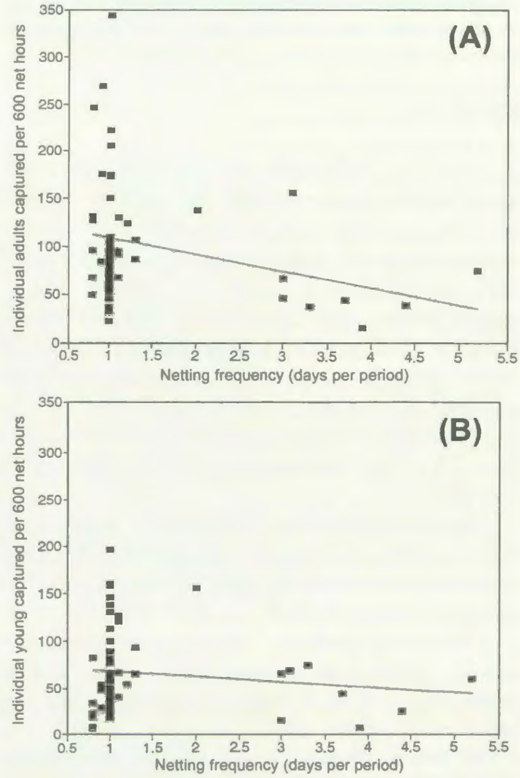

FIGURE 3. Rates of first capture of (A) adults and (B) young vs. netting frequency at 54 MAPS stations in woodland habitats in 1992. (A) $r = 0.27$, slope $= -17.1$; (B) $r = 0.13$, slope $= -5.9$.

so on, and use the average. The first approach would be the simpler, whereas the second could increase the accuracy and precision of the indices.

The problem of net avoidance becomes significant in breeding-bird monitoring programs in two cases. One is when nets are operated prior to the period under investigation, because resident or early-arriving breeders could be captured during this time and might not be captured again that year due to net avoidance. This is especially true if the nets are operated prematurely and frequently, as for a spring-migration monitoring program. This could act to decrease adult population size indices, increase productivity indices, and reduce survivorship estimates.

The second case in which net avoidance may affect population studies is when a station is operated at a very high frequency. Survivorship models using within-year recaptures to identify residents require a certain period of time between captures, typically 10 days (Buckland and Baillie 1987, Peach 1993, Peach et al. 1990). Stations operated at very high frequencies actually may lower their ability to identify residents, since these birds may be captured several times in rapid succession and avoid the nets thereafter, thus not reappearing in the data set after the necessary time interval has elapsed.

An additional issue is the relationship between annual recapture probability and netting frequency. Increasing recapture probability increases the precision of survival estimates, as does increasing the number of samples (Pollock et al. 1990). For the purpose of estimating interannual survivorship, however, an entire season represents a single sample, regardless of netting frequency. Increasing netting frequency undoubtedly does increase recapture probability, but the exact relationship between these two variables has not been examined across a broad spectrum of sites. Increasing netting frequency certainly does not proportionately add adult birds to the catch.

A more formal approach to the study of net avoidance, but beyond the scope of this paper, would be to

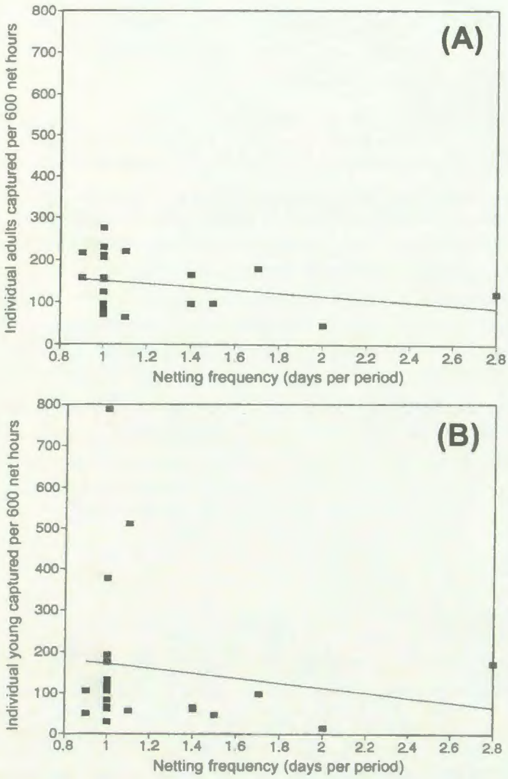

FIGURE 4. Rates of first capture of (a) adults and (b) young vs. netting frequency at 22 MAPS stations in scrub habitats in 1992. (a) r = 0.25, slope = –35.4; (b) r = 0.14, slope = –58.2.

estimate within-year recapture probabilities. Such an approach has been used in closed population estimation models that allow for capture probability to vary by response to capture (Otis et al. 1978), but to our knowledge has not been used to assess the effects of sampling frequency. Such a study could be done on a station-by-station basis, using only a single species or group of related species and a set of stations in similar habitat operated at various frequencies, and it would need to be limited to resident individuals.

Ultimately, the optimum frequency at which to operate a constant-effort mist-netting station will be determined by the specific objectives of the project and the resources available. Data from stations operated at varying frequencies can be combined for large-scale analyses, provided those from stations operated on multiple days per period are adjusted appropriately. In general, however, additional effort, when possible, likely will be more valuable to large-scale monitoring programs if used for establishment of additional stations nearby in similar habitat, rather than repetition. Increasing the number of stations providing data and standardizing the effort expended at these stations will increase the precision and reliability of regional monitoring indices and estimates. Furthermore, clusters of similar stations may provide valuable dispersal and philopatry information, as well as giving more accurate pictures of local conditions and trends.

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MONITORING PRODUCTIVITY WITH MULTIPLE MIST-NET STATIONS

C. John Ralph, Kimberly Hollinger, and Sherri L. Miller

Abstract. We evaluated data from 22 mist-net capture stations operated over 5 to 13 years in northern California and southern Oregon, to help develop sampling designs for monitoring using mist nets. In summer, 2.6% of individuals were recaptured at other stations within 1 km of the original banding station, and in fall, 1.4% were recaptured nearby. We recommend that stations be established 1–5 km apart to promote independent sampling. Percent of young birds in the total captured was similar among stations, both in summer and fall, indicating that large numbers of stations might not be necessary to sample age structure for an entire region, at least for common species. We examined the percent of young captured in fall and summer to determine whether some stations consistently captured lower proportions of young across all species, and found no consistent pattern. Power analysis indicated that about 10 stations were required to detect a 50% change in percent young between years for the Song Sparrow (*Melospiza melodia*), a common species. To detect a 25% change, 10 stations still sufficed in fall, but about 3× more were required in summer. Summer results were similar for the Yellow-breasted Chat (*Icteria virens).* More stations would be needed to reach similar precision targets for uncommon species, and probably also in regions of more heterogeneous habitat. Although the capture rates at stations in our region increased during the study, the capture rates at individual stations declined significantly after the first year of operation.

Key Words: bird, migration, mist net, monitoring, productivity.

Constant-effort mist netting can be used to estimate population composition, species abundance, and demographic parameters such as survivorship and productivity. Coupled with habitat surveys and trend analyses, demographic monitoring has been suggested as a necessary minimum for meeting the monitoring obligations of various resource-management agencies, and for interpreting differences in bird abundance among habitats and over time (e.g., Butcher 1992, Manley 1993). Central to planning and execution of monitoring with mist netting is knowledge of the number of stations necessary to characterize population parameters for a region or a habitat.

Determining the number of netting stations needed to most efficiently monitor birds in a target region requires a balance between effort and the power of the results. If stations produce relatively uniform results, few stations will be needed, as long as sample size requirements can be met. For example, Bart et al. (1999) found that 7 stations could monitor productivity in Kirtland's Warbler (*Dendroica kirtlandii*), using the proportion of young in the total catch as the index of productivity, but the study took place in uniform habitat, for a single species, and in a small area. By contrast, Peach et al. (*this volume*) found that for 17 of 23 species captured, 40–70 netting stations were required to detect annual changes across England with precision of 5% mean standard error. Number of stations required for monitoring productivity at a target level of precision may also differ between the summer season and fall, when more migrants than summer residents are captured.

In this paper, we examine the number of stations needed to sample productivity in summer and fall, in an area approximately 25–50 km in radius and sampled in reasonably homogenous habitat. We also analyzed data from a dense configuration of stations in a larger region of northwestern California and southern Oregon, most established since 1992 to monitor the birds of the region. Our stations were established in riparian habitats along river and stream corridors, and near mountain meadows. We were interested in monitoring permanent and summer residents, as well as migrants, and in monitoring the very important post-breeding period of late summer and fall.

Specifically, this paper addresses the following questions:

(1) To what degree do nearby stations share the same individuals? If movement rates among stations are relatively high, such that nearby stations capture a high number of the same individuals, then stations must be located farther apart to achieve statistical and biological independence of samples.

(2) How much variation is there in percent of young within and among stations? If stations are similar to each other in their percent young, then fewer stations may be needed to provide a good estimate of annual changes in productivity for the region.

(3) How many stations are needed in a region to detect a specific change in our demographic measure of productivity, percent of young?

(4) Is there a consistent effect of year-of-operation on capture rate, which could affect interpretation of trend results?

METHODS

With several cooperators, we established 34 constant-effort stations in northwestern California and southern Oregon, in what is referred to as the Klamath-Siskiyou bioregion. A sub-set of 22 stations with the most similar operating years, schedules, and effort was selected for the analyses presented here (Table 1, Fig. 1). Stations were located along the Klamath River and its tributaries, the major riparian corridors of northwestern California, as well as some nearby rivers. All stations were located in riparian areas bordered by coniferous forests; on the main stem of a river, on a tributary, or in upper elevation meadow–riparian areas. Two coastal stations were in riparian areas within the coast redwood (*Sequoia sempervirens*) zone, and two were along the riparian margin of a coastal pine (*Pinus contorta*) forest.

At each station, 10–12 mist nets were operated during the breeding season, and usually during fall migration as well. Nets were placed in the same locations each year. Except for two stations (HOME and PARK), each station was consistently operated one day during each 10-day period beginning in early May and continuing to the end of August (defined here as the breeding season). During September and October (our definition of the fall migration season), nets were operated once per week. Since 1992, the HOME station has been operated during the breeding season twice every 10 days and in the fall for 3 days a week (usually with at least 1 day between sessions). PARK station was operated during the breeding season once every 10 days, and in the fall for 2 days a week. Regardless of season, nets were opened at all stations from within 15 min of dawn and operated for five hours, weather permitting. Other net operations and processing of birds followed the guidelines in Ralph et al. (1993) and Hussell and Ralph (1998).

Most analyses in this paper included data for the most frequently-captured species; 14 in summer, and 12 in fall (Table 2). The dates defined above for these seasons cover the majority of the breeding and migration seasons of the species involved. However, in many species, at least a proportion of the population does migrate earlier than September. Stations used for each analysis varied (Table 1). Because the effort was similar at all stations, except where otherwise indicated, we did not weight stations in the analyses according to effort.

To determine whether stations close together were sampling the same local population (and therefore not collecting independent samples), we determined the percent of individuals captured between stations as a function of distance. We confined this analysis to eight of the closest stations (analysis A in Table 1).

We used the percent of young of the total of birds captured as an index to productivity. Stations used for this analysis (analysis B in Table 1) represent an area of about 120,000 ha, near the average size of a Forest Service District in the national forests of the Klamath River region. For some of the stations operated for five or more years during the period of 1992–2001, we computed the average annual percent young for each species in summer and fall. To test for differences of the average percent young among stations, we used ANOVA and Duncan's multiple range test (Zar 1984).

To test whether annual percent young was consistently low or high at a given station across species, we calculated an index of productivity for each station. We first calculated the range of percent young for each species over the years of the study period at that station, then calculated an index representing the annual percent young relative to the range of percentages of young of that species captured at that station. For example, if the range for Black-headed Grosbeaks (scientific names of all species are in Table 2) was 25–75% over 10 years at a station, and the percent young in a given year was 65%, 10% lower than maximum value, the relative value for that species at that station was 0.80 (= 1 – (0.10 / (0.75–0.25))). We used a General Linear Model (SAS Institute 1996) to compare the means of these relative percent young by species over all the years when the species was captured (in some years at some stations a species may not have been captured).

We estimated the power of detecting a change in the proportion of young in the total number of birds captured ($\hat{d}$), by species and season (analysis C in Table 1), for two common riparian species, Song Sparrow and Yellow-breasted Chat. We tested for differences in percent young $H_0: d = 1$ vs. $H_1: d \neq 1$ (Cochran 1977), for all pairs of years from 1992 to 1995. We estimated the power of detecting a 50% (d = 0.5 or 1.5) or 25% (d = 0.25 or 1.25) decrease or increase, over a range of sample sizes (number of stations) from one to 50.

To determine if capture rate at a station changed according to year of operation, we compared annual capture rates for the first year of operation (1991, 1992, 1993 or 1994) to the three subsequent years for 17 of the stations (analysis D in Table 1). We used a mixed-effects model (Littell et al. 1996) to estimate the structure of capture rates with year of operation (Year 1, Year 2, Year 3 or Year 4) and capture year (1991–1997), testing capture year both as a categorical and as a continuous variable. We used Tukey-Kramer test for multiple pairwise comparisons of capture rates by years and by year of operation. Station was the random effect in the model, and we accounted for potential serial correlation among years assuming an autoregressive correlation structure (SAS Institute 1996).

RESULTS

INDEPENDENCE OF STATIONS

For the stations less than 1 km apart, 2.6% of individual birds were recaptured at another station in the summer, and 1.4% in fall (Table 3). At stations more than 1 km from the original capture stations, in both

TABLE 1. MIST-NET CAPTURE STATIONS, THE ANALYSES IN WHICH THE STATION'S DATA WERE USED, NUMBER OF NETS, THE YEARS OPERATED, AND SEASONS OF OPERATION (S = SUMMER, F = FALL).

Station	Operator	Analyses[a]	N nets	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Aiken's Creek (AKEN)	Redwood Sciences Laboratory	A	10	S	–	–	–	–	–	–	–	–	–
Antelope Creek (ANT1)	Klamath National Forest	D	10	–	–	S,F	S,F	S,F	S,F	S,F	S,F	S,F	–
Big Bar (BBAR)	Trinity National Forest	B	12	S,F	S	S,F	S	S,F	S	–	–	–	–
Bondo Mine (BOND)	Redwood Sciences Laboratory	A, B, C, D	10	S	S	S	S	S	–	–	–	–	–
Camp Creek (CAMP)	Redwood Sciences Laboratory	A, B, C, D	10	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
Red Cap Creek D (CAPD)	Redwood Sciences Laboratory	A, B, C, D	13	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
Carberry Creek (CARB)	Rogue River National Forest	D	10	–	S,F	S,F	S,F	S,F	S	–	–	–	–
Emmy's Place (EMMY)	Redwood Sciences Laboratory	D	10	–	–	S,F	S,F	S,F	S,F	–	–	–	–
Grayback Creek (GBCR)[b]	Siskiyou National Forest	D	8	S	S	S	S	S	S	S	S	S	–
Grove's Prairie (GROV)	Redwood Sciences Laboratory	D	10	–	–	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
HBBO HQ (HOME)	Humboldt Bay Bird Observatory	A	17.5	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	–
Indian Valley (INVA)	Redwood Sciences Laboratory	D	10	–	–	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
Delaney Farm (LADY)	Redwood Sciences Laboratory	A, B, C, D	10	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
Long Ridge (LORI)	Siskiyou National Forest	D	10	S	S	S	S	S	S	–	–	–	–
Molier (MOLI)	Redwood Sciences Laboratory	A, B, C, D	12	S	S	S	S	S	–	–	–	–	–
DeMello pasture (PARK)	Humboldt Bay Bird Observatory	A	14	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F	–
Pacific Coast Trail 1 (PCT1)	Klamath National Forest	B, D	13	–	S,F	S,F	S,F	S,F	S,F	S,F	S,F	–	–
Redwood Creek (RECR)	Redwood Sciences Laboratory	D	11	–	–	S,F	S,F	S,F	S,F	S,F	S,F	S,F	S,F
Red Cap Creek 2 (RED2)	Redwood Sciences Laboratory	A, B, C, D	13	S,F	S,F	S,F	S,F	S,F	–	–	–	–	–
Whitmore Creek (WHIT)	Redwood Sciences Laboratory	A	10	S	–	–	–	–	–	–	–	–	–
Wright Refuge (WREF)	Humboldt State University	D	10	–	S,F	S,F	S,F	S	S	–	–	–	–
Yager Creek (YACR)	Pacific Lumber Company	D	12	–	–	S,F	S,F	S,F	S	S	S	S	S

Notes: "–" denotes no data were taken.

[a] Stations used in each analysis: A = Independence between stations from movement among stations (includes all years); B = Variation in percent young among stations and years (1992–1995); C = Number of stations needed to detect declines in productivity (includes years 1992–1995); D = Effect of running nets on capture rate (includes summer data from first four years of operation – years used indicated with underline).

[b] This station was also operated in the summer of 1991.

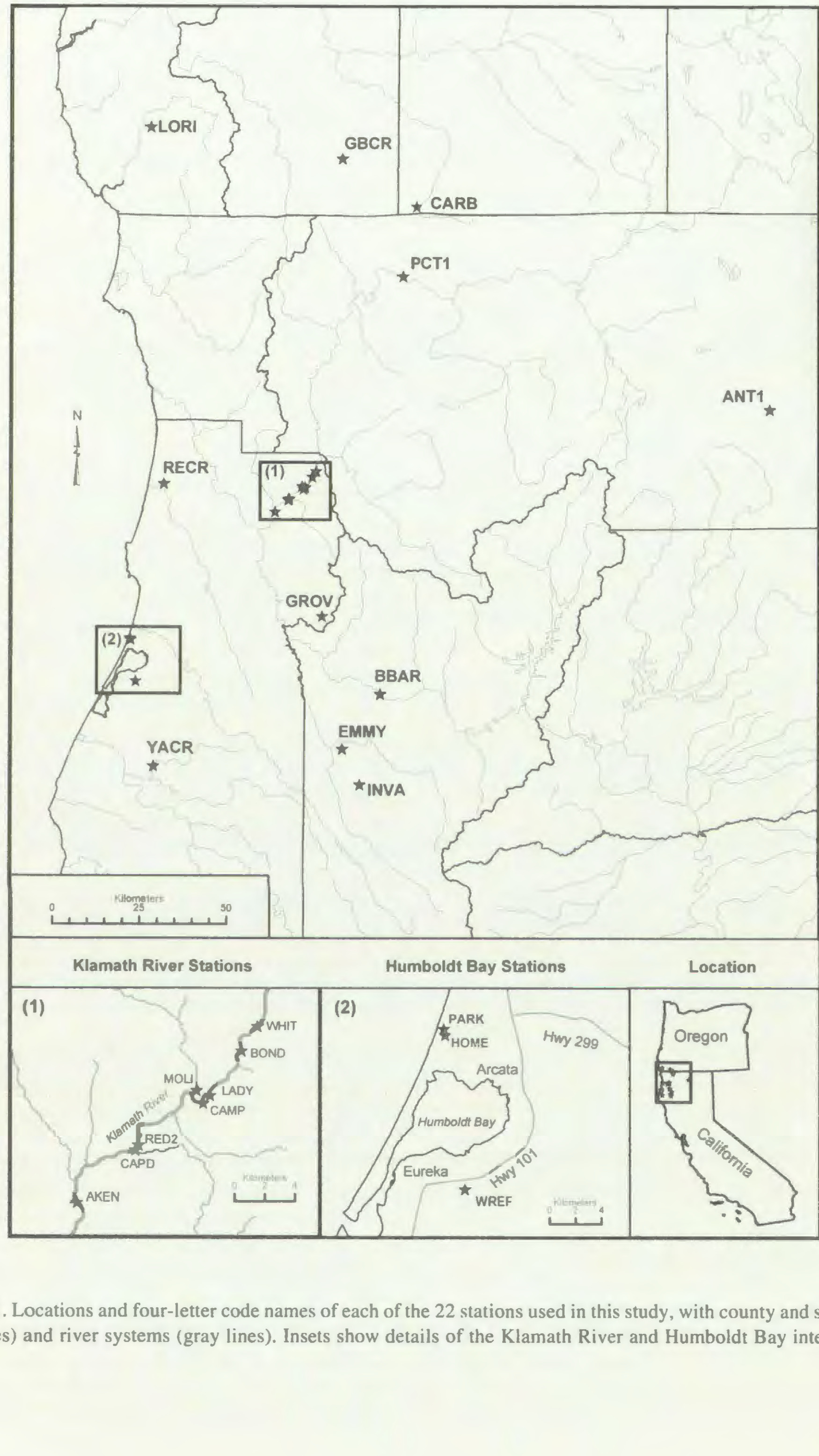

FIGURE 1. Locations and four-letter code names of each of the 22 stations used in this study, with county and state borders (black lines) and river systems (gray lines). Insets show details of the Klamath River and Humboldt Bay intensive study areas.

TABLE 2. SPECIES USED IN THE ANALYSES FOR EACH SEASON

Code	Species	Summer	Fall
WIFL	Willow Flycatcher (*Empidonax trailii*)	X	X
PSFL	Pacific-slope Flycatcher (*E. difficilis*)	X	
BUSH	Common Bushtit (*Psaltriparus minimus*)	X	
RCKI	Ruby-crowned Kinglet (*Regulus calendula*)		X
SWTH	Swainson's Thrush (*Catharus ustulatus*)	X	X
HETH	Hermit Thrush (*C. guttatus*)		X
AMRO	American Robin (*Turdus migratorius*)		X
VATH	Varied Thrush (*Ixoreus naevius*)		X
WREN	Wrentit (*Chamaea fasciata*)	X	X
OCWA	Orange-crowned Warbler (*Vermivora celata*)	X	
YWAR	Yellow Warbler (*Dendroica petechia*)	X	
MYWA	Myrtle Warbler (*D. coronata*)		X
MGWA	MacGillivray's Warbler (*Oporornis tolmiei*)	X	
WIWA	Wilson's Warbler (*Wilsonia pusilla*)	X	
YBCH	Yellow-breasted Chat (*Icteria virens*)	X	
WETA	Western Tanager (*Piranga ludoviciana*)	X	
SPTO	Spotted Towhee (*Pipilo maculatus*)	X	X
FOSP	Fox Sparrow (*Passerella iliaca*)		X
SOSP	Song Sparrow (*Melospiza melodia*)	X	X
GCSP	Golden-crowned Sparrow (*Zonotrichia atricapilla*)		X
BHGR	Black-headed Grosbeak (*Pheucticus melanocephalus*)	X	

seasons, the number of birds recaptured was $\leq 0.5\%$, indicating that stations more than 1 km apart were collecting largely independent samples.

CONSISTENCY IN PERCENT OF YOUNG AMONG STATIONS

Percent of young differed little among stations for most species in summer (Table 4). Six of the stations were quite close together, in similar riverine–riparian habitat, and had statistically indistinguishable percents of young. Two more distant stations (BBAR and PCT1) appeared to have lower percents of young for some species (Table 4). However, each of these stations also had the highest percent young for at least one species. Two resident species, Wrentit and Song Sparrow, tended to have more variable percents of young among stations than did the other species, most of which are migratory.

In the fall, percent young was more consistent among stations than during the summer (Table 5). However, for five species, the BBAR station had significantly different percent young than the other stations.

TABLE 3. PERCENT OF INDIVIDUALS CAPTURED AT A STATION LOCATION OTHER THAN WHERE PREVIOUSLY CAPTURED, 1992–2001

Distance between capture and recapture locations	Summer		Fall	
	Total captures	Percent recaptured	Total captures	Percent recaptured
< 1.0 km	5646	2.65	5243	1.39
≥ 1.0 ≤ 5.0 km	4326	0.46	1924	0.10
≥ 5.1 ≤ 10.0 km	3719	0.22	1142	0.09
≥ 10.1 ≤ 17.5 km	1483	0.20	0	–

We did not find a pattern in standardized percent young that would indicate consistently low or high productivity across years at some stations (all target species combined; Table 6). BBAR was consistently lowest in percent young in summer across all years, although the difference was significant in only one year. In the fall, CAPD usually had the highest percent young, but this was significantly higher in only one of the years.

A station with the highest percent young in one year did not necessarily have the highest in other years. The percent young was indistinguishable across all stations in the summers of 1992 and 1995, and in the falls of 1993 and 1995. However, in the summer of 1993, three stations had fewer young than the other stations. In summer 1994, stations were evenly divided, with some stations having higher percents of young and others having lower percents.

NUMBER OF STATIONS NEEDED TO DETECT ANNUAL CHANGES IN PRODUCTIVITY

Power analysis showed that for the Song Sparrow, 10 stations were required in summer to detect a 50% change in percent young between years with a 0.95 probability and a significance level of 0.05 (Table 7). The number of stations required to detect a 25% change at the same level of probability is three times as large, at 32 stations. In the fall, when percent young was more consistent among stations, only four stations were needed to detect a 50% change, and 10 to detect a 25% change. Summer data for the much-less common Yellow-breasted Chat gave similar results (Table 7; this species is not captured in fall). With 10 stations, the probability of detecting a 50% change in percent young between years was

TABLE 4. PERCENT OF YOUNG (SUMMER) AVERAGED OVER 10 YEARS (1992–2001)

	Station							
Species code	BBAR	BOND	CAMP	CAPD	LADY	MOLI	RED2	PCT1
PSFL	88.8	76.4	49.6	73.0	70.2	66.3	72.8	47.6
	A[a]	AB	B	AB	AB	AB	AB	AB
WIFL	93.3	85.3	84.0	80.7	77.6	94.7	78.7	46.1
	A	A	A	A	A	A	A	B
BUSH	50.9	79.2	0	94.5	100	–	60.0	65.8
	AB	AB	B	A	A	–	AB	AB
WREN	100.0	71.8	58.9	76.1	65.2	64.6	73.1	79.2
	A	BC	C	BC	C	C	BC	AB
SWTH	58.3	44.5	37.3	31.2	18.2	21.8	32.8	23.8
	A	AB	B	B	B	B	B	B
OCWA	21.3	30.6	33.2	48.5	51.0	74.0	59.7	19.5
	B	B	B	AB	AB	A	AB	B
MGWA	3.9	39.7	31.0	42.9	40.2	39.5	35.9	35.6
	B	A	AB	A	A	A	AB	AB
WIWA	1.8	53.6	32.1	61.4	59.3	67.5	60.9	2.9
	B	A	AB	A	A	A	A	B
YWAR	16.6	55.0	17.6	56.5	36.2	38.3	33.3	32.6
	A	A	A	A	A	A	A	A
YBCH	25.8	39.4	49.2	44.1	30.4	34.2	28.2	44.5
	A	A	A	A	A	A	A	A
WETA	52.6	63.7	54.9	75.5	61.8	54.2	68.3	77.8
	A	A	A	A	A	A	A	A
BHGR	13.3	75.2	58.8	69.6	62.2	69.8	68.4	60.3
	B	A	A	A	A	A	A	A
SPTO	67.6	70.1	61.8	74.2	66.9	70.1	81.0	72.6
	A	A	A	A	A	A	A	A
SOSP	61.5	68.9	54.0	70.7	35.9	50.2	56.9	68.0
	ABC	A	ABC	AB	C	BC	ABC	AB

Note: Species codes are explained in Table 2.

[a]Stations with the same letter are not significantly different in average percent young (ANOVA, Duncan's multiple range test, $P > 0.05$).

0.97, and 29 stations were needed to detect a 25% change with 0.95 probability.

CHANGE IN CAPTURE RATE ACCORDING TO YEAR OF OPERATION

We compared capture rates in the first and subsequent three years of station operation to test the assumption that there is no effect of year of operation on capture rates. When capture rate was calculated by the year of operation (i.e., Year 1, Year 2, Year 3 and Year 4) for all 17 stations combined, there was a noticeable (>20%) decline after Year 1 (Table 8). However, many stations were established in the same years, so the decline could have been related to differences in bird abundance among years. To determine if the decline was significant, and related to initiation of the mist-net station or simply a difference in bird abundance, we examined two models: year of operation and capture year as categorical variables and then as continuous variables. Both year of operation and capture year had significant effects on capture rates, in both models (year of operation: categorical, $F = 6.81$, $P = 0.002$, continuous, $F = 11.65$, $P = 0.003$; capture year: categorical, $F = 2.52$, $P = 0.043$, continuous, $F = 6.63$, $P = 0.021$). The predictability of the alternate models, as measured by the estimated variance of a single prediction, was similar. The AIC_c value was considerably lower for the categorical model, 760.4 vs. 845.3, indicating the categorical model was a better fit to the data.

Capture rate at the 17 stations generally increased from 1991 to 1997, with stations that began operation later in the period tending to have higher captures rates. At each individual station, however, capture rates declined after the first year. The mean capture rate averaged over all 17 stations for the first

TABLE 5. PERCENT YOUNG (FALL) OF THE MOST COMMON SPECIES CAPTURED OVER 10 YEARS (1992–2001)

	Station					
Species codes	BBAR	CAMP	CAPD	LADY	RED2	PCT1
WIFL	100.0	97.1	96.7	89.1	96.0	100.0
	A[a]	A	A	A	A	A
RCKI	0.0	35.8	60.7	54.2	20.0	54.8
	A	A	A	A	A	A
SWTH	100.0	67.9	76.5	69.4	74.9	79.9
	A	B	B	B	B	B
HETH	22.9	71.4	78.2	70.8	78.2	78.6
	B	A	A	A	A	A
AMRO	50.0	50.0	75.9	44.1	44.4	49.0
	A	A	A	A	A	A
VATH	0.0	60.6	45.8	66.8	40.0	60.0
	A	A	A	A	A	A
WREN	–	97.5	96.0	94.9	80.6	96.0
	–	A	AB	AB	B	AB
MYWA	–	82.3	94.1	94.0	85.2	86.2
	–	A	A	A	A	A
SPTO	13.9	87.6	86.8	81.4	92.7	85.4
	B	A	A	A	A	A
FOSP	22.9	53.2	69.2	60.8	60.2	72.6
	B	A	A	A	A	A
SOSP	57.8	79.6	71.4	76.6	72.8	82.0
	A	A	A	A	A	A
GCSP	21.4	59.0	57.6	45.6	62.0	62.1
	B	A	A	A	A	A

Note: Species codes are explained in Table 2.

[a]Stations with the same letter are not significantly different in average percent young (ANOVA, Duncan's multiple range test, $P > 0.05$).

year of operation was significantly higher than the capture rate in years 2, 3, and 4.

DISCUSSION

INDEPENDENCE OF STATIONS

Recapture rate between stations >1 km apart was very low. We make the conservative recommendation that stations be established a minimum of 1–5 km apart to approach independence of sampling, while still allowing multiple samples to be collected within an area of relatively homogeneous habitat.

CONSISTENCY IN PERCENT OF YOUNG AMONG STATIONS

If stations in an area are similar in percent of young, then relatively few stations should be needed to sample regional productivity at target levels of precision. The few differences we found between stations in percent young captured in summer seemed to reflect distance from other stations, rather than differences in habitat. Six of the stations used in this analysis (Table 4) were in similar, riverine–riparian habitat, in close proximity on a 12-km section of the main stem Klamath River near Orleans (Fig. 1). The two more distant stations appeared to have, in general, lower productivity. The BBAR station on the Trinity River, a tributary of the Klamath, and PCT1 (109 km upstream along the Klamath River) had the lowest percent young for five of the 14 species analyzed. Together, these two stations accounted for most of the significant differences in percent young among stations. Percents were not consistently low, however, as each of these stations also had the highest percent young for at least one species.

Some resident species had more variable annual percent young than migratory species (Table 4; Wrentit and Song Sparrow), suggesting that there might be real spatial differences in local productivity. It is possible that residents are better able to fine tune their productivity to local conditions, whereas productivity of migrant species might be more affected by wintering ground conditions and factors operating on a broader scale. Variability among stations in percent young for resident species may

TABLE 6. STANDARDIZED PERCENT YOUNG FOR ALL TARGET SPECIES COMBINED, BY STATION AND SEASON, FOR 1992–1995

	Summer				Fall			
Station	1992	1993	1994	1995	1992	1993	1994	1995
BBAR	38.3	17.6	33.2	29.6	63.9	–	20.0	–
	A[a]	D	B	A	AB		C	
BOND	50.1	78.2	47.4	57.7	–	–	–	–
	A	A	B	A				
CAMP	59.4	41.5	38.2	52.8	61.1	37.4	70.0	39.4
	A	DC	B	A	AB	A	AB	A
CAPD	61.2	60.5	86.6	48.6	82.9	61.2	81.2	71.2
	A	AB	A	A	A	A	A	A
LADY	63.3	28.0	50.0	58.4	58.7	58.0	69.4	37.8
	A	DC	B	A	AB	A	AB	A
MOLI	45.7	66.9	64.2	56.2	–	–	–	–
	A	AB	AB	A				
RED2	43.6	68.7	60.1	54.6	32.1	49.4	49.9	43.7
	A	A	AB	A	B	A	B	A
PCT1	–	52.8	39.0	56.7	–	40.0	85.8	70.7
		ABC	B	A		A	A	A

Notes: See Methods for means of standardization. Species codes are explained in Table 2.
[a]Stations with the same letter are not significantly different in average percent young (ANOVA, Duncan's multiple range test, P > 0.05).

TABLE 7. PROBABILITY OF DETECTING ANNUAL CHANGE (DECLINE OR INCREASE) IN THE PERCENT OF YOUNG CAPTURED, WITH A SIGNIFICANCE LEVEL OF 0.05, AMONG KLAMATH RIVER STATIONS

			Probability of detecting	
Species	Season	Number of stations	50% change	25% change
Song Sparrow	Summer	4	0.78	0.37
		6	0.86	0.49
		8	0.91	0.58
		10	0.95	0.65
		32	>0.99	0.95
	Fall	2	0.92	0.58
		4	0.98	0.75
		6	>0.99	0.86
		8	>0.99	0.92
		10	>0.99	0.95
Yellow-breasted Chat	Summer	6	0.72	0.26
		8	0.79	0.33
		10	0.97	0.60
		29	>0.99	0.95

reflect differences in the quality of the immediate and nearby habitats, allowing us to identify source and sink areas. However, Nur and Geupel (1993b) showed that summer mist-net captures reflected local productivity in Song Sparrows, but not Wrentits. In many species, percent young in summer and fall, when dispersers and migrants are being captured, may represent average productivity across the region rather than local productivity at each netting station. In the Klamath network, many species use the riparian habitats during migration, and variability in percent young is low among stations. That fewer stations are needed in fall than in summer to detect annual changes in percent young is an indication that young and adults are distributed among stations in more even proportions during the fall.

TABLE 8. SUMMER CAPTURE RATES OVER THE FIRST FOUR YEARS OF MIST-NET OPERATIONS (17 STATIONS). YEAR 1 RANGED FROM 1991 TO 1994

Year	Mean annual capture rate	SE
1	567.77	29.40
2	440.07	20.72
3	448.99	25.27
4	412.97	23.06

NUMBER OF STATIONS NEEDED TO DETECT ANNUAL CHANGES IN PRODUCTIVITY

For two species in our region, 10 stations were needed to detect a 50% annual change in regional productivity at target precision levels, and about 30 to detect a 25% change (at least in summer). If detecting changes smaller than 25% is of interest, or for detecting similar changes in less common species, a larger number of samples may be required. More stations may also be needed if habitat is more heterogeneous than in our study area.

Here we examined changes in productivity between adjacent years of sampling, both consecutive and non-consecutive years. When additional years of sampling are available, we will examine our power for detecting multi-year trends in productivity.

CHANGE IN CAPTURE RATE IN FIRST AND SUBSEQUENT YEARS

The decline in capture rates following the first year of operation is perplexing. The drop could be due to several causes, including net shyness. The presence of investigators even for as little as one morning in 10 could result in birds avoiding the study area, or, alternatively, learning the location of nets and avoiding them in subsequent years. Net avoidance resulting from long-term memory would result in capture rates suggesting a decline in abundance when none actually occurred. If net shyness was the cause, then decline of captures should be greater in adults than young of the year, so percent young should increase after the first year of operation. This will be tested in future work. It is crucial to that we continue to investigate patterns in capture rate at mist-netting stations that may affect interpretation of monitoring efforts using this technique.

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INFLUENCE OF MIST-NETTING INTENSITY ON DEMOGRAPHIC INVESTIGATIONS OF AVIAN POPULATIONS

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Abstract. We evaluated capture rates of juvenile and adult passerines, comparing two different netting regimes on the same study plot at the Palomarin Field Station, Point Reyes National Seashore, California. One set of nets was run approximately 5× as often as the other during the breeding season. For four resident species breeding in the immediate vicinity of the nets, results were compared to direct measures of productivity and breeding density as determined from nest monitoring, color banding of nestlings, and known densities of adults from spot-mapping censuses of color-banded individuals. Nets run 6 days/week captured an average of 42% of the Song Sparrows (*Melospiza melodia*) breeding within 100 m of the nets, whereas nets run 1 day/week averaged 10%. Capture rates of adult Wrentits (*Chamaea fasciata*) did not differ significantly between netting regimes. Nets run with higher frequency detected direction of change in productivity in Song Sparrows accurately, whereas nets run with lower frequency did not. The reverse was true for Wrentits, though Wrentit fledglings were twice as likely to be caught in the higher frequency nets. Distance from nest to net also influenced juvenile capture probability. Results indicate the importance of using standardized netting protocol, and show that demographic indices based on mist netting should not be directly compared among species. Optimal netting frequency to attain study goals should be evaluated separately for each species. We caution investigators from drawing conclusions regarding songbird population size and demography based on mist-netting data alone.

Key Words: capture probability, *Chamaea fasciata*, demographic monitoring, *Melospiza melodia*, mist netting, passerine, population size, sampling effort, spot mapping, Song Sparrow, Wrentit.

Constant effort mist-netting has been widely used as a method for monitoring breeding populations of passerines (DeSante 1991b, Ralph et al. 1993), although few studies have attempted to validate the technique (but see du Feu and McMeeking 1991; Nur et al. 2000, *this volume*; S. Baillie et al. unpubl. report).

In this paper we compare capture rates in two arrays of mist nets operated with different protocols, established on a plot where spot-mapping and nest-monitoring of color-banded individuals of four species provided an independent measure of population parameters (Lebreton et al. 1992). The two netting regimes differed in both the frequency of netting and the number of nets employed. We examine whether more intensive mist-netting effort leads to more accurate estimates of population size, productivity, and survivorship.

The use of mist nets to estimate the size of a breeding population requires knowledge of the likelihood of capture of adults (Jenni et al. 1996, Sauer and Link *this volume*). Capture likelihood could vary with many factors, including bird species, distance of territory to nets, number of intervening territories, year, and netting intensity (Nur et al. *this volume*). Here we compare capture rates of adults of four species for individuals known to be breeding within 100 and 200 m of each set of nets in each year.

Another important variable for estimating population size is the breeding status of individuals that are caught. Nur and Geupel (1993b) found that varying percent of breeding season captures consisted of transient individuals that did not breed on the study area, and Nur et al. (*this volume*) found that most Wrentits (*Chamaea fasciata*) captured during the breeding season were not territory holders. Whether or not an individual is recaptured at least once within a season has been used as a means of separating transients from local breeders (Peach 1993, Chase et al. 1997, Gardali et al. 2000). We compare within season recapture rates of known breeders between the two netting regimes.

If mist nets recapture sufficient numbers of individuals from one year to the next, the data may be used in adult survivorship calculations (Clobert et al. 1987, Nur et al. 1999). Knowledge of adult survivorship is important to understanding population dynamics. We examine recapture rates of breeders known to have bred in 1992 that returned to breed on the study plot in 1993, for each netting regime and study species.

Finally, mist netting can be used to estimate productivity of breeding populations (DeSante and Geupel 1987, DeSante et al. 1993, Nur et al. 2000). Capture rates of hatch year (HY) individuals are often assumed to be an index of annual productivity. However, due to variation in natal dispersal strategies and catchability of juveniles produced from nests close to nets, the area being sampled is difficult or impossible to determine (Baker et al. 1995). We compare numbers of HY individuals caught with each netting regime to numbers known to have been produced on the study plot, and we determine the proportion of individuals produced locally and subsequently caught in each netting regime.

METHODS

Field work was conducted on a 36-ha plot at the Palomarin Field Station in the Point Reyes National Seashore in central coastal California. Densities of Song Sparrows (*Melospiza melodia*), Wrentits, Spotted Towhees (*Pipilo maculatus*), and Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) were determined by almost daily spot-map censusing throughout the breeding season (mid-March to July 31). These four species are obligate coastal scrub breeders at Palomarin; that is, 90% of their territories are located in scrub habitat as opposed to in adjacent forested habitats (Geupel and Ballard 2002; Point Reyes Bird Observatory [PRBO], unpubl. data). We located and monitored most nests of the study species, as described by Geupel and DeSante (1990) and Martin and Geupel (1993). In summary, we individually color-banded all nestlings surviving until their primaries broke sheath (usually a few days before fledging). Nestlings missing from the nest after banding were presumed fledged unless there was evidence of depredation. We recorded each nest's location, and its distance from the nearest mist net in each of the two net arrays. Further description of the study site and methods have been provided elsewhere (DeSante 1981, Geupel and DeSante 1990, Johnson and Geupel 1996, Nur et al. *this volume*).

Two arrays of 12-m mist nets were run with different frequency during the summers (May 1 to August 18) of 1992 and 1993 (Fig. 1). One array (the "daily nets") consisted of 20 nets placed relatively close together at 14 sites (6 were stacked 2 high), situated near the southeastern edge of the study area close to the border of coastal scrub and mixed evergreen forest (DeSante and Geupel 1987, Johnson and Geupel 1996). These nets were run at least 6 days/week during both breeding seasons. The other array (the "weekly nets") consisted of 10 nets at ten sites spaced at maximum distances for safe operation (usually 5–20 m), situated in the center of the study area in continuous coastal scrub habitat. These nets were operated once and occasionally twice in 10 days through both breeding seasons. Captured birds were aged by combination of skull pneumatization and plumage characteristics (Pyle et al. 1987). Unbanded birds were given new bands. Netting effort was consistent for the two years of the study. Nets were made by Avinet (Dryden, New York), and were 36- and 30-mm mesh.

We evaluated the differences between netting regimes using log-likelihood tests (G-test) or Fisher's exact tests, depending on sample size (we used the latter where sample size was small). Results were considered significant if $P < 0.05$. We used logistic regression to model the effect of distance from nest to nearest net on capture probability.

RESULTS

Capture Rates of Adults

The weekly nets captured 10% of adult Song Sparrows breeding within 100 m of nets, significantly fewer than the daily nets, which captured 42% (G-test, controlling for year, $G = 7.22$, $df = 1$, $P = 0.007$) (Table 1, Fig. 2). For Wrentits, the netting regimes did not differ significantly, with 42% of those breeding within 100 m captured in the daily nets and 36% in the weekly nets ($G = 0.15$, $df = 1$, $P = 0.69$). There was no significant change in the proportion of breeders captured when we extended the distance to include all breeders within 200 m. No Wrentit breeding more than 150 m from either set of nets was captured (Fig. 2).

Within-season Recapture Rates of Adults

Song Sparrows were more likely to be caught twice or more within a season in the daily nets than in the weekly nets (Table 2). In fact, no Song Sparrows at all were recaptured in the weekly nets (Fisher's exact test, pooling years, $P = 0.025$). The

Table 1. Capture rates for breeders nesting at different distances from nets, comparing daily to weekly nets

			Breeders within 100 m			Breeders within 200 m		
				Captured			Captured	
Species	Netting intensity	Year	Number present	Number	Percent	Number present	Number	Percent
Song Sparrow	Daily	1992	13	5	39	22	6	27
		1993	9	4	44	23	4	17
	Weekly	1992	18	2	11	49	3	6
		1993	13	1	8	37	1	3
Wrentit	Daily	1992	18	6	33	32	6	19
		1993	12	6	50	30	7	23
	Weekly	1992	50	20	40	66	20	30
		1993	45	14	31	65	17	26

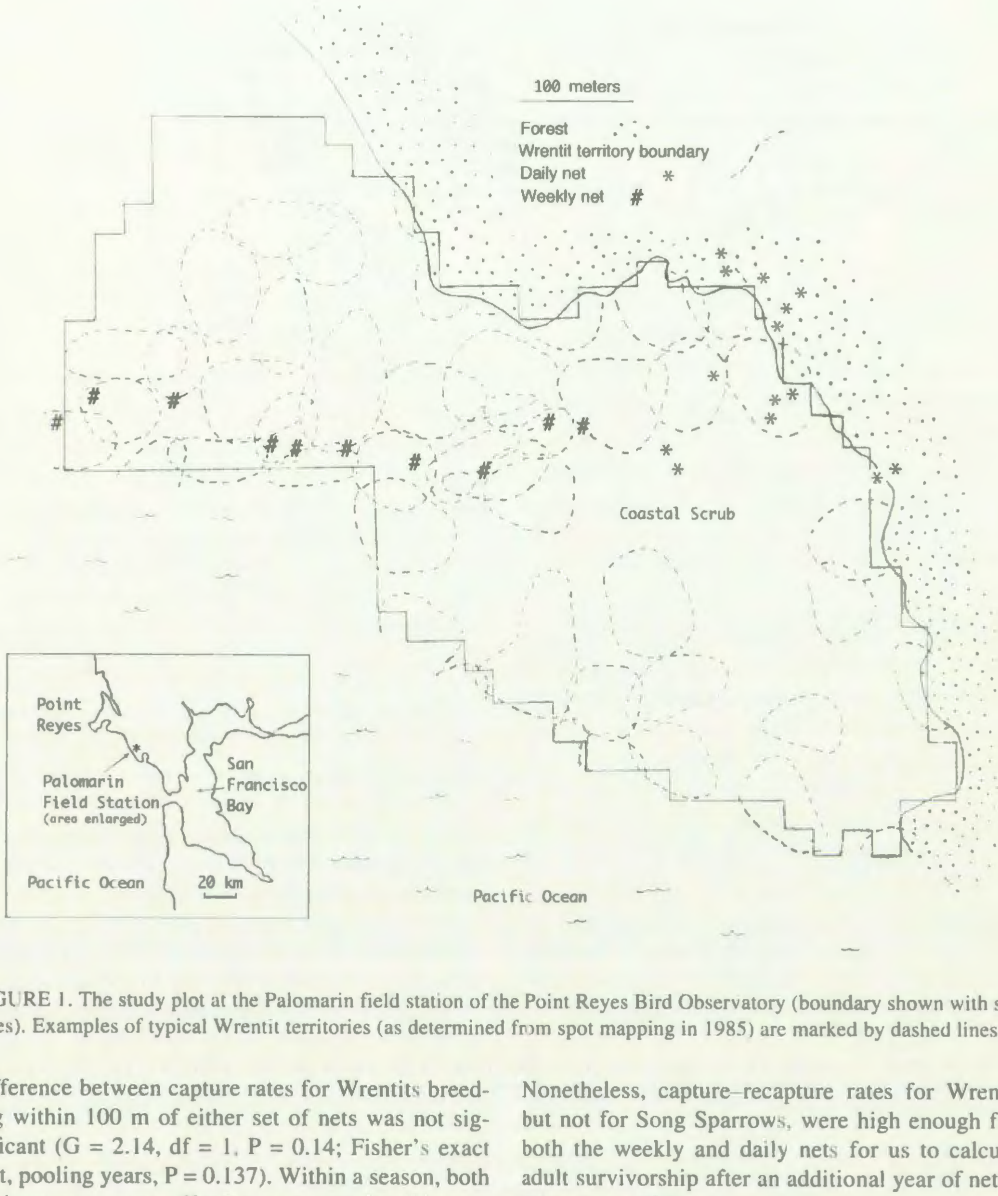

FIGURE 1. The study plot at the Palomarin field station of the Point Reyes Bird Observatory (boundary shown with solid lines). Examples of typical Wrentit territories (as determined from spot mapping in 1985) are marked by dashed lines.

difference between capture rates for Wrentits breeding within 100 m of either set of nets was not significant (G = 2.14, df = 1, P = 0.14; Fisher's exact test, pooling years, P = 0.137). Within a season, both regimes were more effective at recapturing Wrentits than Song Sparrows.

Between-year Recapture Rates of Adults

The daily nets caught more returning Song Sparrows than did the weekly nets, which recaught none (P = 0.044; Table 3). The daily nets caught fewer returning Wrentits than the weekly nets, but this difference was not significant (P = 0.668). Thus, for Song Sparrows, but not for Wrentits, between-year capture rates declined as netting frequency declined. Nonetheless, capture–recapture rates for Wrentits, but not for Song Sparrows, were high enough from both the weekly and daily nets for us to calculate adult survivorship after an additional year of netting (Nur et al. 1999).

Capture Rates of HY Birds Compared to Number Fledged

For Song Sparrows, the capture rates of hatching year birds in the daily nets reflected a decrease in productivity between 1992 and 1993, showing an 11% decrease in HY birds/100 net-h, and thus matched the change in productivity known to have taken place over the entire study plot (–13%), but underestimated the change for birds nesting within

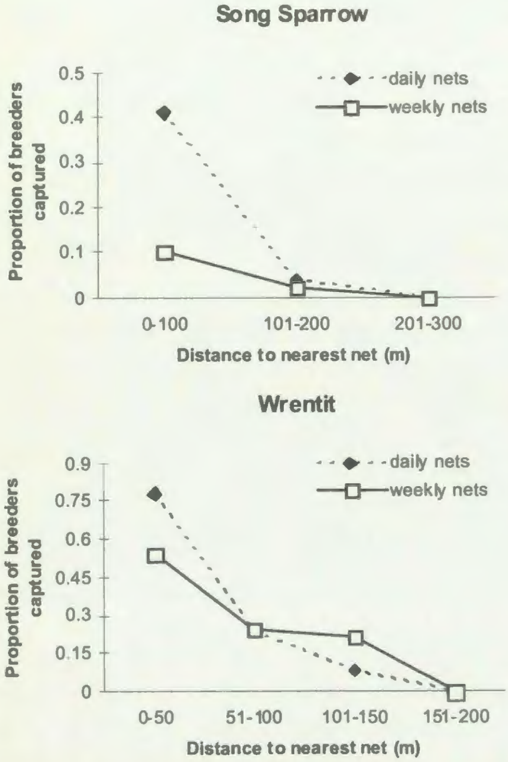

FIGURE 2. Recapture rates of adult breeding Song Sparrows and Wrentits related to distance from nest or territory center to nearest mist net.

200 m of nets (–28%; Table 4). Capture rates in the weekly nets failed to track the number of nestlings known to have fledged at either distance from nets. In fact, capture rates went up whereas the number fledged went down.

For Wrentits, capture rates in the daily nets did not reflect productivity changes at any distance, showing a 32% decrease in HY birds caught/100 net-h between 1992 and 1993 whereas known productivity went up 39% overall, and up 20% within 200 m of nets. The weekly nets performed better; capture rates went up 21% whereas total number fledged on the study plot went up 39%, though within 200 m they went up by 98%. Thus, whereas capture rates

TABLE 2. PROPORTION OF BREEDERS WITHIN 100 M OF THE NETS THAT WERE CAUGHT MORE THAN ONCE PER YEAR, 1992 AND 1993, COMPARING DAILY TO WEEKLY NETS

Species	Netting intensity	Year	Breeders	Captured > once	Percent
Song Sparrow	Daily	1992	13	2	15
		1993	9	2	22
	Weekly	1992	18	0	0
		1993	13	0	0
Wrentit	Daily	1992	18	3	17
		1993	12	4	33
	Weekly	1992	50	9	18
		1993	45	2	4

in the weekly nets reflected the general direction of productivity change on the study plot, they did not reflect the magnitude of this change, particularly for Wrentits breeding closer to the nets.

CAPTURE RATES OF FLEDGLINGS PRODUCED ON THE STUDY PLOT

Compared to weekly nets, the daily nets caught significantly more locally produced White-crowned Sparrows ($G = 8.65$, $P = 0.003$) and Song Sparrows ($G = 20.12$, $P < 0.001$), and more (but not significantly more) Spotted Towhees and Wrentits (Table 5). For White-crowned Sparrows and Song Sparrows, the ratio of captures was about 5 to 1 (daily vs. weekly), similar to the ratio in netting frequency. For Spotted Towhees, the ratio was 2.5 to 1, and for Wrentits, only 1.17 to 1 (i.e., 17% more HY birds were caught in the daily nets compared to the weekly nets).

The number of fledglings captured was biased somewhat by differing distributions of breeding birds in relation to the different netting regimes. That is, the weekly nets were located closer to higher bird densities, especially for Wrentits. Using logistic regression to control for the effect of proximity, the predicted capture probability of a Wrentit fledged 100 m from the daily nets (combining both years) was 0.35. For the weekly nets it was 0.17 (Table 6). This difference was significant ($P < 0.01$). Thus, the daily nets were approximately twice as likely as the

TABLE 3. RETURN RATES OF BANDED BREEDERS NESTING WITHIN 100 M OF THE NEAREST NET, COMPARING DAILY TO WEEKLY NETS

	Daily nets			Weekly nets		
Species	Number returning	Number captured	Percent captured	Number returning	Number captured	Percent captured
Song Sparrow	6	3	50	9	0	0
Wrentit	7	2	29	19	8	42

TABLE 4. DETECTING PRODUCTIVITY WITH DAILY AND WEEKLY NETTING

Species	Netting intensity	Year	HY birds captured	Number/ 100 net-h	Number fledged	
					In study plot	<200m
Song Sparrow	Daily	1992	77	0.75	76	21
		1993	66	0.67	66	13
Percent change				-11%	-13%	-28%
	Weekly	1992	16	1.40	76	47
		1993	13	1.67	66	43
Percent change				+19%	-13%	-9%
Wrentit	Daily	1992	77	0.75	86	24
		1993	51	0.52	120	29
Percent change				-32%	+39%	+20%
	Weekly	1992	41	3.60	86	45
		1993	34	4.35	120	89
Percent change				+21%	+39%	+98%

weekly nets to catch Wrentits fledged 100 m from the closest net. There were too few captures to carry out similar analyses for other species.

DISCUSSION

We demonstrated important differences in capture rates among species and netting strategies, which argue against drawing conclusions regarding adult survivorship, breeding population size, or productivity from mist-netting data alone. For one species, increased effort increased the proportion of the actual breeding population sampled, whereas for another this was not true. Increased effort increased proportion of the locally produced young captured in all four species evaluated, but not to the same extent. There was also substantial annual variation in these parameters, as N. Nur and G. Geupel (unpubl. report), using the same daily nets in the period 1980–1991, found that 71% (versus our 17 to 33%) of Wrentit breeders were caught more than once within a given year. Given this level of annual variation in capture probability, the importance of standardization of techniques among years and study sites cannot be overstated.

Numerous factors have been shown to affect capture rates, and these should be expected to vary among species. For example, differences in post-fledging movement may have been responsible for our low capture rates in weekly nets for locally fledged sparrows, but not Wrentits. Song Sparrows have higher dispersal distances and tend to be less sedentary than Wrentits (Nur and Geupel 1993b; PRBO, unpubl. data). It is likely that young Song Sparrows range farther from their natal territories and do this relatively abruptly, therefore spending less time in the vicinity of mist nets that intersect their territories (Nice 1937). Wrentit juveniles have been observed to stay with family groups near their natal territory an average of thirty days after fledging, and thus have a greater likelihood of being captured in mist nets, even if these nets are run only once or twice per week (Geupel and DeSante 1990). However, Song Sparrows are probably more similar to most North American passerines in dispersal strategy, flying ability, and escape frequency than Wrentits, which are known for their uniqueness in these areas (Geupel and Ballard 2002).

Other studies have also found different capture rates for different species. Du Feu and McMeeking

TABLE 5. PROPORTION OF LOCALLY PRODUCED FLEDGLINGS CAUGHT DURING 1992 AND 1993 COMBINED, COMPARING DAILY WITH WEEKLY NETS

Species	Number fledged	Daily nets		Weekly nets		P	Ratio (daily:weekly)
		Number captured	Percent captured	Number captured	Percent captured		
White-crowned Sparrow	76	12	15.8	2	3.9	0.003	6.0
Song Sparrow	142	34	23.9	8	5.6	<0.001	4.3
Spotted Towhee	39	5	12.8	2	5.1	ns	2.5
Wrentit	206	41	19.9	35	16.9	ns	1.2

TABLE 6. EFFECT OF DISTANCE TO NEAREST NET ON CAPTURE PROBABILITY OF LOCALLY PRODUCED WRENTITS, COMPARING DAILY WITH WEEKLY NETS

	Daily nets		Weekly nets	
Distance from nest to nearest net (m)	Capture probability estimate	95% confidence interval	Capture probability estimate	95% confidence interval
0	0.488	0.33–0.65	0.221	0.14–0.33
100	0.350	0.12–0.47	0.169	0.12–0.23

Notes: Results of logistic regression analysis. $P < 0.001$ for model including distance and netting frequency.

(1991) found that a netting regime's captures of Eurasian Blackbirds (*Turdus merula*) was correlated with local productivity, but that with Song Thrushes (*Turdus philomelos*) this correlation did not exist. Also, Nur and Geupel (1993b), using 12 years of data from the same daily nets we used, found that HY Song Sparrow capture rates mirrored true local production whereas capture rates of HY Wrentits did not.

Net shyness is another factor that probably differs among species. The fact that breeding Wrentits were caught less frequently in the daily nets than in the weekly nets may indicate learned net avoidance. If nets are run infrequently, it may be harder for birds (Wrentits, at least) to remember net locations (see also Faaborg et al. *this volume*). However, analyses conducted by Nur et al. (*this volume*) using capture–recapture techniques indicated no evidence of learned net avoidance in Wrentits, as recapture probability in the daily nets was high (71%) 1981–1991, and all breeders with territories within 50 m of nets were recaptured each year. Also (in our study), Song Sparrows were not captured unless nets were run fairly often, and therefore net avoidance did not appear to be a factor.

Habitat may also affect capture rates differently between species (Ballard et al. 2003). In our study, the daily nets were situated closer to and in the forest adjacent to the coastal scrub study plot. All study species nested in much higher densities in coastal scrub habitat at Palomarin than in the forested habitat. Neither Wrentits nor Song Sparrows regularly held territories in the forested habitat, so forest nets were not expected to capture as many of either species. Still, it is possible that Song Sparrows were more likely than Wrentits to venture into the forest habitat, which could also be an explanation for why the daily nets captured more of this species. It would be instructive to evaluate the effect of habitat by repeating our study using a design that varies netting frequency within each habitat type.

We did not test for effects of net density on capture rates, but this factor should also be expected to affect species differently, depending on territory size and movement patterns.

Other authors have related differences in capture rates between species to the birds' different morphologies. Jenni et al. (1996) found that all study species showed similar ability to avoid nets, but that certain species were significantly less likely to escape from the net after being caught. They related this finding to skull width and overall size and mass of the bird. Wrentits and Song Sparrows are relatively similar in size and weight, but Wrentits have longer tarsi, which may be more easily tangled in nets (Wrentit: mean = 25.07 mm, N = 238, SE = 0.24; Song Sparrow: mean = 21.07 mm, N = 216, SE = 0.32).

Capture rates are probably influenced also by the placement of individual nets, but this is difficult to assess (Ballard et al. 2003, Berthold *this volume*). Micro-habitat differences, exposure to sun or wind, and density of net placements relative to number of bird territories are some of the variables that could have significant effects on the effectiveness of different nets for different species. We found that individual nets caught a high percentage of Song Sparrows, and other nets caught a high percentage of the Wrentits. In fact, nets side by side often had completely different capture rates (PRBO, unpubl. data). Jenni et al. (1996) found that exposure to wind and sunlight both affected capture rates, varying by habitat and bird-species composition. These considerations warrant further investigations of sampling effectiveness of various net locations.

For most species at our site, capture rates were not high enough for estimating relative abundance, adult survivorship, or relative productivity of our locally breeding birds. Increased effort generally improved our ability to determine these population parameters, even for species in which net shyness may have been an issue (see above), but never reached an adequate sample size for most other species breeding nearby. Possibly we could increase netting intensity without increasing frequency (e.g., use

100 nets, each run 1 day in 10, rather than running the same 10 nets daily). However, as the coverage area is increased, details of local populations might be lost. Our nets captured a surprisingly small segment of the local population (birds breeding within 200 m, at best), and sometimes only if nets were run with high frequency.

CONCLUSIONS

Our results and others discussed here indicate the importance of standardizing all aspects of mist netting, from using the same net locations to maintaining the same netting frequency throughout a study. However, regardless of netting frequency, different species were not equally represented in mist nets. To obtain sufficient sample size to attain study objectives, it may not be possible to use the optimal netting frequency for each species individually.

Validation of results provided by mist nets requires knowledge of true population size and productivity data, which are best provided by daily nest-searching and territory mapping of color-banded individuals. We recommend continued investigations of true breeding population sizes for disparate species and locales, which will greatly enhance the interpretability of data gathered by mist-netting alone.

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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 ±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.

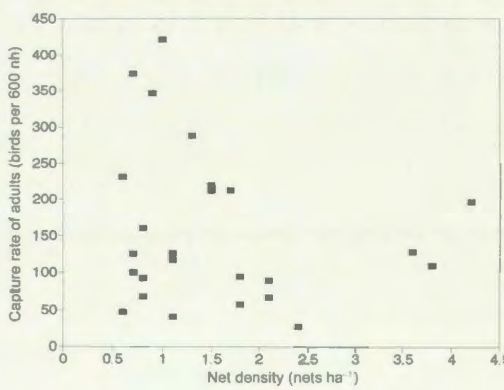

FIGURE 1. Capture rate of adult birds (all species pooled) at varying net densities. Data are from 25 MAPS stations operated in forest or forest-edge habitats for one or two days per 10-day period in 1990.

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 ± 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

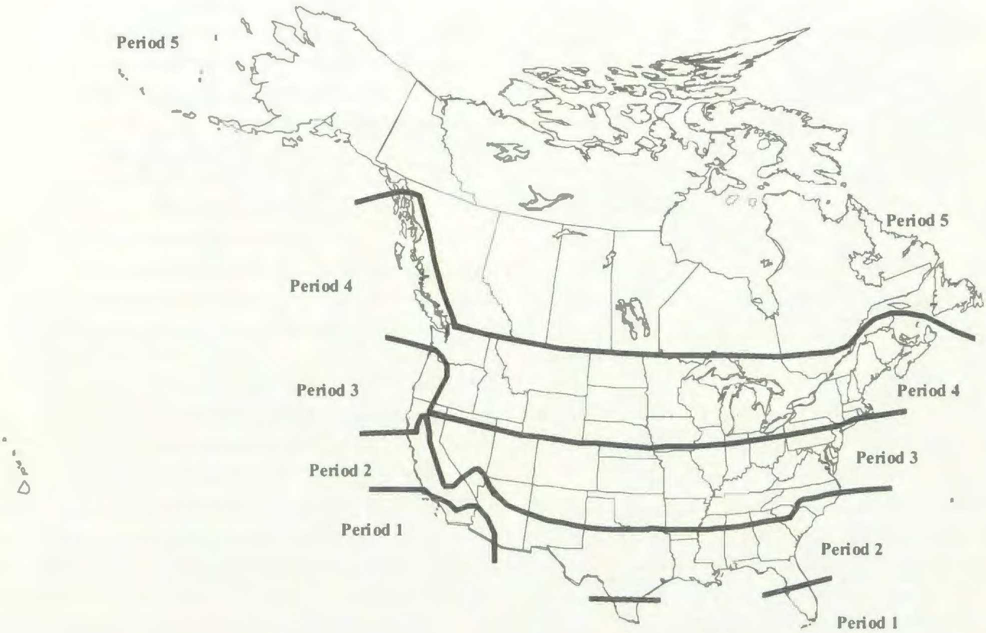

FIGURE 2. Recommended starting periods for MAPS stations in five geographic regions. Period 1 = May 1–10; Period 2 = May 11-20; Period 3 = May 21–30; Period 4 – May 31 –June 9; Period 5 = June 10–19.

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 ± 0.02 (N = 11 species) at Shenandoah, 0.09 ± 0.02 (N = 24) at Wenatchee, and 0.08 ± 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% depending 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 ≥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.

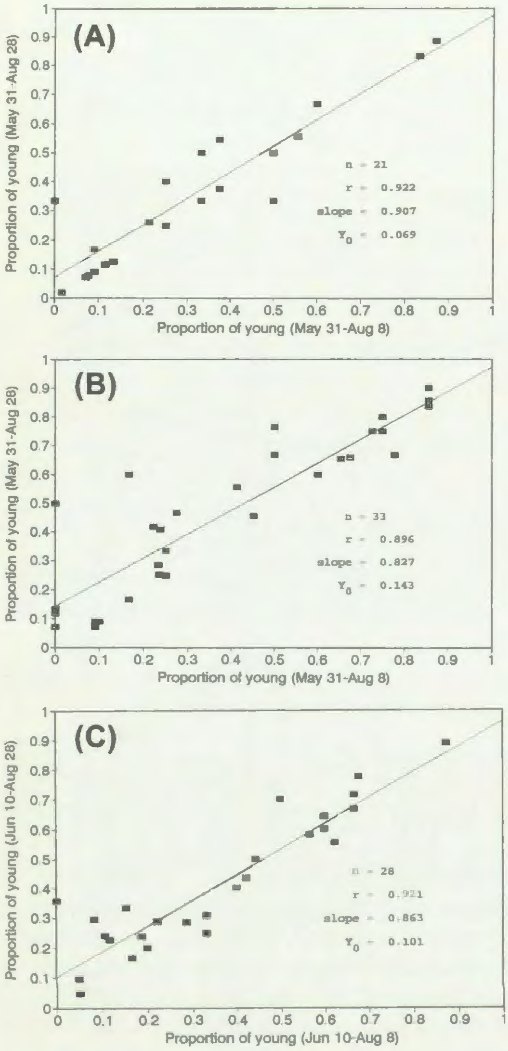

FIGURE 3. Regression of the proportion of young caught during all 10-day periods vs. the proportion of young caught in all but the last two 10-day periods during 1992 for all stations (N) at three stations.

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

	1992							1993						
	One-day station			Two-day station				One-day station			Two-day station			
Species	Adult	Young	Proportion young	Adult	Young	Proportion young	Difference[a]	Adult	Young	Proportion young	Adult	Young	Proportion young	Difference
Yellow-billed Cuckoo (*Coccyzus americanus*)	–	–	–	0.0	0.6	1.00		0.9	0.0	0.00	0.5	0.0	0.00	
Red-bellied Woodpecker (*Melanerpes carolinus*)	–	–	–	1.2	0.0	0.00		1.8	0.0	0.00	–	–	–	
Downy Woodpecker (*Picoides pubescens*)	1.2	–	0.00	0.6	0.0	0.00		–	–	–	0.0	0.5	1.00	
Northern Flicker (*Colaptes auratus*)	1.2	–	0.00	–	–	–		–	–	–				
Eastern Wood-Pewee (*Contopus virens*)	–	–	–	0.6	0.0	0.00		1.0	0.0	0.00	–	–	–	
Acadian Flycatcher (*Empidonax virescens*)	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 (*Myiarchus crinitus*)	1.2	0.0	0.00	–	–	–		0.9	0.0	0.00	–	–	–	
White-eyed Vireo (*Vireo griseus*)	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 (*V. flavifrons*)	–	–	–	0.6	0.0	0.00		–	–	–	–	–	–	
Red-eyed Vireo (*V. olivaceus*)	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 (*Cyanocitta cristata*)	–	–	–	–	–	–		–	–	–	1.5	0.5	0.25	
Carolina Chickadee (*Poecile carolinensis*)	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 (*Baeolophus bicolor*)	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 (*Thryothorus ludovicianus*)	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 (*Catharus fuscescens*)	1.2	0.0	0.00	–	–	–		–	–	–	0.5	0.0	0.00	
Wood Thrush (*Hylocichla mustelina*)	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 (*Turdus migratorius*)	–	–	–	–	–	–		0.9	0.0	0.00	–	–	–	
Gray Catbird (*Dumetella carolinensis*)	1.2	0.0	0.00	0.6	0.0	0.00		–	–	–	1.0	0.0	0.00	
Brown Thrasher (*Toxostoma rufum*)	–	–	–	0.6	0.6	0.50		–	–	–	0.5	0.0	0.00	
Pine Warbler (*Dendroica pinus*)	–	–	–	0.6	0.0	0.00		–	–	–	0.5	0.5	0.50	
Black-and-white Warbler (*Mniotilta varia*)	–	–	–	0.0	0.6	1.00		0.0	2.8	1.00	0.5	2.5	0.83	-0.17
American Redstart (*Setophaga ruticilla*)	–	–	–	1.2	0.0	0.00		–	–	–	–	–	–	
Prothonotary Warbler (*Protonotaria citrea*)	–	–	–	–	–	–		0.9	0.0	0.00	–	–	–	
Worm-eating Warbler (*Helmitheros vermivorus*)	2.5	0.0	0.00	–	–	–		0.9	0.9	0.50	0.5	1.0	0.67	+0.17
Ovenbird (*Seiurus aurocapillus*)	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 (*S. motacilla*)	–	–	–	–	–	–		1.8	0.9	0.33	0.0	1.0	1.00	+0.77
Kentucky Warbler (*Oporornis formosus*)	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 (*Geothlypis trichas*)	–	–	–	–	–	–		0.9	0.0	0.00	1.0	0.0	0.00	
Hooded Warbler (*Wilsonia citrina*)	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 (*Icteria virens*)	–	–	–	–	–	–		–	–	–	0.5	0.0	0.00	
Summer Tanager (*Piranga rubra*)	–	–	–	–	–	–		0.9	0.0	0.00	1.5	0.0	0.00	
Scarlet Tanager (*P. olivacea*)	–	–	–	1.2	0.0	0.00		–	–	–	0.5	0.0	0.00	

TABLE 1. CONTINUED

Species	1992 One-day station Adult	Young	Proportion young	1992 Two-day station Adult	Young	Proportion young	Difference[a]	1993 One-day station Adult	Young	Proportion young	1993 Two-day station Adult	Young	Proportion young	Difference
Northern Cardinal (*Cardinalis cardinalis*)	2.5	0.0	0.00	4.7	0.6	0.11	+0.11	4.6	0.9	0.17	2.0	0.5	0.20	+0.03
Eastern Towhee (*Pipilo erythrophthalmus*)	–	–	–	–	–	–		0.9	0.0	0.00	0.5	0.0	0.00	
Swamp Sparrow (*Melospiza georgiana*)	–	–	–	0.6	0.0	0.00		–	–	–	–	–	–	
Common Grackle (*Quiscalus quiscula*)	–	–	–	0.6	0.0	0.00		3.7	0.0	0.00	1.0	0.0	0.00	
Brown-headed Cowbird (*Molothrus ater*)	1.2	0.0	0.00	0.0	0.6	1.00	+1.00	–	–	–	–	–	–	
All species pooled	62.5	18.8	0.23	53.3	18.1	0.25	+0.02	73.7	25.8	0.26	47.4	27.5	0.37	+0.11
Number of species	18	6		22	12		7/10 +	22	13		25	16		11/14 +
Total number of species		18			25				23			27		

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

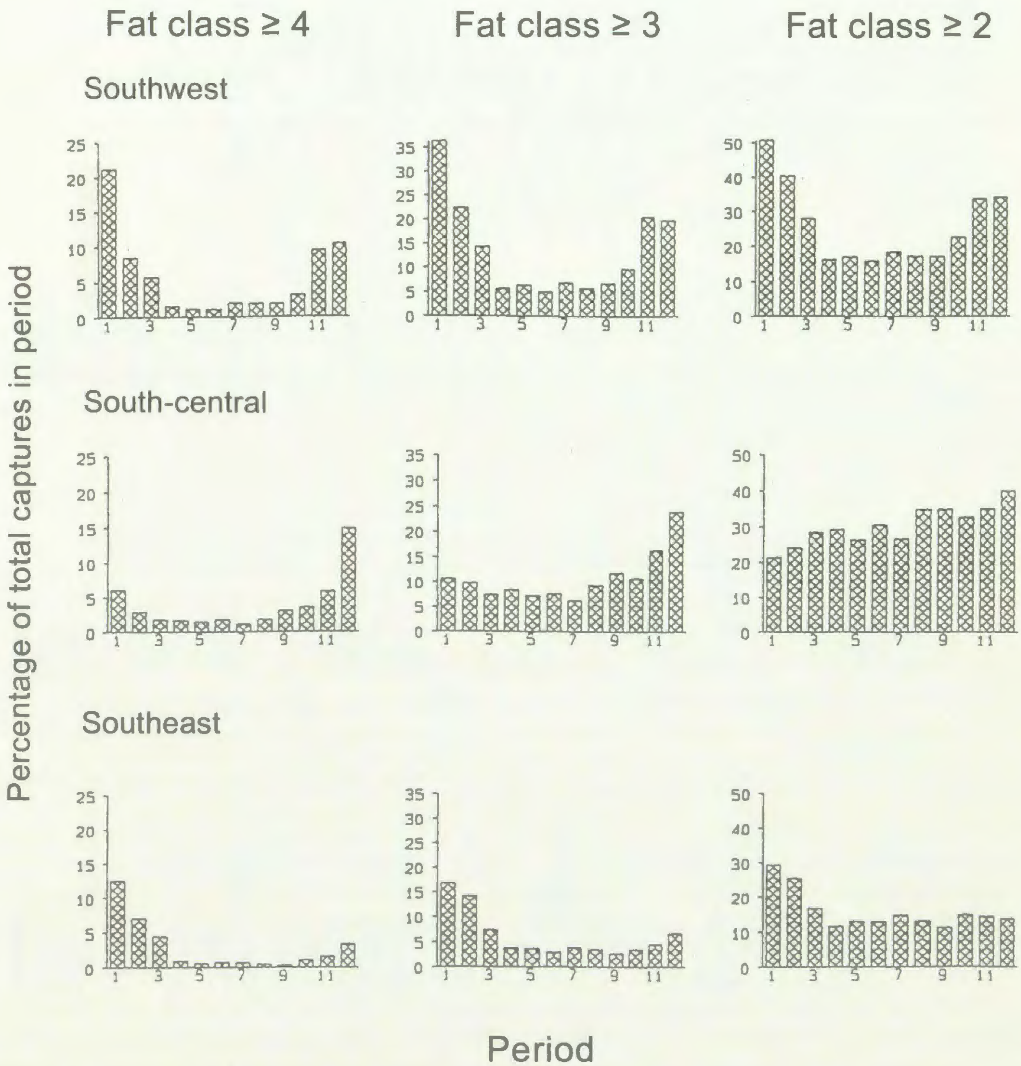

FIGURE 4. Frequency distributions of classes of subcutaneous fat carried by birds captured in the MAP Program as a function of 10-day period for three southern regions. Periods: 1 = May 1–10; 2 = May 11–20; 3 = May 21–30; 4 = May 31–Jun 9; 5 = Jun 10–19; 6 = Jun 20–29; 7 = Jun 30–Jul 9; 8 = Jul 10–19;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

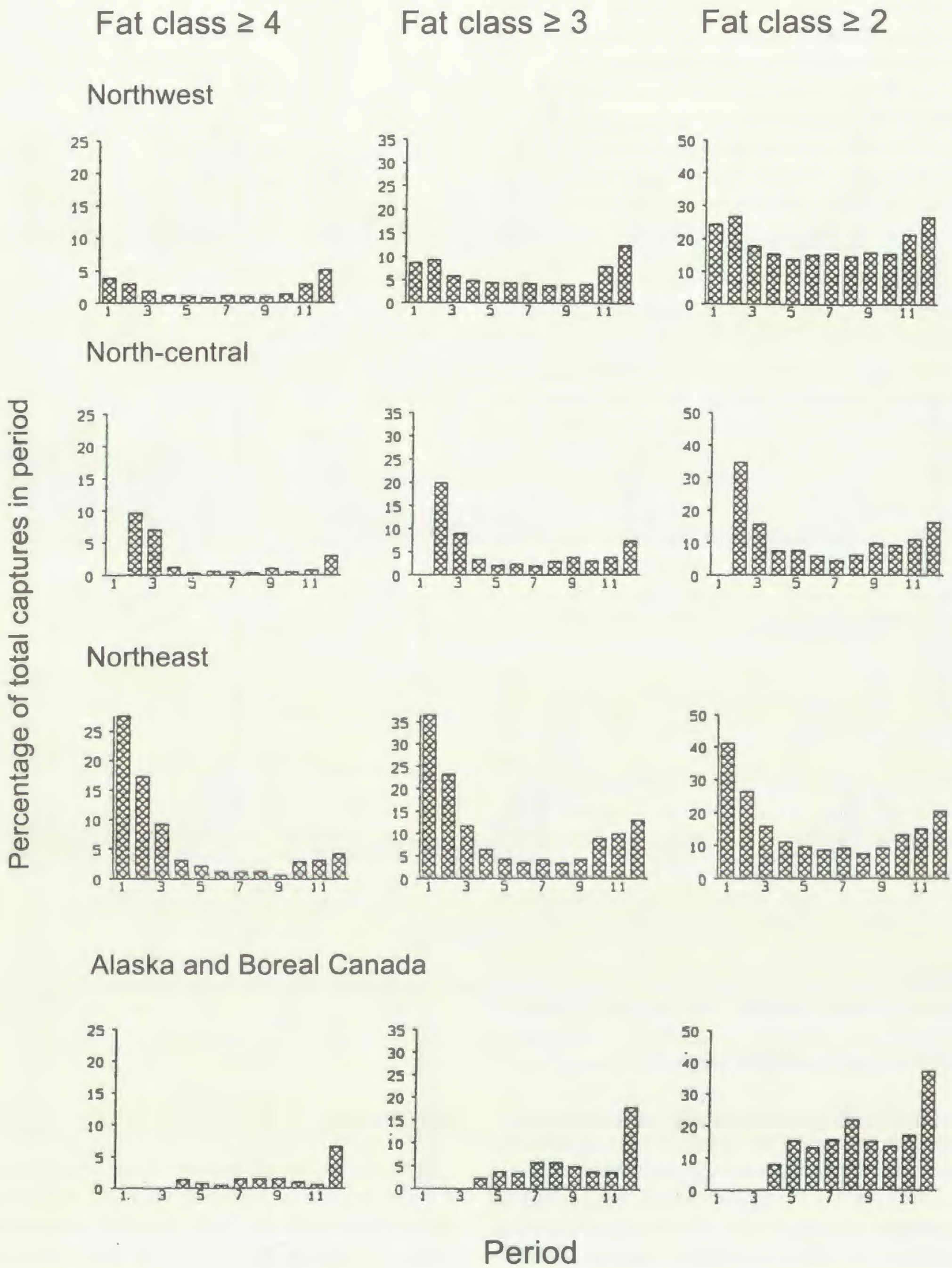

FIGURE 4. Continued. Four northern regions.

Table 2. Productivity indices (proportion of young in the catch) calculated by two methods from data collected at a MAPS station operated daily

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

[a] Number of first captures of adult birds during all days of operation.

[b] Calculated using data from all days of operation each 10-day period.

[c] Calculated using data from only the first complete day of operation each 10-day period.

[d] 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).

[e] 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

	Percent change in numbers of adults					Percent change in numbers of young					Change in proportion of young				
		All days[a]		One day[b]			All days		One day			All days		One day	
Species	N[c]	Birds[d]	Birds/ 600 nh[e]	Birds	Birds/ 600 nh	N	Birds	Birds/ 600 nh	Birds	Birds/ 600 nh	N	Birds	Birds/ 600 nh	Birds	Birds/ 600 nh
Changes between 1990 and 1991															
Dusky Flycatcher *(Empidonax oberholseri)*	2	+19	+144	+33	+15	1	-76	-78	-91	-92	1	-0.26	-0.26	-0.34	-0.34
"Western" Flycatcher (*E. difficilis* or *occidentalis*)	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 *(Dendroica petechia)*	5	-23	+5	+8	+18	5	+8	+53	0	+3	5	+0.08	+0.08	+0.02	-0.02
MacGillivray's Warbler (*Oporornis tolmiei*)	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 (*Melospiza lincolnii*)	2	+14	+54	+56	+53	2	0	+50	+500	+525	2	-0.03	-0.01	+0.20	+0.20
Dark-eyed Junco *(Junco hyemalis)*	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[f]		0.75	0.75	0.83*	0.75		0.42	0.42	0.42	0.50		0.33	0.33	0.33	0.25
Changes between 1991 and 1992															
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[f]		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).

[a] Calculated using data from all days of operation during each 10-day period.

[b] Calculated using data from only the first complete day of operation during each 10-day period.

[c] 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.

[d] Total number of first captures.

[e] Total number of first captures/600 net-h.

[f] 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

	1990						1991					
	All days per period[a]			One day per period[b]			All days per period			One day per period		
Station number	Total net-h	Birds[c]	Birds/ 600 nh[d]	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).

[a] Using data from all days each period that the station was run.

[b] Using data from only the first complete day each period that the station was run.

[c] Using the total number of first captures of adults.

[d] 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 [*Cocothraustes 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[a]	r	Station	N[a]	r
Mount Baker NF			*Siuslaw NF*		
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 ***
Wenatchee NF			*Willamette NF*		
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 ***
Umatilla NF			*Fremont NF*		
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.

[a] 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

	Number of			Survival probability[a]		Recapture probability[b]	
Species	Stations[c]	Individuals[d]	Captures[e]	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 (*Passerina cyanea*)	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
Group means for							
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.

[a] Defined as the probability of an adult bird surviving and returning in 1991 to the area where it was captured in 1990.

[b] 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.

[c] Number of stations operated for three consecutive years (1990–1992) where the species was known to be breeding.

[d] 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.

[e] 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 ± 0.03 (Karr et al. 1990a), that for Black-capped Chickadee (*Poecile atricapilla)* in Connecticut was 0.59 ± 0.02 (Loery et al. 1987, Pollock et al. 1990), and that for European Dipper (*Cinclus cinclus*) in France was 0.57 ± 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 increased 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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CURRENT PRACTICES IN THE BRITISH TRUST FOR ORNITHOLOGY CONSTANT EFFORT SITES SCHEME AND COMPARISONS OF TEMPORAL CHANGES IN MIST-NET CAPTURES WITH CHANGES IN SPOT-MAPPING COUNTS AT THE EXTENSIVE SCALE

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Abstract. The Constant Effort Sites (CES) scheme of the British Trust for Ornithology (BTO) aims to monitor changes in abundance, breeding productivity, and survival rates for a range of common passerines breeding in scrub and wetland habitats in Britain and Ireland. Changes in the size of the annual catch from a set of standard mist nets operated during 12 summer (May–August) visits, are combined across stations to produce estimates of the percent change in adult and juvenile numbers. We use the proportion of juveniles in the catch as a relative measure of breeding productivity. Methods are presented for calculating standard errors of between-year changes in both adult and juvenile catches, and changes in the proportion of juveniles. We compared the changes in the numbers of adults caught between 1982 and 1992 with changes in the numbers of territories counted on farmland and woodland Common Birds Census (CBC) plots. For 9 of 21 species considered, between-year changes in catches and counts were significantly and positively correlated, and long-term trends in abundance were consistent across the two monitoring schemes. For six species, long-term trends, but not between-year changes, were consistent across the two monitoring schemes. For a further six species, between-year changes and long-term trends were inconsistent between monitoring schemes, although for several of these species the disparity may be due to heterogeneous population trends across habitats. We discuss priorities for further validation studies of CES, including possible effects of habitat succession and station turnover on long-term trends in catch sizes.

Key Words: abundance monitoring, Common Birds Census, Constant Effort Sites, productivity, validation.

The Constant Effort Sites (CES) scheme is organized by the British Trust for Ornithology (BTO), and aims to monitor changes in the abundance, breeding success, and survival rates of a range of common passerine species breeding in wetland and scrub habitats in Britain and Ireland. Standardized mist netting and banding are used to assess changes in the abundance of adult and juvenile birds. The percent of young birds in the overall catch is taken as an index of annual productivity, while between-year recaptures are used to estimate apparent survival (i.e., return rates) of adults. Changes in the catches of adults and young of 23 species (including eight warblers and five finches), and updated trends in abundance and productivity, are published annually (e.g., Balmer and Milne 2002, Baillie et al. 2002). The CES scheme complements other BTO monitoring schemes that provide information on changes in population levels (Common Birds Census; Waterways Bird Survey; and, since 1994, the Breeding Bird Survey), nesting success (Nest Records Scheme), and survival rates (Ringing Scheme). The BTO has developed an Integrated Population Monitoring (IPM) programme, which aims to monitor changes in bird populations and to identify the mechanisms and causes of these changes (Baillie 1990, Greenwood et al. 1993, Thomson et al. 1997). The most important contribution of the CES scheme to the IPM programme is the provision of demographic information (productivity and survival), although for species that are difficult to census by traditional counting methods (e.g., Reed Warbler) the information on changes in the abundance of breeding adults will also be important.

The CES scheme was initiated in 1981 as a pilot project with a volunteer organizer. From an initial set of 17 participating study locations in 1981, the scheme expanded to 47 stations by 1984. Following an evaluation of the scientific potential of the CES scheme (Baillie et al. 1986), the BTO took over full responsibility for the project and devoted approximately half of one full-time staff member to its organization and promotion. The popularity of the CES scheme has continued to grow, and in 2000 data were received from 144 stations.

In this paper we describe the methodology of the CES scheme and the data currently being collected. Methods are presented for estimating between-year changes and associated standard error of adult and juvenile catches, and changes in the proportion of young birds (Peach et al. 1996). Finally, we compare between-year changes and trends in the numbers of adult birds caught on CE stations between 1982 and 1992 with changes in the numbers of territories counted on CBC plots during the same period. Since undertaking the work reported here, we have developed methods for modelling long-term changes in numbers and productivity from CES data (Peach et al. 1998). Results of these analyses are now reported annually along with those from other BTO monitoring schemes (Baillie et al. 2002).

STUDY SITES AND METHODS

STATION COMPOSITION AND NETTING REGIMES

All CE stations are operated by one or more fully trained volunteer banders who have proposed their study sites for registration in the national project. British and Irish banders are encouraged to propose locations at which experience has shown that reasonable numbers of passerines are netted during spring and summer. Under-represented regions (such as Scotland and Ireland) and species (such as Redpoll and Linnet; scientific names in Table 1) are highlighted in articles and publicity sent to banders and in presentations given at conferences and meetings. Proposed locations have generally been accepted into the scheme provided they do not contain a significant growth of coniferous trees (which will increase in height at a relatively rapid rate) and provided banders undertake to operate the station in a standardized manner for at least four years. Although banders are encouraged to control scrub growth, particularly around net positions, in most cases where this is attempted, it probably only entails the cutback of growth on the tops and sides of bushes.

At the time of proposing a new station, the bander must also specify the number and positions of a set of standard mist nets. These are usually determined by the bander based on previous experience of netting at the station. Once agreed, these net positions are not normally changed. Banders proposing locations at which they have not previously netted are usually asked to experiment with net positions during an initial trial year, after which the fixed set of standard CES nets is determined. In 1992 the mean standard net length on the 111 stations at which at least eight main visits were completed was 110.2 m (range 46–274 m). There are currently no guidelines concerning the density or number of nets to be used, because when the scheme was initiated it was felt that individual station characteristics and the number of banders available would have a large influence on the number and spacing of nets. We are now encouraging groups of banders to operate relatively large stations and to erect as many standard nets as possible. In

TABLE 1. MEAN STANDARD ERRORS (PERCENT) OF BETWEEN-YEAR CHANGES IN CATCHES, AND MEAN NUMBERS (IN PARENTHESES) OF CE SITES CONTRIBUTING DATA, DURING THE PERIOD 1987–1988 TO 1991–1992

Species	Adults (visits 1–6)	Adults (visits 1–12)	Juveniles (visits 1–12)	Percent juveniles (visits 1–12)
Wren (*Troglodytes troglodytes*)	7.7 (79.0)	7.0 (67.2)	7.7 (68.2)	2.5 (66.8)
Dunnock (*Prunella modularis*)	6.6 (78.4)	6.7 (67.0)	9.8 (67.2)	3.4 (66.6)
Robin (*Erithacus rubecula*)	9.1 (75.2)	9.0 (64.6)	7.1 (67.8)	2.3 (65.6)
Blackbird (*Turdus merula*)	6.5 (80.6)	6.5 (68.2)	10.3 (65.4)	3.9 (66.2)
Song Thrush (*T. philomelos*)	10.8 (71.2)	10.8 (62.8)	16.2 (59.0)	5.1 (54.4)
Sedge Warbler (*Acrocephalus schoenobaenus*)	8.2 (51.4)	8.0 (47.0)	12.6 (46.0)	4.8 (43.0)
Reed Warbler (*A. scirpaceus*)	7.2 (41.6)	5.8 (41.0)	10.3 (42.8)	3.9 (38.0)
Lesser Whitethroat (*Sylvia curruca*)	11.9 (46.0)	10.8 (42.8)	16.4 (49.0)	5.9 (36.2)
Whitethroat (*S. communis*)	10.7 (53.2)	11.4 (48.0)	13.6 (52.4)	4.6 (45.4)
Garden Warbler (*S. borin*)	9.7 (62.2)	9.5 (56.0)	17.0 (56.8)	5.2 (51.6)
Blackcap (*S. atricapilla*)	8.6 (69.4)	7.5 (61.8)	11.2 (63.2)	3.8 (60.4)
Chiffchaff (*Phylloscopus collybita*)	14.2 (47.2)	14.8 (50.8)	12.1 (57.6)	3.7 (50.6)
Willow Warbler (*P. trochilus*)	4.9 (78.4)	5.1 (66.6)	7.0 (68.2)	3.1 (67.0)
Long-tailed Tit (*Aegithalos caudatus*)	14.3 (64.0)	14.2 (56.0)	22.6 (52.4)	4.4 (49.2)
Blue Tit (*Parus caeruleus*)	9.1 (79.0)	8.3 (67.6)	9.3 (68.4)	2.7 (68.2)
Great Tit (*P. major*)	9.6 (74.6)	8.9 (64.2)	11.3 (67.2)	3.2 (64.6)
Treecreeper (*Certhia familiaris*)	35.6 (36.6)	24.2 (32.8)	16.8 (49.4)	6.9 (36.0)
Chaffinch (*Fringilla coelebs*)	9.2 (66.6)	9.9 (58.0)	23.4 (46.4)	6.3 (50.2)
Greenfinch (*Carduelis chloris*)	25.7 (34.8)	23.0 (35.2)	27.3 (23.4)	11.2 (23.8)
Linnet (*C. cannabina*)	21.6 (20.6)	20.5 (20.0)	34.4 (15.8)	8.3 (13.8)
Redpoll (*C. flammea*)	29.4 (26.2)	27.3 (24.0)	33.6 (13.2)	11.6 (13.6)
Bullfinch (*Pyrrhula pyrrhula*)	9.1 (70.2)	7.5 (63.4)	14.9 (55.4)	4.4 (59.0)
Reed Bunting (*Emberiza schoeniclus*)	9.9 (50.0)	9.3 (45.0)	20.5 (36.4)	6.5 (37.4)

Notes: Species are separated into taxonomic groups. For a station to be included in the analysis, at least eight out of 12 paired visits must have been completed (or four out of six paired visits for adults caught during visits 1–6). The precision of changes in adult captures is presented for all 12 CES visits (1–12) and for the first six visits only (see text for rationale).

1992 the median number of individual birds of all species trapped in standard nets at stations at which at least eight visits were completed was 112 adults (range 28–262) and 174 juveniles (range 43–425).

All CES banders are asked to make 12 visits to their stations between early May and late August, one in each of 12 10-day or 11-day periods. The dates of these periods vary slightly from year to year to ensure that at least three non-working days (weekends or public holidays) are included in each visit period. The interval between main visits should normally not be less than 6 days and must be at least 3 days. At least 10 of the 12 main visits were completed at 87% of all CES stations in 1991 (N = 108) and at 84% of all stations in 1992 (N = 122). Banders are asked to operate their set of standard nets for a set duration of at least 6 h on each visit, and to standardize their chosen netting duration across years, but not necessarily across visits within a year. A typical regime would be to begin netting at dawn and continue until midday on each of the 12 visits. Different netting durations between visits is allowed for in the analysis by only comparing between-year changes in catches for paired visits (i.e., visits completed in both years under consideration; see below).

To increase volunteer participation in the CES scheme, banders have the option of carrying out extra visits to their CE stations between May and August, and of erecting additional nets during main CES visits. However, extra visits are not permitted during the three days preceding a main visit and the length of additional netting should not exceed the combined length of all the standard nets. During 1989 a mean of 3.0 extra visits were made per CE station with no extra visits being made at 53% of stations. The mean length of additional netting per visit in 1989 was 8.6% of the standard net length. Captures made during extra visits or from additional nets are collected and computerized but are not used in calculations of between-year changes in catch sizes. These captures are used in analyses of mark–recapture data and might also contribute to analyses of adult:juvenile ratios.

Data Collection and Routine Analysis of Between-year Changes

For each bird trapped on a CE station between May and August the following information is recorded in a station- and year-specific file on the BTO computer: band number, species, age ("adult" = after hatching year or "juvenile" = hatching year), sex (in the case of adults), date(s) of capture, and an additional net code to indicate whether the bird was trapped in a standard CES net or in an additional net. To minimize the costs of collecting and computerizing the CES data, information on biometrics, molt, and brood patches have not been collected routinely as part of the CES scheme. However, most banders now submit these data electronically as part of their main banding returns and they can be linked to the CES files as required. In particular, CES banders have been encouraged since 2001 to record brood patches to provide information on the length of the breeding season. Until 1993, simple, descriptive habitat information was collected, accompanied by detailed station sketch maps. Starting in 1994, habitat codes, vegetation height, and scrub density were recorded on each side of each standard mist net.

CES capture data are submitted either on paper forms or on computer disc. Paper submissions are computerized and checked by BTO staff, after which printouts of the data are returned to the bander for final checking. The BTO has developed various computer software packages for banders that enable the user to computerize their banding and recapture data and to carry out most of the paperwork required for administrative purposes (Coker 1993, Cubitt 2002). The latest software is freely available and includes a program to extract CES capture data from larger data sets. In 1992, data from 35 out of 122 stations were submitted on disc and this figure rose to 130 out of 144 stations operated in 2000.

Calculation of the Magnitude and Precision of Between-year Changes in Adult and Juvenile Abundance

Between-year changes in the catches of adults and young birds (r) are computed by aggregating the numbers of birds caught across those stations at which at least eight paired visits (at least four out of the first six visits, and four of the second six visits) were completed in each of the two years under consideration. Only captures from paired visits contribute to the annual total. For example, if all 12 visits are completed in year one but only visits 1 to 10 in year two, then the comparison of between-year change is based upon catches from the 10 paired visits only. Stations are excluded from the analyses of between-year change if netting effort was not standardized or if major habitat changes occurred.

An index of between-year changes in the adult or juvenile catch at CE stations is calculated as

$$r = \frac{\sum_{j=1}^{n} y_j}{\sum_{j=1}^{n} x_j}$$

where x_j = last year's catch at station j, y_j = this year's catch - last year's catch at station j, n = the number of stations worked in the same way during both years. We define q = $100(r)$ = percent change between years.

The measure of change r is a ratio estimator with approximate standard error (Cochran 1963)

$$\mathrm{SE}(r) = \sqrt{\frac{n\sum_{j=1}^{n}\left(y_j - r.x_j\right)^2}{(n-1)\left(\sum_{j=1}^{n}\right)^2}}$$

and the standard error of q is found as

$$\mathrm{SE}(q) = 100\ \mathrm{SE}(r)$$

An approximate 95% confidence interval for the true ratio R (after Cochran 1963) is

$$r\left\{\frac{\left(1-1.96^2 c_{\bar{y}\bar{x}}\right)\pm 1.96\sqrt{\left(c_{\bar{y}\bar{y}}+c_{\bar{x}\bar{x}}-2c_{\bar{y}\bar{x}}\right)-1.96^2\left(c_{\bar{y}\bar{y}}c_{\bar{x}\bar{x}}-c^2_{\bar{y}\bar{x}}\right)}}{1-1.96^2 c_{\bar{x}\bar{x}}}\right\},$$

where

$$c_{\bar{x}\bar{x}}=\{c.v.(\bar{x})\}^2=\left\{\frac{\sum_{j=1}^{n}\left(x_j-\bar{x}\right)^2}{n\,(n-1)\left(\bar{x}\right)^2}\right\},$$

$$c_{\bar{y}\bar{y}}=\{c.v.(\bar{y})\}^2=\left\{\frac{\sum_{j=1}^{n}\left(y_j-\bar{y}\right)^2}{n\,(n-1)\left(\bar{y}\right)^2}\right\},$$

and $c_{\bar{y}\bar{x}}=\left\{\dfrac{\sum_{j=1}^{n} y_j\left(x_j-\bar{x}\right)}{n(n-1)\,\bar{x}\,\bar{y}}\right\}$

These limits should be multiplied by 100 to give limits for Q, the true percentage change between years.

The formulae presented here do not require that between-year changes in captures be homogeneous across CE stations. The calculation of a binomial standard error for a between-years change would not be valid because some individuals are caught in both years under consideration and because of the observed heterogeneity in capture trends across stations (see below). The methods presented here are appropriate for any monitoring programs that aim to draw inferences from between-year changes in abundance at a sample of stations or plots.

Standard errors of between-year changes in the numbers of territories on Common Birds Census or Waterways Bird Survey plots have until recently been calculated using a modification of Cochran's (1963) cluster sample method. Cluster sampling would be appropriate if a random sample of stations (clusters) was drawn, and the fate of all birds in sampled stations was recorded. That is clearly not the case in monitoring programs. The ratio sampling method requires only the first of these two assumptions.

Calculation of the Magnitude and Precision of the Between-year Change in the Percent of Juveniles

A simple estimate of change in productivity between years i-1 and i is

$$v_i - v_{i-1}$$

where v_i and v_{i-1} are the proportions of young birds in the entire catches, summed over all stations operated in the same manner in year i and year i–1.

In any year,

$$v_i=\frac{\sum_{j=1}^{n} b_j}{\sum_{j=1}^{n}(a_j+b_j)}$$

where b_j is the number of juveniles caught at the jth station in any year i, and a_j is the number of adults caught at the jth station. The standard error of the overall proportion v_i is then calculated as

$$\mathrm{SE}\,(v_i)=\sqrt{\frac{n\sum_{j=1}^{n}\left(b_j-v\left(a_j+b_j\right)\right)^2}{(n-1)\left(\sum_{j=1}^{n}\left(a_j+b_j\right)\right)^2}}$$

The standard error of the difference v_i - v_{i-1} is

$$\mathrm{SE}\left(v_i - v_{i-1}\right)=\sqrt{(\mathrm{SE})^2+(\mathrm{SE})^2}\,.$$

Adult Captures Compared to Territory Counts

The Common Birds Census

Between 1962 and 1994, the Common Birds Census (CBC) was the main monitoring scheme for common breeding birds in the United Kingdom. The scheme involves the counting of breeding territories on typically 200–300 plots in farmland and woodland each year using the spot-mapping method. Farmland plots can be any type of arable, horticultural, or grazing land (except unenclosed sheepwalk), and must be at least 40 ha, and preferably 60 ha, in area, which can include up to 10% of small woods and copses. Woodland plots include all kinds of semi-natural and broadleaved woodlands, but not parkland, scrubby heathlands, or coniferous plantations, and must be at least 10 ha in area. For a full account of the methods, history, and long-term trends of bird species monitored by the CBC, see Marchant et al. (1990).

The CBC provides an independent source of information on between-year and long-term changes in abundance for 21 of the 23 species currently monitored by the CES scheme. The CBC has been the subject of a large number and wide range of validation studies (O'Connor and Marchant 1981, O'Connor and Fuller 1984, Baillie and Marchant 1992) and is generally accepted to provide reliable extensive information on population changes of a wide range of common bird species in lowland Britain. If strong positive correlations exist between population changes as measured by CBC and CES data, then this would constitute good evidence that the latter is providing meaningful measures of changes in the size of the breeding population. However, a lack of correlation between measures of population change would be more difficult to interpret, because the two schemes are using different methods to assess changes in population size in different habitats. The CBC measures changes in the numbers of territories, whereas the CES scheme measures changes in the numbers of adult birds caught, which might include transient or non-breeding individuals. The CBC covers woodland and farmland whereas most CES plots are located in scrub and reedbed habitats. Although the CBC methodology is generally considered to be reliable for most territorial passerines, it may not perform well for some species, such as those having short song periods or very large or highly aggregated territories (Bell et al. 1968, Fuller and Marchant 1985). A lack of correlation between the CBC and CES might also occur if the population level of a species had remained unchanged during the period of study. Between-year changes would then largely reflect sampling error, rather than real changes in the bird population.

A further question considered here is whether between-year changes in adult captures made during the first six CES visits correlate more strongly with those measured from the CBC, or are more precise than those derived from captures made during all 12 visits. CBC census workers carry out their field work between late March and early July, which corresponds more closely with the first six CES visits (May–June) than the full 12 visits (May–August). For most species a high proportion of adults are caught during the first six visits (Baillie et al. 1986) and late season captures might include a relatively high proportion of transients, as well as individuals embarking on second or late breeding attempts. If changes in adult captures from the first six CES visits were more closely correlated with changes from the CBC (or were much more precise) than changes based on captures from all 12 visits, then it might be concluded that adult abundance on CE stations would be better monitored using captures from the first six visits only.

Analysis

Weighted correlation was used to compare between-year changes in the number of territories recorded on farmland and woodland CBC plots during the period 1983–1984 to 1991–1992 with changes in the captures of adults on CES stations during visits 1–6 and during visits 1–12. Each pair of between-year changes was weighted by the reciprocal of the mean of the standard errors of the between-year changes from the CBC and CES schemes. This weighting procedure has the effect of down-weighting changes from the early years of the CES scheme when fewer stations were operated and precision was relatively poor.

At the time of conducting these analyses, methods for the indexing of long-term monitoring data were under development (Peach and Baillie 1994, Peach et al. 1998, Siriwardena et al. 1998) and in this paper we use the simple chain index in which successive between-year changes in abundance are linked together around an arbitrary base year (Marchant et al. 1990). Although the chain indexing method has various shortcomings (Peach and Baillie 1994), we use it here to compare long-term trends in abundance across monitoring schemes and not to draw biological conclusions concerning changes in abundance. Our approach therefore assumes there is no differential sensitivity of the two monitoring schemes to the use of the chain index. We recommend that the chain index should not be used for future analyses of CES trends, as more robust methods are now readily available (Peach et al. 1998, Baillie et al. 2002).

Long-term trends in chain indices derived from the CBC and CES data for the period 1982 to 1992 were compared using a test for homogeneity of linear slopes. This involved fitting an analysis of covariance model using the GLM procedure of SAS (SAS Institute 1988) in which year was the covariate and monitoring scheme the main factor, with an interaction term between year and scheme. A significant interaction term was taken as evidence of different average rates of change in the abundance of adult birds as measured by the two monitoring schemes. Comparisons of slopes from the CBC and CES schemes were carried out for both farmland and woodland CBC indices and for CES indices derived from visits 1–6 and visits 1–12. In all such analyses, indices were weighted by the square root of the sum of the number of birds caught, or the number of territories counted, during the year of the index and the preceding year. We note that the use of linear regression to assess the significance of trends in chain indices may be statistically unreliable (because the observations are not independent), and more robust techniques have been developed since these analyses were conducted.

Finally, we compare the precision of between-year changes in captures of adults on CE stations based on captures during the first six visits and all 12 visits.

RESULTS

Precision of Between-year Changes in Catches

The precision with which between-year changes in abundance are measured by the CES scheme has increased as the number of contributing stations has risen. The average precision attained for between-year changes in the catches of adults, young and the percent of young during the period 1988–1989 to 1991–1992 for 23 species is summarized in Table 1. For 16 of the 23 species, between-year changes in the catches of adults (between May and August) are currently estimated with standard errors of 10% or less. Between-year changes in the catches of juveniles are more variable across stations, with mean standard errors of 10% or less being attained for only seven species. Between-year changes in the percent of young birds caught are measured with mean standard errors of 5% or less for 17 of the 23 species (Table 1).

Adult Captures Compared to Territory Counts

Average standard errors of between-year changes in CES adult captures are presented in Table 1. Weighted correlation coefficients comparing between-year changes in abundance of common passerines on CBC plots and CE stations are presented in Table 2, whereas tests for differing overall trends in abundance between the two monitoring schemes are summarized in Table 3. The information summarized in Tables 1–3 is considered below according to the taxonomic groupings used in the tables.

Resident insectivores and thrushes

For this group of five common species, between-year changes in adult CES catches were highly correlated with changes in counts in both woodland and farmland CBC plots (Table 2), suggesting that the CES is providing reliable measures of changes in adult abundance for all five species. Temporal trends in abundance were generally consistent across the two monitoring schemes (Table 3), although catches of Blackbirds have declined at a greater rate on CE stations than have territory counts on CBC plots. Exclusion of late season adult captures did not improve precision of between-year changes, and, in the case of Wren, resulted in lower precision (Table 1).

Migratory warblers

For this group of eight species, comparative CBC data were available for all species except Reed Warbler. For Sedge Warbler, Whitethroat, and Chiffchaff, between-year changes in CES catches were generally consistent with changes in counts on CBC plots (Table 2). In the case of Whitethroat, trends in CES catches were more consistent with trends in CBC counts on farmland when captures made during July and August were excluded (Table 3). The precision of between-year changes in the captures of adult Whitethroats (and Chiffchaffs) was also higher when data from July and August were excluded (Table 1). For Blackcap, Willow Warbler, and Lesser Whitethroat, long-term trends were reasonably consistent across the two schemes (Table 3). In the case of Willow Warbler, there was some evidence of a greater rate of decline in CE catches compared to territory counts on farmland CBC plots (Table 3).

TABLE 2. WEIGHTED PEARSON'S CORRELATION COEFFICIENTS COMPARING BETWEEN-YEAR CHANGES (1983/1984 TO 1991/1992) IN THE NUMBER OF ADULTS CAUGHT ON CE SITES AND THE NUMBERS OF TERRITORIES RECORDED ON CBC PLOTS IN FARMLAND AND WOODLAND

	Farmland CBC		Woodland CBC	
Species	CES 1–6	CES 1–12	CES 1–6	CES 1–12
Wren	0.97 ***	0.92 ***	0.93 ***	0.87 ***
Dunnock	0.95 ***	0.90 ***	0.79 *	0.82 **
Robin	0.97 ***	0.96 ***	0.84 **	0.79 *
Blackbird	0.83 **	0.78 *	0.65 (*)	0.63 (*)
Song Thrush	0.89 **	0.84 **	0.68 *	0.68 *
Sedge Warbler	0.78 *	0.76 *	–	–
Reed Warbler	–	–	–	–
Lesser Whitethroat	-0.29	-0.22	–	–
Whitethroat	0.86 **	0.86 **	0.93 ***	0.96 ***
Garden Warbler	-0.47	-0.51	0.35	0.13
Blackcap	0.57	0.47	0.59	0.64 (*)
Chiffchaff	0.72 *	0.80 **	0.65 (*)	0.74 *
Willow Warbler	0.38	0.50	0.34	0.43
Long-tailed Tit	0.71 *	0.75 *	0.58	0.62
Blue Tit	0.24	0.15	-0.07	-0.07
Great Tit	-0.24	-0.71 *	-0.11	-0.41
Treecreeper	-0.29	0.09	0.01	0.14
Chaffinch	-0.11	0.03	-0.67 *	-0.31
Greenfinch	0.27	0.33	-0.06	-0.14
Linnet	0.13	0.17	-0.09	-0.01
Redpoll	–	–	–	–
Bullfinch	0.46	0.18	–0.15	–0.30
Reed Bunting	-0.10	-0.10	–	–
Number significant	9+	9+, 1-	5+, 1-	6+

Notes: Changes in the numbers of adults caught on CE stations were considered using data from all 12 visits (May–August) and from the first six visits only (May–June). Species are separated into groups as in Table 1.
*** denotes $P < 0.001$; ** denotes $P < 0.01$; * denotes $P < 0.05$; (*) denotes $P < 0.10$; – denotes no comparative CBC data available.

Trends in the catches of adult Garden Warblers on CE stations differed significantly from trends in abundance on both woodland and farmland CBC plots (Table 3), although the difference was only marginally significant on woodland (0.05 < P < 0.06). Trends in the abundance of Garden Warblers also differed between woodland and farmland CBC habitats (P < 0.02). Catches of Garden Warblers on CE stations have declined since 1982, whereas numbers on CBC plots have increased on farmland and shown no trend in woodland.

Tits and Treecreeper

For Long-tailed Tit, both between-year changes and long-term trends in abundance were consistent between the CBC and CES schemes (Tables 2 and 3), particularly for annual indices derived from CES visits 1–6 (Table 3). Between-year changes in the catches of adult Treecreepers were generally not consistent between the two monitoring schemes (Table 2). However, long-term trends in the catches of Treecreepers made during all 12 CES visits did not differ significantly from those derived from CBC counts in both woodland and farmland habitats (Table 3). Relatively small numbers of adult Treecreepers are caught on CE stations (for example the 1991–1992 change was based upon 59 adults trapped in 1991 and 41 in 1992) and hence between-year changes are measured imprecisely (Table 1).

The most pronounced inconsistencies between long-term trends in CES catches and CBC counts were for Blue Tit and Great Tit (Table 3). In the case of Great Tit, between-year changes in abundance were negatively correlated (Table 2). For both species, CES captures have declined strongly since 1982, whereas there have been no significant trends in counts of tits on either farmland or woodland CBC habitats.

TABLE 3. COMPARISON OF LONG-TERM TEMPORAL TRENDS IN CHAIN INDICES DERIVED FROM CBC AND CES DATA (1982–1992)

	Farmland CBC		Woodland CBC	
Species	CES 1–6	CES 1–12	CES 1–6	CES 1–12
Wren	0.00	0.72	0.32	0.08
Dunnock	2.90	1.64	0.00	0.28
Robin	0.41	0.06	3.90	1.14
Blackbird	3.62	5.98 *	4.55 *	7.17 *
Song Thrush	0.03	0.11	5.43 *	3.08
Sedge Warbler	2.12	0.23	–	–
Reed Warbler	–	–	–	–
Lesser Whitethroat	1.32	1.19	–	–
Whitethroat	1.36	8.47 **	0.01	2.94
Garden Warbler	17.26 ***	12.49 **	11.73 **	4.35 (*)
Blackcap	2.59	3.42	0.47	0.78
Chiffchaff	1.99	2.90	0.00	0.17
Willow Warbler	5.46 *	4.04 (*)	0.04	0.74
Long-tailed Tit	1.62	5.90 *	0.21	2.56
Blue Tit	19.13 ***	39.13 ***	20.91 ***	45.58 ***
Great Tit	9.87 **	13.42 **	21.10 ***	26.06 ***
Treecreeper	7.36 *	0.27	12.21 **	0.05
Chaffinch	21.02 ***	8.98 **	7.73 *	0.90
Greenfinch	7.54 *	6.12 *	14.86 **	17.65 ***
Linnet	3.42	16.96 ***	0.49	5.31 *
Redpoll	–	–	–	–
Bullfinch	2.86	0.89	2.77	0.63
Reed Bunting	41.72 ***	10.12 **	–	–
Number of species with different trends	8/21	11/21	8/18	6/18

Notes: F-statistics and associated significance levels are presented for the interaction between monitoring scheme (factor) and year (continuous covariate). Significant interactions indicate different average annual rates of change in abundance. Changes in the numbers of adults caught on CES stations were considered using data from all 12 annual visits (May–August) and from the first six visits only (May–June).

*** denotes P < 0.001; ** denotes P < 0.01; * denotes P < 0.05; (*) denotes P < 0.10; – denotes no comparative CBC data available.

Finches and Reed Bunting

For one of the six species in this group (Redpoll) there are no comparable CBC data. For Chaffinch, between-year changes in CES captures were not positively correlated with those derived from CBC data (Table 2), and long-term trends in CES catches were inconsistent with trends in counts on farmland, but not woodland (Table 3). Woodland is probably the preferred breeding habitat of Chaffinches in Britain (Gibbons et al. 1993).

For Greenfinch and Linnet, trends in abundance were generally inconsistent between the two monitoring schemes, although not when CES catches of Linnets were limited to the first six visits (Table 3). For both of these species, changes in adult abundance are measured with relatively low precision by the CES scheme (Table 1), due to small sample sizes.

Bullfinch is a relatively late-breeding species and a relatively high proportion of adults are caught for the first time in any year during visits 7–12 (Baillie et al. 1986). Between-year changes are therefore measured with greater precision when they are based upon captures from all 12 visits, rather than only from the first six visits (Table 1). Although between-year changes were not consistent with those derived from CBC data (Table 2), longer-term trends in abundance were consistent across the two monitoring schemes (Table 3).

In the case of Reed Bunting, between-year changes in CES catches and counts on CBC farmland plots were not correlated (Table 2), and long-term trends in abundance differed significantly (Table 3). However, changes in numbers on farmland may not be representative of wider population changes because wetland habitats are the main and probably preferred breeding habitat for this species (Gordon 1972, Gibbons et al. 1993). Drier farmland probably serves as a suboptimal, overspill habitat for Reed Buntings when population levels in wetland habitats are high (Bell 1969, Marchant et al. 1990).

DISCUSSION

Comparison of CES and CBC

Despite the problems of interpretation outlined above, several general conclusions emerge from this analysis.

(1) For at least nine species, between-year changes in adult captures combined across CE stations were consistent with extensive changes in abundance as measured by spot-mapping of breeding bird populations. These species are Wren, Dunnock, Robin, Blackbird, Song Thrush, Sedge Warbler, Whitethroat, Chiffchaff, and Long-tailed Tit (Table 2).

(2) For a further six species, long-term trends in CES captures (but not between-year changes) were generally consistent with trends in abundance derived from extensive CBC counts (Table 3). These species are Blackcap, Willow Warbler, Treecreeper, Linnet, Bullfinch, and Lesser Whitethroat.

(3) For the remaining six species, between-year and long-term changes in CES adult catches were inconsistent with concurrent changes in territory counts on CBC plots for at least one of the two CBC habitats. In the case of Reed Bunting, this may reflect the unrepresentative habitats covered by the CBC. In the cases of Garden Warbler, Chaffinch, and Greenfinch, trends in abundance differ significantly between woodland and farmland CBC plots suggesting that population processes may differ between habitats. The preferred habitats of Garden Warblers are probably woodland and scrub close to canopy closure (Gibbons et al. 1993). Because the CES monitors Garden Warblers mainly in scrub and woodland habitats it is perhaps not surprising that the trend in abundance on CE stations is more similar to the CBC trend for woodland than for farmland (Table 3).

In the case of the two titmouse species (Blue Tit and Great Tit), trends in abundance were consistent across CBC woodland and farmland habitats, but inconsistent between the CBC and CES data. Because between-year changes in the numbers of adult titmice caught at CE stations were measured with reasonable precision (Table 1), the observed disparity between the CES and the CBC data is difficult to explain, and casts some doubt over the reliability of the CES data for these species. One possible cause of declining catches of adult tits on CE stations could be net-avoidance, which might be promoted by winter and spring mist-netting activities on or adjacent to constant effort stations, often in association with artificial feeders. Such netting activities would be unlikely to involve other species caught on CE stations. This possibility could be investigated by comparing trends in captures on stations with and without winter and spring mist-netting activities. Habitat succession on CE stations might also serve to reduce catching efficiency as tits in mixed-aged flocks tend to fly along the tops of bushes and trees. As the vegetation grows higher, fewer of these flocks might be caught in mist nets.

(4) For most species monitored by the CES

scheme, there was little difference in between-year changes, long-term trends, and precision based on captures made during all 12 visits and captures made during visits 1–6 only. However, in the case of Whitethroat, long-term trends in catches were more strongly correlated with trends in counts on CBC plots, and the precision of between-year changes was higher, when CES changes were based upon captures during visits 1–6 only. Similarly, long-term trends in the captures of Linnets and Long-tailed Tits were more closely correlated with those derived from CBC data when the CES changes were based on captures made during visits 1–6 only. For these three species, changes in adult abundance might be better measured by using captures from the first six CES visits only.

For Treecreeper and Bullfinch, long-term trends in CES captures were more closely correlated with those from the CBC, and precision of between-year changes improved, when captures from all 12 visits were used.

To summarize, for 15 of the 21 species considered, long-term trends in the abundance of adult songbirds as recorded by spot-mapping (CBC) and standardized mist netting (CES) were similar (see also Peach et al. 1998). This suggests that, for most common songbirds, the CES methodology is providing reliable information on extensive changes in the size of breeding populations. Our conclusions are broadly similar to those of Silkey et al. (1999) who found that capture rates from standardized mist netting in coastal scrub did reflect changes in breeding densities for three out of four species considered. These authors noted that the form of the relationship between capture rates and breeding densities differed between species, thus highlighting the need for caution when relating changes in catch rates to breeding densities.

Priorities for Further Validation of CES

Effects of habitat succession

Successional changes at CE stations could cause two potentially serious problems for long-term monitoring. First, the catching efficiency of particular net locations may decline as the vegetation height increases and birds increasingly fly over the tops of nets. Second, the composition of breeding passerine communities can be sensitive to successional changes to the vegetation (Fuller 1987, 1995), and therefore long-term population trends derived from CES data may be negatively biased for species which prefer early successional habitats, and positively biased for species which prefer later successional habitats. Little is known about the habitat preferences of juvenile passerines during the post-fledging period, though successional changes on CE stations have the potential to bias CES results for both adult birds and young birds.

A new system of habitat recording was introduced in 1995 to collect quantitative information on the extent and rate of habitat change on CE stations. This system involves the collection of three types of information describing an area extending 10 m from both sides of each standard mist net: (1) five habitat codes giving details of the major habitat type (following Crick 1992) and the presence of water; (2) the average maximum height of the scrub vegetation within 5 m of the net; and (3) the percent scrub cover within 10 m of the net. Fuller (1987) has shown that percent scrub cover is a useful predictor of the overall density of passerine birds and the total number of species breeding in scrub in southern England. Habitat codes are also requested for land surrounding the CE station.

At a smaller sample of CE stations we plan to collect net-specific capture and habitat data, which should allow us to consider relationships between habitat changes and capture rates at a finer scale. It might also be useful to have CE banders manage and maintain vegetation at fixed heights at some of their standard net locations (i.e., through regular cut back) while allowing the vegetation to grow up at others, and comparing changes in catch rates in managed and unmanaged net locations on the same stations.

Some insight into the likely importance of habitat succession as a factor affecting capture rates might be gained through analyses of the existing CES data. Trends in catch rates of species thought to be sensitive to successional change or changes in species composition could be compared in habitats considered to be sensitive and insensitive to successional change (e.g., scrub and woodland respectively). Analyses might allow for widescale population changes through the calculation of station-specific deviations in catches from those expected according to known regional population changes (derived, for example, from the British Breeding Bird Survey).

Effects of station turnover

Each year a number of CE stations drop out of the scheme and a number of new stations are enrolled. During the period 1987–1993, the average loss rate of CE stations was 8% per annum. If between-year changes in catches differ between stations which have just entered the scheme and stations just about to leave the scheme, then bias could be introduced into long-term indices of abundance or productivity. This might be the case if stations tended to be registered when they were catching relatively large numbers of birds and tended to be discontinued when they were catching relatively small numbers of birds.

Analyses of existing data could compare between-year changes in captures for stations at the beginning of their (CES) lives with those at stations that have been operated for some minimum number of years, or which are in their last few years as CE stations. This sort of analysis has been applied to CBC territory count data (S. Baillie and S. Gates, unpubl. data) and for most species considered, between-year changes in territory counts did not differ between plots at the beginning and end of their lives.

Representativeness of CE stations

For practical reasons relating to the efficiency of mist netting in different habitats, most CE stations are operated in either scrub or wetland habitats, and fewer than 10% of stations are operated in deciduous woodland. The CES scheme therefore monitors bird populations only in these habitats. Because banders choose the locations of their CE station, the national sample of CE stations may not be representative of scrub, wetland, and woodland habitats within Britain and Ireland.

Various land-use databases are now available for the U.K. region that could be used to examine the degree to which CE stations are representative of the wider landscape. The Centre for Ecology and Hydrology (CEH) has provided the BTO with remotely sensed land cover data for each 1-km square of Great Britain (Fuller et al. 1993). In 1990, the percent of each of 25 land cover types was measured in each 1-km square. The 25 land cover types are general categories such as "lowland bog," "scrub/orchard," and "deciduous wood." Recently a further land-cover survey has been completed and more up-to-date data are now available (Fuller et al. 2002). Such information will be used to assess whether the habitat within 1-km squares containing CE stations is broadly representative of the squares containing predominantly scrub and wetland (and perhaps woodland) habitat. This could be done both for the entire United Kingdom and within broad regions. An obvious problem here will be the definition of a subset of squares which represents the "scrub and wetland" component of Great Britain.

Validation of annual CES productivity indices

The proportion of young birds in catches made on CE stations represents an integrated measure of annual productivity, which incorporates the number of nesting attempts per pair, nesting success, and immediate post-fledging mortality. Any comparative assessment of annual productivity should ideally incorporate all these factors.

Each year the BTO Nest Records Scheme collects information on approximately 30,000 nest histories (Greenwood et al. 1993). This information can be used to estimate average laying dates, clutch sizes, egg survival rates, and chick survival rates for a wide range of species, including most of those currently being monitored by the CES scheme. For some CES species, annual estimates of post-fledging mortality could be attained from the U.K. national banding recovery data using the methods developed by Thomson et al. (1999).

For species that are essentially single-brooded (like Willow Warbler and the *Parus* tits), it should be possible to combine estimates of nesting success with those for post-fledging mortality, producing independent annual estimates of productivity that could be compared with the percent of young birds caught at CE stations. For multi-brooded species, it may be difficult to obtain any extensive measure of the number of breeding attempts. The distribution of laying dates from nest record cards, or the temporal distribution of heavy (gravid) females (Naylor and Green 1976) or brood patches at differing stages of development (Boddy 1992) as recorded by banders, may provide some information on annual variation in the number of breeding attempts, although all such approaches would require critical evaluation. Intensive studies may be required to measure annual variation in the number of breeding attempts.

Comparison of results from CES and intensive studies

Intensive local studies have an important role to play with respect to both the validation and the interpretation of data generated through extensive monitoring programs like the CES scheme. Where possible, intensive studies should be replicated across many locations in order to allow general conclusions to be drawn.

For example, independent assessments of the abundance of adults birds on CE stations would be useful to compare against catches. Between 1985 and the early 1990s, timed point counts were carried out during May and June at a sample of CE stations (34 stations in 1985 and 10 stations in 1993). These count data will provide useful independent estimates of local breeding population sizes and between-year changes in those populations. Some additional comparative count data are available from a small number of stations in the form of intensive territory mapping counts (e.g., Peach et al. 1995).

Another source of high quality count data is observation of individually marked adult birds, which can also provide a range of information concerning territorial and breeding behavior and site fidelity. Color-banding of chicks or of juveniles could provide useful information on site fidelity and dispersal, and could be a useful tool for the study of net avoidance.

Intensive banding programs for nestlings can provide useful information on local nesting success, for comparison with productivity indices from mist netting (as shown by Nur and Geupel 1993b, du Feu and McMeeking *this volume*). Species using nest boxes are obviously convenient for such studies, whereas finding nests of open-nesting passerines can be time consuming. If a high proportion of locally fledged young are banded as chicks, then it is also possible to apportion the total juvenile catch into local and non-local components. For some species, a high proportion of the total juvenile catch may be of non-local origins (Naylor and Green 1976, Nur and Geupel 1993b).

Finally, the BTO is seeking to develop a small network of Integrated Population Monitoring (IPM) Stations at which intensive standardized mist netting is combined with intensive territory mapping, nest-finding, and color-banding of nestlings and adults. The main aim of these IPM stations is to generate high quality demographic data over long runs of years, but a secondary aim is to provide locations for replicated validation studies.

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RELATIONSHIP OF JUVENILES CAPTURED IN CONSTANT-EFFORT NETTING AND LOCAL ABUNDANCE

CHRIS R. DU FEU AND JOHN M. MCMEEKING

Abstract. Numbers of juvenile Blackbirds (*Turdus merula*), Song Thrushes (*T. philomelos*), Blue Tits (*Parus caeruleus*), and Great Tits (*P. major*) caught during constant effort mist-netting were compared with numbers of nestlings of these species banded during the years 1979–2002 in Treswell Wood, Nottinghamshire, England. There was a significant relationship between the annual numbers of juveniles captured and the annual numbers of nestlings banded in all four species. Mortality and immigration between fledging and mist-netting periods probably vary among years, reducing the strength of correlation. Results suggest that number of young birds captured in the British Trust for Ornithology Constant Effort Sites scheme across many sites is a good index of the number of young in the population following juvenile dispersal.

Key Words: constant-effort mist netting, Constant Effort Sites, productivity, banding.

The index of productivity used by the Constant Effort Sites (CES) scheme of the British Trust for Ornithology is the ratio of juveniles to adults totalled over a large number of study sites (Peach and Baillie 1990). The assumption underlying this index is that the numbers of adults and young birds captured are proportional to the true numbers of each age group in the population. This has been tested for adults by comparing CES data from many sites with results from the Common Birds Census (Peach et al. *this volume*), with positive results. Here we present evidence to support the assumption that young birds are also captured in proportion to their abundance, using data from a single site. Some of the data were previously published (du Feu and McMeeking 1991), but this paper includes additional data and discussion.

We compared numbers of nestlings banded that were deemed to have fledged with numbers of young birds captured in mist nets during the summer. There are many reasons to expect that these numbers might not be correlated. Not all birds produced at the study site will be banded as nestlings. All nestlings do not fledge at the same time as each other, or at the same time each year, which affects numbers captured in mist nets. Dispersal and mortality of young occurs throughout the netting period, and captures are affected by weather. Captures of juveniles of flocking species in mist nets may not be independent of each other. Such factors could potentially invalidate the use of juvenile captures in mist netting as an index of local fledging success.

METHODS

Treswell Wood is composed of 47 ha of mature broad-leaved trees, mainly ash (*Fraxinus excelsior*) with some oak (*Quercus robur*), with an understory predominantly of hazel (*Corylus avellana*). It is an ancient woodland designated as a Site of Special Scientific Interest, owned and managed by the Nottinghamshire Wildlife Trust. Since 1972 the Trust has restored the traditional system of "coppice with standards" (Cramp and Simmons 1977) to parts of the wood.

We have carried out year-round constant-effort mist netting at seven sub-sites in Treswell Wood since 1978. Our netting regime differs from that of the CES regime, which specifies 12 evenly spaced visits to each site throughout the months May to August inclusive. Instead, we visit each of our seven sites in the Wood five times a year, approximately once every 10 weeks. The exact order of visiting the sites varies according to weather, for some sites are more affected by wind than others, but it is kept as constant as possible from year to year. On each visit we use ten 18-m nets, in fixed positions, set for five hours from shortly after dawn. If conditions allow, extra nets are erected. Such extra nets are not sited immediately adjacent to the standard nets, to prevent interference with the standard nets. Birds caught in additional netting are not included in our constant effort analyses.

About 100 nest boxes, primarily for tits (*Parus* spp.), have been placed in the northern two-thirds of the wood. The number and distribution of boxes have remained relatively constant since 1979. We record all nests in boxes, and band all chicks. Although we make no attempt to find non-box nests, we record all natural nests of any species we detect while on the nest box rounds (e.g., when an adult is flushed from the nest), and chicks in those nests are also banded. Nest checks have been done by the same person (CdF) each year. Because the distribution of boxes is much the same from year to year, the opportunity for finding other nests is also approximately the same. No nestling tits have been banded other than those in boxes, but we have banded enough Blackbirds (*Turdus merula*) and Song Thrushes (*T. philomelos*) to analyze them here.

We assume that any bird banded has also fledged, unless there is evidence to the contrary. Such evidence includes finding carcasses of young in the nest when the boxes are emptied at the end of the season. Sometimes predators attack nests and leave a few partially dismembered bodies, in which case we assume that all chicks failed to fledge. Evidence for success includes finding undamaged but flattened empty nests with many flakes of feather sheath, nestlings capable of fledging when last seen in the nest, and newly fledged juveniles in the vicinity of nest boxes. There have been almost no direct observations of birds fledging from nests.

A Common Bird Census (CBC) is carried out in the wood by other workers. For all years, we have a record of the total numbers of territories recorded, but a breakdown of where these territories lay within the Wood is available only for some years (1981–1994 and 1997–1998).

In this paper, we compared the numbers of banded Blackbirds and Song Thrushes deemed to have fledged each year with the numbers of free-flying juveniles caught in mist nets between 28 May and 15 August (1979–2002). These dates correspond approximately to the CES breeding season sampling period. We also compared the numbers of nestling Blue Tits (*Parus caeruleus*) and Great Tits (*P. major*) fledging from boxes with the numbers of juveniles mist netted in the same period. We use the terms "sampling period" for the late May through August netting period and "study period" for the years 1979–2002.

Because data for both numbers of nestlings banded and juveniles caught are count data, we used log(N+1) transformations in correlation analyses, as described in Fowler and Cohen (1986). Scatter diagrams were plotted on logarithmic axes and all regression lines were fitted using the model 2 reduced major axis regression described by Fowler and Cohen (1986).

RESULTS

Annual numbers of each species banded as nestlings within the wood, and the numbers of juveniles captured in constant effort nets in the sampling period are given in Table 1. We found a significant, positive correlation between these annual numbers for all four species: Blackbird ($r = 0.49$, $N = 24$, $P = 0.02$), Song Thrush ($r = 0.40$, $N = 24$, $P = 0.05$), Blue Tit ($r = 0.64$, $N = 24$, $P = 0.001$), Great Tit ($r = 0.46$, $N = 24$, $P = 0.03$). Only four points lay more than two standardized residuals away from any regression line

TABLE 1. NUMBERS OF NESTLINGS BANDED AND FLEDGED AND OF JUVENILES CAPTURED IN CONSTANT-EFFORT MIST NETTING BETWEEN 28 MAY AND 15 AUGUST EACH YEAR

	Blackbird		Song Thrush		Blue Tit		Great Tit	
Year	Nestlings banded	Juveniles captured	Nestlings banded	Juveniles captured	Nestlings banded	Juveniles captured	Nestlings banded	Juveniles captured
1979	14	16	33	2	91	0	65	4
1980	9	8	10	4	222	7	51	5
1981	0	5	6	4	215	45	55	9
1982	0	3	4	2	171	10	49	0
1983	7	4	14	4	117	5	48	5
1984	12	5	27	2	147	8	60	5
1985	9	10	14	0	175	11	104	3
1986	13	9	26	2	226	0	125	0
1987	3	3	15	1	261	30	133	30
1988	5	2	6	0	104	8	74	5
1989	0	5	3	2	242	46	132	14
1990	0	0	0	1	173	17	38	2
1991	3	0	0	0	120	1	44	4
1992	0	0	4	4	130	0	66	9
1993	0	1	0	0	85	1	22	0
1994	0	6	6	6	120	4	21	1
1995	5	6	8	0	171	18	66	2
1996	4	6	2	2	113	3	18	3
1997	3	6	0	0	93	2	65	2
1998	0	1	0	1	41	1	20	2
1999	0	4	0	2	108	2	90	6
2000	3	1	5	2	88	0	43	1
2001	4	1	0	0	87	0	46	1
2002	4	2	8	2	63	2	70	3
Totals	96	104	191	43	3363	221	1505	116

(Fig. 1). These were the points for Blue Tit in 1986 and 1998 and for Great Tit in 1986 and 1996.

There was significant correlation between numbers of Song Thrush nests (1981–1994 and 1997–1998) and the numbers of Song Thrush territories recorded by CBC in the section of the Wood in which boxes were present ($r = 0.77$ for transformed annual indices, $N = 16$, $P < 0.001$; Fig. 2). The correlation for Blackbirds was not significant ($r = 0.39$, $N = 16$, $P = 0.14$).

DISCUSSION

Here we examine some of the probable causes of variance in the correlations between number of nestling-banded birds deemed to have fledged and number of juveniles captured during summer mist netting.

Proportions Banded

The relationship between nestlings banded and juveniles captured was weaker for Song Thrush and Blackbird than for the tit species. A contributing factor was the relatively low proportions of the nestling populations of Song Thrush and Blackbird that were banded. The correlation between Song Thrush nests found and CBC territories (Fig. 2) suggests there was fairly constant nest finding effort, although data for Blackbirds do not support this as strongly. Nest-finding effort was not exhaustive, however, and although 605 Blackbird and 327 Song Thrush CBC territories were recorded in the study period, only 55 and 104 nests were found, respectively. Because both species are multiple brooded, the overall percentage of nests found is unlikely to be higher than 10%. The percentages of juveniles banded at nests and later caught in constant effort nets, 0% for Blackbirds and 9.7% for Song Thrushes, are compatible with this low figure. The number of juvenile Song Thrushes netted has always been so low that chance factors are relatively important in determining variation in numbers. Thus, it is not surprising that the correlation between the numbers of nestlings banded and the numbers of juveniles netted was weakest in this species.

For tits, the number of nests in natural sites is

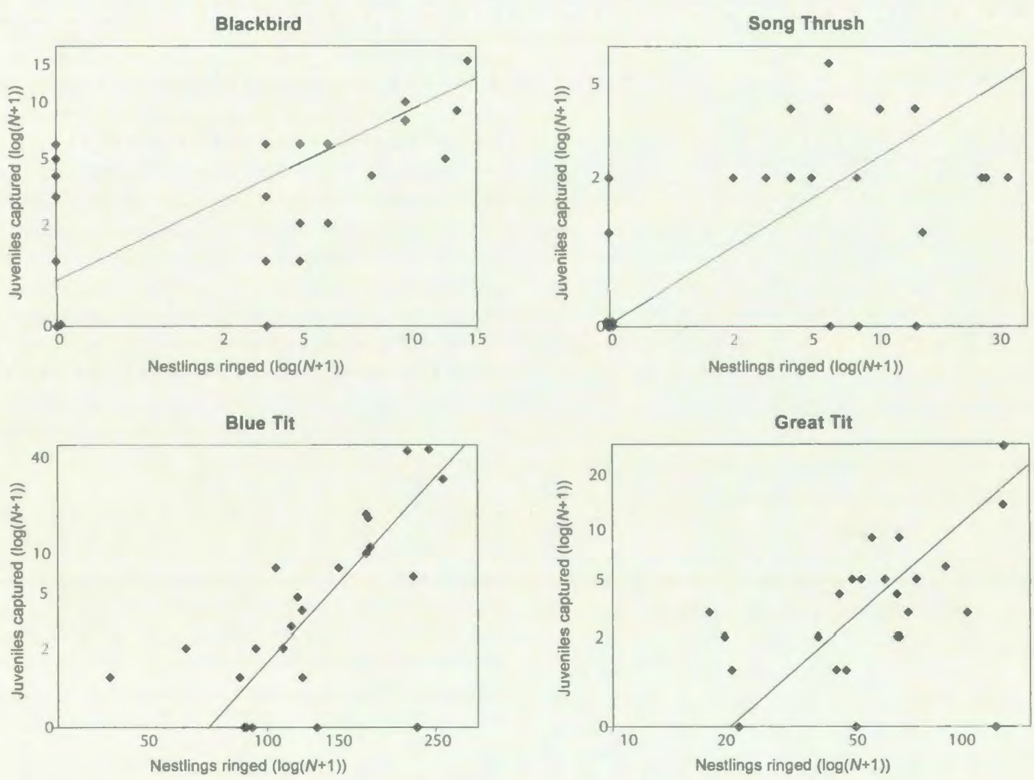

FIGURE 1. Nestlings banded and juveniles captured in constant-effort mist nets in Treswell Wood, 1979–2002 (model 2 reduced major axis regression method).

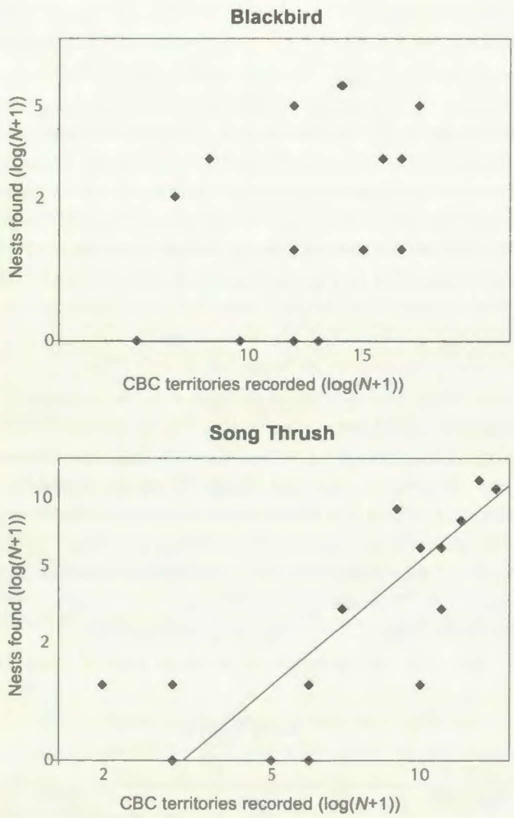

FIGURE 2. Blackbird and Song Thrush Common Bird Census (CBC) territories recorded vs. nests found, 1981–1994 and 1997–1998.

unknown, as is the number of young fledged from such sites. We have never banded nestling tits in natural sites. During the study period, 41% and 37% respectively of the juvenile Great Tits and Blue Tits captured in constant effort nets in the sampling period had been banded as nestlings. This suggests either that there are many natural nests (producing up to 60% of all nestlings), or that many juveniles captured in mist nets had moved in from elsewhere (see below). Several lines of evidence indicate that the first explanation is correct and the second has little influence.

Over 24 years, the percent of adult female tits captured in the spring in constant-effort mist nets that were later found nesting in boxes was 27% for Great Tits and 17% for Blue Tits. These percentages are lower than those given by Perrins (1979) for the percentage of these tits using boxes in Wytham Wood. However, in Treswell Wood we did not capture all females nesting in boxes every year. (For Blue Tits, 86% of females nesting in boxes were captured, but the figure for Great Tits was only 56%.) Moreover, one-third of the Wood contained no nest boxes. Another estimate of the proportion of tits nesting in boxes is the ratio of occupied nest boxes to the number of CBC territories found in the same part of the Wood. This ratio was 0.29 for Great Tit nests and 0.31 for Blue Tits, although the ratio may be biased by miscounts due to unsuccessful and replacement clutches, and by the use of nest box data in CBC.

Whereas all lines of evidence indicate that less than half of nestling tits were banded each year, the proportion is much higher than for Song Thrush and Blackbird, and is less likely to have varied among years simply as a result of chance.

Fledging Period

Song Thrush and Blackbird are multi-brooded, and it is probable that many of the year's juveniles were already dead by the time the sampling period began, whereas others had not yet fledged. Because mist-net data were collected over several visits, however, the total sample of juveniles should be relatively unaffected by variation in timing of the breeding season. Tits, on the other hand, are almost exclusively single brooded, all fledge within a relatively short period, and fledging dates vary from year to year. This means that in late years there were fewer mist-netting sessions after nestlings had fledged and become available for capture.

To gain insight on the effect of fledging date variation on the correlation between nestlings banded and juveniles captured, we reanalysed data omitting the last two netting visits in each year. Although correlations remained more or less the same for the two thrushes and Blue Tits, the correlation was considerably weakened for Great Tits. In Treswell Wood, Great Tits nest nearly a week later than do Blue Tits. This result demonstrates the importance of ensuring that sampling periods extend far enough into the summer to ensure a representative number of individuals will be trapped.

It is likely that the complete absence of juvenile tits captured in 1986 (Table 1) was primarily a consequence of the very late season (which was also followed by high post-fledging mortality caused by lack of food late in the season). The percentage of nest box-banded birds recaptured by the end of the study period was also lower for the 1986 cohort than for any other year.

Movement and Dispersal

Lack of correspondence between mist-net samples of juveniles and number of locally banded nestlings could reflect changes in the local population of young birds between the two samples. Such changes could reflect dispersal and immigration, or mortality.

Perrins (1979) states that after the first month after fledging, there is local redistribution of tit populations, with some new birds moving into the area and some natives moving out. Our sampling period ends during this redistribution period, and we have only a little evidence for it. Two young Blue Tits and one Great Tit were captured between 4 and 8 km away from the Wood within the sampling period, and several more were captured elsewhere shortly after the end of the sampling period. Evidence of movement into the Wood came from one Blue Tit that fledged from a nest box on a farm to the south of the Wood and was captured 1.5 km away within 10 days, in the northern part of the Wood. However, because the proportions of nest box-banded tits captured later in constant effort netting were so close to the estimates of percentages of all nests that were in boxes, it appears that juvenile dispersal did not have a great effect by the time our sampling period ended.

Reanalysis of the data with the last two sessions removed made little overall difference to the strength of the relationships for the three earliest fledging species. This provides further evidence that any local dispersal has not had a major impact by the time the sampling period ends.

Mortality

Two of the four points in Figure 1 with standardized residuals >2 were 1996 for Great Tits and 1998 for Blue Tits (the left-most points on the graphs in Fig. 1). In both of these years there was massive mortality of nestlings in nest boxes, largely through predation. Both species suffered in each of these years, although Great Tits rather more in 1996 and Blue Tits more in 1998. It is not known whether the predation was equally great amongst tits that nested in natural sites. Neither is it known whether predation of nests was equally great in the area surrounding the Wood. Although very few juveniles were mist netted in the standard nets in these years (three Great Tits 1996, one Blue Tit in 1998), these numbers were higher than expected (Fig. 1). Possibly this was a chance result, but may also have represented immigration from areas with lower predation.

Lack (1966) discussed the causes, timing, extent, and variation of post fledging mortality for Great Tits and Blue Tits. He found that there is heavy mortality before the beginning of November, most of it in the first month after fledging. W. Peach (pers. comm.) suggests that this mortality is greatest in the first few days after fledging. In these few days juveniles will be relatively immobile, waiting high in the tree canopy for parents to bring food, and so are particularly vulnerable to predators. Instances of early death caused by predators have been provided by bands, from one Blue Tit and two Great Tits, recovered from owl pellets within our sampling period. In some years, we also noted very heavy predation on Song Thrush nests, often at a late stage. In some cases a Tawny Owl (*Strix aluco*) systematically raided Song Thrush nests, as shown by bands of nestlings being found in the owl's nest. Blackbirds seem not to have suffered systematic nest predation by the owls, as we have only ever recovered one single Blackbird nestling band from any owl nest.

The level of immediate post-fledging mortality depends, among other things, on population size, weather, food availability, predator activity, and brood sizes. It varies greatly from year to year, and therefore weakens the relationship between number of juveniles mist netted and number of nestlings banded. However, the fact that there is correlation between number of juveniles captured and numbers banded in the nest suggests the immediate post-fledging mortality is generally similar from year to year (with the possible exception of 1986).

Capture Patterns

A major problem in any estimate of productivity based on captures of tits in mist nets lies in the erratic nature and non-independence of captures. In the early post-fledging period, tits may remain in family parties. Thus whole families are often captured together rather than as individuals. Later young tits join mixed species flocks and, again, captures tend to be of groups rather than of individuals. The flocks often spend much of their time high in the tree canopy, out of range of mist nets. Therefore tits can be abundant, but not be captured. Nonetheless, there are very few years in which we missed capturing at least some of the flocking birds. The distorting effect of flocking on mist-net captures is well illustrated by the 1980 data. Tits were abundant in 1980 (Table 1) and there was high survival, but the constant effort captures were relatively low. In fact many juvenile tits were caught but, by chance, these captures were in netting that was not part of the constant effort program, and so did not contribute data to this analysis.

CONCLUSION

For all four species considered, there was significant correlation between the numbers of young birds caught in mist nets and the numbers of banded nestlings deemed to have fledged. Despite variance introduced by the factors discussed above, number of juveniles captured in summer appeared to provide a good index of local productivity in most years.

The CES productivity index is compiled using data from many sites (typically well over 100), such that atypical captures at one site are unlikely to bias the national index. Moreover, the CES productivity index is meant to reflect numbers of juveniles surviving the immediate post fledging period, and the index was neither intended nor expected to represent site-specific productivity. Early post-fledging mortality and dispersal therefore pose little problem for the CES scheme. Nonetheless, the fact that relationships can be demonstrated between constant effort captures and known numbers of nestlings on a single site encourages confidence that constant effort data from many sites combined will provide a measure of juvenile abundance that can reliably be used in calculating indices of adult productivity.

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ESTIMATES OF ADULT SURVIVAL, CAPTURE PROBABILITY, AND RECAPTURE PROBABILITY: EVALUATING AND VALIDATING CONSTANT-EFFORT MIST NETTING

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Abstract. We evaluate the use of capture–recapture data gathered with constant-effort mist-netting to infer adult survival, comparing estimates obtained using the program SURGE with direct observations on color-banded individuals. In addition, we determined capture probability of breeding adults in relation to several factors, such as distance from nest to nearest net. Data were collected as part of a long-term, on-going study of species breeding at the Palomarin Field Station, Point Reyes National Seashore, concentrating on Wrentits (*Chamaea fasciata*). Capture probability of breeding Wrentit adults was strongly related to distance from nest to nearest net and, independently, to the number of intervening territories between nest and net. In addition, females (and their mates) laying early in the season were less likely to be caught than those laying later. Breeding adults whose nests were more than 200 m from the closest mist net were rarely caught. Most adults caught were transient individuals, not holding local breeding territories. Territory-holders were caught repeatedly; non-territory holders were not. Recapture probability of territory-holders in the following year (if alive) was estimated at 71%, but only at 5% for those not holding local territories. Survival of Wrentit breeding adults was estimated to be 57%, which was slightly below estimates based on re-sightings (59% to 64%). However, survival estimated on the basis of capture–recapture of all adults (ignoring territorial status) was only 38%. We suggest that, in the absence of information regarding territorial status, survival analyses be restricted to individuals caught at least twice in a season. This is an effective method for screening out transient individuals.

Key Words: capture–recapture, constant effort netting, productivity, survival, transients, validation, Wrentit.

Populations of certain North American landbird species appear to be declining strongly (reviewed in Hagan and Johnston 1992, Finch and Stangel 1993). For effective management responses to be formulated, underlying causal factors responsible for the declines must be identified. To understand the causes of population decline requires detailed demographic information. However, the primary, long-established North American monitoring programs, specifically the Breeding Bird Survey, do not provide this information.

The three most critical demographic processes underlying population growth and decline are (1) adult survivorship, (2) reproductive success (i.e., production of young, or "productivity"), and (3) recruitment of young into the breeding population. These three demographic components are the most critical because the change in breeding population size from one year to the next, representing decline or recovery of a species, can be directly attributed to a combination of these three components (provided that immigration balances emigration). The need for researchers, managers, and agencies to assess such primary demographic parameters has been repeatedly stressed by many authors (Temple and Wiens 1989, DeSante et al. 1993b, Nur and Geupel 1993b).

Mist-netting appears to be a potentially powerful and efficient means of collecting critical data on demographic parameters such as annual survival and reproductive success, and is the cornerstone of several monitoring programs, including the Constant Effort Sites (CES) Scheme of the British Trust for Ornithology (Baillie et al. 1986, Bibby et al. 1992, Peach 1993, Peach et al. *this volume*), and, more recently, the Monitoring Avian Productivity and Survivorship (MAPS) program of the Institute of Bird Populations (DeSante et al. 1993b, *this volume*). However, the accuracy and validity of inferences based on mist-netting data have only recently been studied (though see du Feu and McMeeking 1991), and we know little about the limitations of data derived from constant effort mist-netting (CEM). Finally, in the absence of information on the specific portion of the sampled population to which mist-netted birds belong, it is impossible to develop methods of data collection and data analysis that best measure demographic parameters of the target portions of the population (such as local breeders).

Both CEM and intensive observations of color-banded individuals have been underway at the Point Reyes Bird Observatory (PRBO) since 1980. Because the same population has been studied with different methodologies, we are able to evaluate demographic inferences made using the CEM methodology, by comparing results with inferences made using a second methodology. In addition, we are able to estimate capture probability, which is rarely known for natural populations, and evaluate whether captured individuals are a random sample of those present at the breeding site.

Here we report selected results of a project that we refer to as "The Mist-Net Validation Study," with regard to adult survival, capture probability, and recapture probability. We consider factors influencing capture and recapture probability, which could therefore bias demographic estimates. In this paper, we report results from a single site over the period 1981–1991. Additional aspects of the project have been reported in Silkey et al. (1999) and Nur et al. (2000).

METHODS

The study species is the Wrentit (*Chamaea fasciata),* which has been the subject of relatively little prior study (Erickson 1938, Geupel and DeSante 1990, Geupel and Ballard 2002). Wrentits are monogamous, year-round, territorial residents, and both parents share in parental care such as nest-building and incubation. The Wrentit is considered to be quite sedentary (Erickson 1938, Johnson 1972), and we found that <1% of breeders move their territories between years on our study site (Geupel and DeSante 1990, Geupel and Ballard 2002). This make the species well suited for estimating survivorship on the basis of capture–recapture data. Wrentits maintain year-round territories and that, together with the sedentary nature of this species, makes them good candidates for a validation study, because birds observed on the study grid are likely to be the same ones caught in the nets.

The field work was conducted at PRBO's Palomarin Field Station, located just within the southern boundary of the Point Reyes National Seashore and adjacent to the Pacific Ocean. On the main 36 ha study site, we simultaneously carried out constant effort mist-netting, nest searches, intensive spot-mapping, and behavioral observations of color-banded individuals.

Constant effort mist-netting was conducted using 20, 12-m mist nets comprising 14 netting sites (Fig. 1). Eight sites (14 nets) were located on the edge of mixed, evergreen forest habitat comprised primarily of coast live oak (*Quercus agrifola*), California bay (*Umbellularia californica*), Douglas-fir (*Pseudotesuga menziesii*), and California buckeye (*Aesculus californicus*). The other six single nets were located in disturbed coastal scrub, which is the preferred habitat of Wrentits (Erickson 1938, AOU Check-list 1983). This was composed primarily of coyote bush (*Baccharis pilularis*), California sage *(Artemisa californica*), bush monkey flower (*Mimulus aurantiacus*), poison oak (*Rhus diversiloba*), California blackberry (*Rubus vitifolius*), and California coffeeberry (*Rhamnus californica*) interspersed with introduced grasses. For further description of the study area see DeSante and Geupel (1987) and Silkey et al. (1999).

Net locations were adjacent to, and extended across, approximately 25% of the 36 ha study plot (Fig. 1). Net locations were selected so as to maximize the number of birds caught (L. R. Mewaldt, pers. comm.). The standardized mist-netting procedure was described by DeSante and Geupel (1987) and continued with only minor change during the study period, 1981–1991. Briefly, nets were run 7 days/week for 6 h, beginning 15 min after local sunrise (weather permitting) from 1 May (from 1 April prior to 1989) to approximately 25 November, and 3 days/week (Wednesday, Saturday, and Sunday) from December through end of March (through end of April, since 1989).

Detailed monitoring of individuals was conducted on the 36-ha study plot and has been described elsewhere (Geupel and DeSante 1990). In brief, identities and territory boundaries of color-marked individuals were determined from detailed spot-mapping censuses conducted a minimum of 3 days/week during the breeding season (15 March–31 July) throughout the 11 years of the study. Each territorial individual was observed a minimum of once every two weeks, and normally at least once per week.

Concentrated efforts were made to locate and monitor all nest attempts of all territorial pairs on the study area from 1981 through 1985, and from 1987 through 1991. No attempt was made to locate nests in 1986 and effort was reduced in 1980, hence we excluded those years from analyses of fledged young. The method of locating and monitoring Wrentit nests was described in Geupel and DeSante (1990). Nearly all successful nests (those fledging one or more young) were found before fledging, and nestlings were individually color-banded. Additional individuals were color-banded when first caught in mist-nets as hatching year (HY) or as after-hatching year (AHY) birds.

Here we analyze survival and capture probability with respect to territorial status; all individuals were classified as "territory holders" or "non-territory holders" according to whether or not they were known to maintain breeding territories on or adjacent to the study grid. Whereas all territory holders were presumed breeders (which could be confirmed through nest-finding and monitoring), non-territory holders were mostly transient individuals. Non-territory holders may have been "floaters" (*sensu* Stutchbury and Zack 1992), but it is also possible that some individuals bred outside the study area. Note that some non-territory holders were floaters displaying local site fidelity (Nur et al. 2000).

We examined differences in capture rates (per season and over the observed lifetime of individuals) for adults, comparing territory holders and non-territory holders, using Poisson regression (StataCorp 1997). We used linear models to test for differences in capture dates between known territory holders and non-territory holders (Neter et al. 1990), after determining that assumptions of this method were met (Nur et al. 1999). We evaluated differences in capture probability of territorial (breeding) adults with respect to distance of the nest from nearest net, number of