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SURVIVAL, PRODUCTIVITY, AND ABUNDANCE IN A WILSON'S WARBLER POPULATION

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ABSTRACT.—We analyzed patterns in the abundance, productivity, and survivorship of a coastal California population of Wilson's Warbler (*Wilsonia pusilla*) using capture-recapture data from 18 years of standardized mist-netting conducted during the breeding season. The numbers of adult and hatching-year birds captured each year showed no consistent trend through time. The total number of adults captured annually, an index of adult abundance, was positively related to productivity in the previous year as indexed by the number of hatching-year birds captured. In addition, the number of adults captured for the first time at the study site, an index of new adults entering the population, was positively related to the previous year's productivity. There was a positive correlation between the numbers of summer residents and transients captured in each year. Estimated annual adult survival of summer residents was 50.3%. The annual recapture probability for summer residents (68.8%) was much greater than for presumed transients (7.2%). When the difference in recapture probability between summer residents and transients was ignored, annual survival was underestimated (30.5 %). Year-to-year variation in survival showed no relationship to annual fluctuations in adult abundance. These patterns of survival and productivity parameters suggest that abundance in this population has been influenced primarily by circumstances on the breeding grounds. *Received 17 May 1996, accepted 10 January 1997.*

EVIDENCE OF DECLINES in North American landbird populations has led to widespread efforts to monitor population trends and to identify the causes of population fluctuations (Robbins et al. 1989, Hagan and Johnston 1992, Finch and Stangel 1993). In theory, fluctuations in population size may be influenced by variation in reproductive success, survival and recruitment of young into the breeding population, adult survivorship, immigration, or emigration (Nur and Geupel 1993a). Variation in reproductive success has been suggested as a major cause of fluctuations in the abundance of Neotropical migrants, and several studies have found evidence that the recruitment of new breeders into populations of long-distance migrants is positively correlated with reproductive success in the previous summer (Nolan 1978, Sherry and Holmes 1991, Holmes et al.1992, Johnson and Geupel 1996). Evidence also suggests that variation in mortality during migration and over winter are important factors influencing the abundance of migratory birds (Holmes et al. 1989, Robbins et al. 1989, Peach et al. 1991, Rappole and McDonald 1994). Clearly, studies examining the demographic parameters of migratory bird populations are critical to identifying the proximate causes of population fluctuations (Temple and Wiens 1989; Sherry and Holmes 1991, 1992; Verner 1992).

We studied the dynamics of a coastal California population of Wilson's Warbler (*Wilsonia pusilla*) using 18 years (1979 to 1996) of standardized mist-net data. We estimated three demographic parameters: abundance, productivity, and adult survival. Using the capture rate of adults as an index of abundance, we looked for evidence of long-term trends. To generate insight into the demographic mechanisms influencing population fluctuations, we investigated the relative influence of productivity and adult survival on adult abundance. To examine the influence of productivity on the variation we observed in abundance, we investigated the relationship between productivity in one year and the number of adults captured in the following year. We estimated annual recapture and survival probabilities of adult Wilson's Warblers by analyzing capture/recapture data (Lebreton et al. 1992). To examine the influence of survival on annual variations in abundance, we investigated the relationship between an-

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nual survival estimates and the number of adults captured in the following year.

STUDY AREA AND METHODS

As part of ongoing research and monitoring efforts, constant-effort mist netting was conducted at the Palomarin Field Station of the Point Reyes Bird Observatory from 1979 through 1996. The study area is located within the Point Reyes National Seashore, Marin County, California, adjacent to the Pacific Ocean. Twenty 12-m mist nets were placed at 14 different sites (at six sites two nets were stacked vertically) along an ecotone between forest and scrub habitats, and each net was located within 200 m of all other nets. Eight sites (14 nets; mesh size = 30 mm) were located along the edge of a riparian woodland containing a small perennial stream. The predominant forest plant species were coast live oak (*Quercus agrifolia*), California bay (*Umbellularia californica*), Douglas fir (*Pseudotsuga menziesii*), and California buckeye (*Aesculus californicus*). The other six single nets (mesh size = 36 mm) were located in adjacent coastal scrub, composed primarily of coyote bush (*Baccharis pilularis*), California sagebrush (*Artemisia californica*), bush monkeyflower (*Mimulus aurantinius*), and poison oak (*Rhus diversiloba*). Only three of these six nets were located more than 10 m from the riparian woodland habitat. A more detailed description of the study area is found in DeSante and Geupel (1987) and Johnson and Geupel (1996).

Study species.—The Wilson's Warbler is a Neotropical migrant with a wide breeding range in North America and a wide wintering range in Mexico and Central America (AOU 1983). Spring migration occurs in California from mid-March through May (Grinnell and Miller 1944, Otahal 1995). Fall migration begins in early to mid-August, and the majority of southbound migrants pass through California in late August and September (Grinnell and Miller 1944, Small 1994, Otahal 1995). Data from a banding station on Southeast Farallon Island, located 32 km offshore of our study area (where no Wilson's Warblers breed), indicate that approximately 85% of fall migrants pass through after 15 August (Pyle and Henderson 1991). Wilson's Warbler life history in the Palomarin study area was described by Stewart (1973) and Stewart et al. (1978). In summary, territorial males begin to arrive in mid-March, females arrive one to two weeks later, and pair formation begins an average of 15 days after the arrival of the males. Males typically defend territories against their neighbors, although breeding birds occasionally are seen or caught up to 300 m from their territories. Open-cup nests are built 30 to 80 cm above ground almost exclusively in the riparian woodland, especially in dense tangles of blackberry (*Rubus* sp.). Stewart et al. (1978) observed a return rate of 60.8% for color-banded males.

Netting protocol.—Nets were opened 15 min after sunrise and left open for 6 h, weather permitting. In April, nets were operated daily from 1979 through 1988 and three times per week from 1989 through 1996. Nets were operated six to seven days per week from May through August, 1979 to 1996. In all our analyses we used the number of individual birds captured per 1,000 net-hours, to standardize capture rate by netting effort. Captured Wilson's Warblers were banded and aged as either hatching-year or after-hatching-year based on skull pneumatization (Pyle et al. 1987). Second-year birds were not reliably distinguishable from after-second-year birds. Birds were sexed by plumage using the criteria of Pyle et al. (1987) and by the presence or absence of a brood patch or a cloacal protuberance.

Classification of captures.—To estimate adult abundance, we considered captures of adults from 1 April through 15 August. Ideally, our index of adult abundance would be based on captures of local breeders and not on captures of transient individuals. Here we use the term "transients" in a broad sense to refer to migrants, floaters, and other non-territorial adults. We considered several ways to distinguish local breeders from transients. Because locally breeding individuals are among the earliest Wilson's Warblers to arrive at the study area (Stewart 1973), spring arrival dates cannot be used to distinguish migrant adults from local breeders, and 1 April was chosen to include the earliest captures of local adults in most years. The presence of a brood patch or cloacal protuberance also cannot be used to distinguish local breeders, because non-local adults that still have signs of breeding condition move through the study area in June (Stewart 1973). The 15 August ending date was chosen to exclude the majority of fall migrants, based on published information on migration chronology in California (Grinnell and Miller 1944, Pyle and Henderson 1991, Small 1994, Otahal 1995).

Other studies have used within-year recapture data to distinguish site-attached adults (summer residents) from transients (Peach et al. 1991, Nur and Geupel 1993a, Peach 1993, Poulin et al. 1993, Johnson and Geupel 1996). We defined summer residents as those adults that were captured more than once within a season, with at least seven days between first and last captures, and defined the remaining adults as transients. Studies of stopover length in other Neotropical migrants have found that migrants generally do not stay in one area for more than seven days (Rappole and Warner 1976, Moore and Kerlinger 1987). Although we lack data on stopover duration of Wilson's Warblers during autumn, Otahal (1995) reported that most (88%) recaptures of spring migrants occur less than seven days after first captures. Based on the criterion outlined above, we then

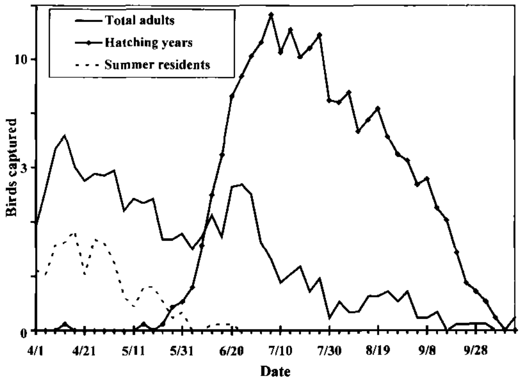

FIG. 1. Mean number of adult, hatching-year, and summer resident Wilson's Warblers captured during four-day periods from 1 April to 14 September, 1979–1996 (first capture of each individual in each year). Summer residents are adults captured more than once in a year with at least seven days between first and last captures. Note logarithmic scale of vertical axis.

examined the relationship between capture rates of summer residents versus transients to determine if these rates provide comparable indices of adult abundance.

In addition, we used the capture rate of new adults as a potential index of recruitment. Because Wilson's Warblers that have bred in previous years tend to return to territories that they established previously (Stewart 1973), birds that are adults at the time of their first capture in the study area are in many cases second-year birds that are making their first northward migrations. The use of "new" captures as an index of recruitment assumes that capture rates of new adults are proportional to the number of adults recruited into the population. We defined the capture rate of new adults to include capture of any unbanded adult and the first after-hatching-year capture of any bird banded previously.

Productivity has been assessed from mist-net data using both the capture rate of hatching-year birds and indices that compare captures of hatching-year birds with captures of adults (DeSante and Geupel 1987, Bibby et al. 1992, DeSante et al. 1993, Nur and Geupel 1993a, Johnson and Geupel 1996). We used two indices to describe productivity: (1) the number of individual hatching-year birds captured per 1,000 net hours, and (2) the ratio of hatching-year birds to total adults captured. We included captures of hatching year birds between 1 April and 15 August. The within-year pattern of captures does not reveal a distinct time period for the presence of migrating hatching-year birds (Fig. 1). Therefore, we chose the 15 August ending date to exclude the majority of fall migrants, based on the distribution of migrant captures at an offshore banding station (Pyle and Henderson 1991).

Statistical analyses.—We used linear regression analysis to detect trends in the number of birds captured over time and to describe relationships among productivity, survival, and population size. Results were considered significant at $P \leq 0.05$. Capture rates were log transformed to improve the normality of the residuals (Zar 1984). There is a potential for autocorrelation problems in performing regressions using the total number of adults captured in a given year and the number of hatching-year birds captured in the previous year (i.e. the same birds may be captured in consecutive years). We accounted for this by testing for a correlation between the number of adults captured in one year and the number of adults captured the following year.

Survival and recapture probabilities were estimated using the program SURGE to fit a Cormack-Jolly-Seber model (Lebreton et al. 1992, 1993; Pradel and Lebreton 1993) to the capture/recapture data. This analysis provided separate estimates for the two components that determine the annual return rate, i.e. survival probability and recapture probability. Survival probability is the probability of an adult surviving from one year to the next, whether or not it is recaptured. Recapture probability is the probability that a bird will be recaptured, given that it is alive. This technique accounts for surviving individuals that are not captured in every year by estimating recapture probability based on the year-to-year recapture history of all individuals. Models were selected to account for the major components of variation in the data, while maximizing parsimony (i.e. including as few parameters as possible), to allow greater precision in estimating survival (Lebreton et al. 1992). Comparisons of survival and recapture parameters were based on the likelihood ratio statistic (LRS; Lebreton et al. 1992). Survival estimates in other landbird species have been shown to be biased if they do not distinguish between breeders and transients, because transient birds have a much lower probability of recapture (Nur and Geupel 1993a); ignoring this heterogeneity of capture rates violates an assumption of capture/recapture methodology. Therefore, we examined the effect of including transient individuals in our survival estimates by comparing the recapture probability of presumed transients versus summer residents.

We defined summer residents as those individuals captured more than once within a season with at least seven days between captures. This criterion is the same as that used to obtain an index of the abundance of summer residents (see above), except that an individual only had to meet this criterion during one breeding season in its lifetime to be considered a summer resident for survival analyses. We estimated survival and recapture probabilities over all years, comparing models pooling all adult captures

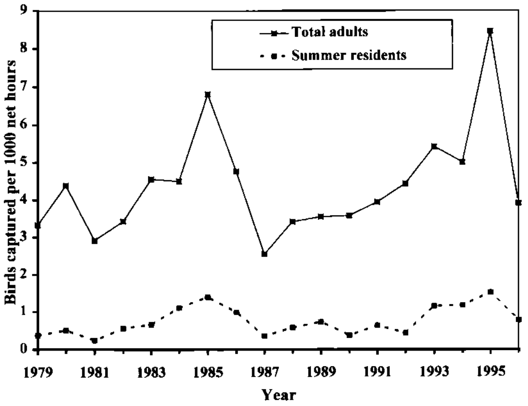

FIG. 2. Capture rates of all adult Wilson's Warblers and of summer residents from 1 April to 15 August, 1979–1996. Summer residents defined as in Figure 1.

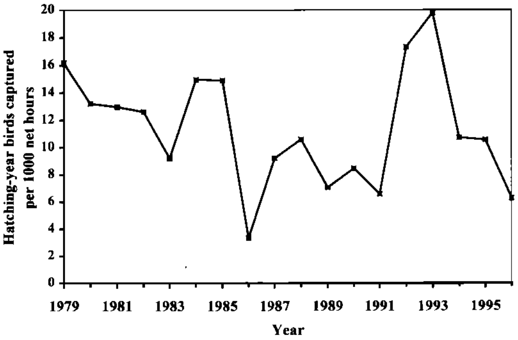

FIG. 3. Capture rates of hatching-year Wilson's Warblers from 1 April to 15 August, 1979–1996.

with models allowing recapture probability to vary between summer residents and transients. We also compared survival and recapture probabilities of male and female summer residents. Finally, we estimated the yearly survival probabilities for adults over the 18-year period of the study, and looked for a relationship between survival rate in a given year and abundance in the following year. In addition, we examined the relationship between adult abundance in a given year and the rate of adult survival to the next year to look for evidence of density-dependent survival. We also examined the relationship between productivity in a given year and adult survival to the following year. All regressions involving annual variation in survival were weighted by the inverse of the standard error of the survival estimates.

RESULTS

Adult abundance.—Two seasonal peaks characterized the distribution of capture rates of adults being captured for the first time in a given year (Fig. 1). The first peak was at the start of the breeding season, and the second peak occurred in late June. First captures of adults that we defined as summer residents peaked early in the season, and 96.9% of summer residents were first captured before 1 June (Fig. 1). Many summer residents were captured more than twice in a single season (out of 161 summer residents, 59% were captured three or more times in one season and 36% were captured four or more times). The second peak in captures was made up of transients. This bimodality indicates that our summer-residence criterion does eliminate captures of post-breeding wanderers and other transients that tend to dominate the population later in the season.

Year-to-year variation in the capture rate of summer residents paralleled the capture rate of transients ($r = 0.76$, $P < 0.001$, $n = 18$). The yearly adult capture rate varied almost 3-fold among years, showing a weakly positive, but nonsignificant, linear trend over time ($r^2 = 0.14$, $F = 2.53$, df = 1 and 16, $P = 0.13$; Fig. 2). There was no evidence of autocorrelation between adult captures in consecutive years ($r = 0.26$, $P > 0.3$, $n = 17$).

Of the total number of adults captured, 53.7% were male, 36.8% were female, and 9.5% could not be reliably sexed. Male and female capture rates were significantly correlated over the years of the study ($r = 0.61$, $P < 0.01$, $n = 18$). Only 3% of all adult captures occurred in the three nets that were located more than 10 m from the riparian woodland habitat.

Productivity.—Capture rates of hatching-year birds showed no significant linear trend over the years of the study ($r^2 = 0.05$, $F = 0.83$, df = 1 and 16, $P > 0.3$; Fig. 3), and neither did the ratio of hatching-year to after-hatching-year birds. Only 49 of 2,289 hatching-year Wilson's Warblers (2.1%) banded between 1979 and 1995 (41 to 198 banded per year) were captured again as adults in a subsequent year. The annual return rate of hatching-year birds ranged from 0 to 11.1%.

Adult abundance was related to productivity in the previous year; i.e. the capture rate of adults in a given year and the capture rate of hatching-year birds in the previous year were positively correlated ($r^2 = 0.25$, $F = 4.96$, df = 1 and 15, $P = 0.042$; Fig. 4). The capture rate of summer residents also was positively related to

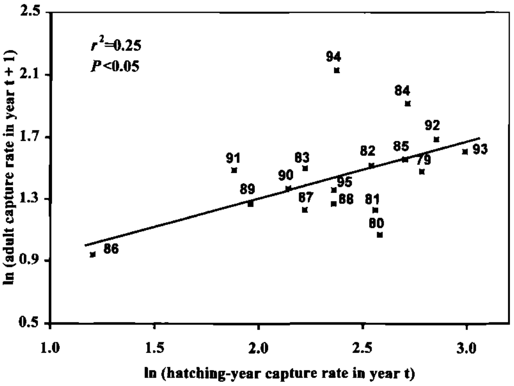

FIG. 4. Capture rates of adult Wilson's Warblers in year t +1 as a function of capture rates of hatching-year birds in year t, 1979–1996. Numerals denote year t. Adult capture rate (A_{t+1}) is related to hatching-year capture rate (H_t) as: $\ln(A_{t+1}) = 0.646 + 0.338 \ln(H_t)$.

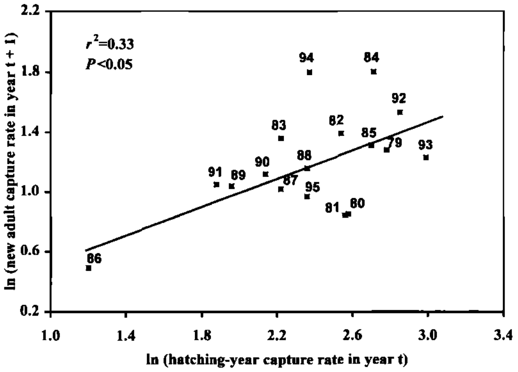

FIG. 5. Capture rates of "new" adult Wilson's Warblers (i.e. not captured in a previous year) in year t + 1 as a function of capture rate of hatching-year birds in year t, 1979–1996. Numerals denote year t. New adult capture rate (NA_{t+1}) is related to hatching-year capture rate (H_t) as: $\ln(NA_{t+1}) = 0.132 + 0.445 \ln(H_t)$.

productivity in the previous year ($r^2 = 0.25$, $F = 4.99$, df = 1 and 15, $P = 0.041$; $b = 0.594$, SE = 0.266). There was a stronger positive relationship between the capture rate of hatching-year birds in a given year and the capture rate of new adults in the following year ($r^2 = 0.33$, $F = 7.32$, df = 1 and 15, $P = 0.016$; Fig. 5). There was no significant relationship between the ratio of hatching-year to after-hatching-year captures and the capture rate of adults ($P = 0.28$) or new adults the following year ($P = 0.09$). We also found no significant relationship between either index of productivity and the number of adults returning to the study site for a second or subsequent season (i.e. adults that were not new adults). Only 3.3% of all hatching-year captures occurred in the three nets located more than 10 m from the riparian woodland habitat.

Recapture and survival probabilities.—A total of 978 adults was captured from 1979 through 1996 and used for survival analyses (Table 1). Of the total sample, 161 individuals met our recapture criterion for classification as summer residents. Of the summer residents captured, 65% were male, 33% were female, and 2% could not be sexed. One model (Model 1) estimated overall survival and recapture probabilities for all adults pooled. An additional model (Model

TABLE 1. Annual survival and recapture probabilities (SE, 95% C.I. in parentheses) for adult Wilson's Warblers estimated from SURGE analysis of capture/recapture data, 1979–1996. Model 1 estimated probabilities for all adults pooled; Model 2 allowed for variation in probabilities between summer residents and transients; Model 3 allowed for variation in probabilities between male and female summer residents.

Sample	n	Survival probability	Recapture probability
		Model 1	
All adults pooled	978	0.305 (0.031, 0.248–0.369)	0.324 (0.048, 0.238–0.423)
		Model 2	
Summer residents	161	0.503[a] (0.035, 0.435–0.571)	0.688[b] (0.058, 0.564–0.789)
Transients	817	0.363[a] (0.072, 0.237–0.511)	0.072[b] (0.025, 0.037–0.138)
		Model 3	
Summer resident males	104	0.523[c] (0.042, 0.441–0.605)	0.709[d] (0.068, 0.560–0.824)
Summer resident females	53	0.452[c] (0.069, 0.324–0.586)	0.663[d] (0.125, 0.397–0.855)

[a] Summer residents vs. transients: LRS = 2.86, df = 1, $P = 0.09$.
[b] Summer residents vs. transients: LRS = 46.51, df = 1, $P < 0.0001$.
[c] Males vs. females: LRS = 1.35, df = 1, $P = 0.25$.
[d] Males vs. females: LRS = 0.67, df = 1, $P = 0.41$.

2) estimated overall survival and recapture probability for summer residents and for transients separately. Comparison of models revealed a significant difference between the recapture probabilities of summer residents and transients ($P < 0.0001$; Table 1). This difference was large; the probability of a surviving summer resident being recaptured in the following year (0.69) was nearly 10 times that for a surviving transient (0.07). This difference in recapture probability was not accounted for in Model 1, in which all adults were pooled. The survival probability obtained for summer residents separately (Model 2) was significantly higher than that for all adults pooled (z test, $P < 0.01$). The difference in survival probability between summer residents and transients, however, was not statistically significant ($P = 0.09$; Table 1).

A third model (Model 3) estimated overall survival and recapture probability for male and female summer residents separately. Survival probability was slightly higher for males than for females, but this difference was not significant ($P = 0.25$; Table 1). Recapture probability also did not vary significantly between males and females ($P = 0.41$; Table 1).

Estimates of the probability of annual survival of adults were obtained for the 18 years of the study using a model (Model 4) that controlled for differences in recapture probability between summer residents and transients (Table 2). In Model 4 we treated recapture probability as constant among years, based on the lack of significant year-to-year variation in recapture probability for summer residents (LRS = 18.59, df = 16, $P = 0.29$). However, due to sparseness of data, we could not test year-to-year variation in recapture probability while simultaneously controlling for the difference in recapture probability between summer residents and transients. Year-to-year variation in survival probability was not statistically significant (LRS = 23.07, df = 16, $P = 0.11$), although survival probability appeared to vary markedly among years (Table 2). Also, survival probability did not vary significantly among years when summer residents and transients were analyzed in separate models (both P values > 0.2). However, the likelihood ratio statistic lacked power for analyzing yearly variation in survival because our sample size of individual recapture histories per year was small.

TABLE 2. Yearly survival estimates for adult Wilson's Warblers estimated from SURGE analysis of all adults ($n = 978$ individuals), controlling for differences in recapture probabilities between summer residents and transients (Model 4).

Year	Survival probability	SE
1979–80	0.595	0.226
1980–81	0.412	0.154
1981–82	0.671	0.221
1982–83	0.311	0.133
1983–84	0.237	0.116
1984–85	0.540	0.142
1985–86	0.392	0.101
1986–87	0.587	0.128
1987–88	0.397	0.134
1988–89	0.222	0.111
1989–90	0.551	0.156
1990–91	0.516	0.154
1991–92	0.626	0.174
1992–93	0.426	0.143
1993–94	0.496	0.113
1994–95	0.891	0.137
1995–96	0.369	0.104

No significant relationships were found between adult survival rates and abundance. Winters with high survival rates were weakly (but nonsignificantly) associated with high abundance in the following breeding season ($r^2 = 0.13$, $F = 2.19$, df = 1 and 15, $P = 0.16$). Conversely, years with high abundance were not necessarily followed by low adult survival rates ($r^2 = 0.00$, $F = 0.01$, df = 1 and 15, $P = 0.92$), suggesting the lack of a density-dependent effect on adult survival. We also found no significant relationship between productivity and adult survival ($r^2 = 0.024$, $F = 0.37$, df = 1 and 15, $P = 0.55$).

DISCUSSION

Adult abundance.—The number of adult Wilson's Warblers caught during the breeding season showed no significant increase or decrease over time, despite high annual variation during the study period (Fig. 2). This lack of a trend in abundance during summer at Palomarin can be compared with results from long-term population monitoring that has taken place in different seasons and at larger spatial scales. Breeding Bird Survey data for California show no significant trend in Wilson's Warbler numbers from 1980 to 1994 (Sauer et al. 1996). Other studies of local population dynamics also have found a concordance between measurements at different scales. Roth and Johnson (1993) found that the abundance of Wood Thrushes (*Hylocichla mustelina*) in a forest fragment declined at a rate very similar to that measured by the Breeding Bird Survey over the entire breeding range. Sherry and Holmes (1992) found that the variation in abundance of American Redstarts (*Setophaga ruticilla*) over 10 years, on both 10- and 180-ha study areas, was correlated with variation in abundance throughout the state of New Hampshire. In contrast, a significant decline was observed in numbers of Wilson's Warblers captured during fall migration from 1980 to 1992 at Palomarin (Dingle 1996). A significant decline was also observed in numbers of migrating Wilson's Warblers censused in the spring from 1968 to 1992 on Southeast Farallon Island, located approximately 32 km west of Palomarin (Pyle et al. 1994). This suggests that the dynamics of the population sampled at Palomarin differed from those of populations in other parts of the western breeding range. Indeed, Breeding Bird Survey data from Oregon and Washington do indicate significant decreases in Wilson's Warblers (Sauer et al. 1996). More knowledge about inter-patch dynamics is needed to understand the relationship between local and regional trends in bird populations (O'Connor 1991). Issues of scale are also discussed below in relation to productivity estimation.

Our data demonstrate a recovery of the Wilson's Warbler population after an exceptional reproductive failure in 1986 that affected many bird species breeding at Palomarin (DeSante and Geupel 1987). The extremely low number of hatching-year birds captured in 1986 was followed by a decline in adult captures the next year to the lowest level in 18 years of monitoring (Figs. 2 and 3). The number of adults captured increased during 1988 and 1989 after two years of higher productivity (Fig. 2).

Productivity.—The abundance of adult Wilson's Warblers at our study site was positively related to productivity in the previous year (Fig. 4). We found no consistent increase or decrease over time in our measures of productivity, which parallels the lack of a significant trend over time in adult captures (Figs. 2 and 3).

The capture rates for hatching-year Swainson's Thrushes (*Catharus ustulatus*) at Palomarin also were correlated with capture rates of adults in subsequent years (Johnson and Geupel 1996). A correlation between mist-net indices of productivity and population size the following year also was found over a large spatial scale at 25 standardized mist-net stations in eastern North America between 1990 and 1991 (DeSante et al. 1993). In that study, five species showed significant decreases in abundance following decreased productivity in the previous year. These results are similar to those found in more intensive studies of Prairie Warblers (*Dendroica discolor;* Nolan 1978), Black-throated Blue Warblers (*Dendroica caerulescens;* Holmes et al. 1992), and American Redstarts (Sherry and Holmes 1992). In these studies, the recruitment of yearlings into the breeding population was strongly related to fledging success in the previous summer. Although we could not identify second-year Wilson's Warblers in our sample, we suggest that the number of new adults captured during the breeding season in a philopatric species such as Wilson's Warbler is a useful index of the recruitment of second-year birds into the breeding population. The relationship between productivity and new adults in this population differs from the results of Roth and Johnson (1993), in which productivity in a Wood Thrush population was positively correlated with the number of adult residents returning to the site in the next year, rather than with the number of new individuals recruited.

The relationship between productivity and captures of new adults (Fig. 5) suggests that years with high productivity are followed by years with high recruitment. However, very few Wilson's Warblers captured in their hatching-year were caught again as adults. In contrast, for Swainson's Thrushes at the same study site, Johnson and Geupel (1996) found a strong relationship between productivity in a given year and abundance in the following year, and also observed exceptionally high return rates of hatching-year birds. However, a combination of low return rates of locally produced young and positive relationships between productivity and subsequent population size has been observed in several other migrant populations. Nolan (1978) observed that although few female Prairie Warblers produced on his study site returned there to breed, there was a significant correlation between annual production of fledglings and the percentage of breeding second-year females in the following year. Similar results were found for male American Redstarts by Sherry and Holmes (1991, 1992), who suggested that the relationship between local nesting success and yearling recruitment might indicate that nesting success on their study area was representative of nesting success over a larger region. This is also supported by the fact that temporal trends in adults on their study area matched those detected at a statewide scale. The evidence we have presented for Wilson's Warblers also suggests that our index of productivity reflects productivity over a larger region. However, we agree with Holmes and Sherry (Holmes et al. 1986; Sherry and Holmes 1991, 1992) that the scale at which demographic processes operate represents a major gap in our knowledge about avian population ecology, and that further long-term studies over a large spatial scale are needed (e.g. DeSante et al. 1993).

Mist-net indices of productivity are affected by several variables including clutch size, nesting success, number of nesting attempts, and postfledging survival (Nur and Geupel 1993a). Thus, mist-netting data cannot identify specific causes of variation in reproductive success. However, this method can provide evidence for a link between breeding-season events and subsequent population changes, indicating that more intensive study of the breeding biology of a species is warranted. Although the population we studied is not declining, our results are consistent with the hypothesis that decreased breeding success can cause population declines in migratory birds (cf. Rappole and McDonald 1994).

Survival and recapture probability.—Our best estimate of overall annual survivorship of breeding adult Wilson's Warblers (i.e. 50.3%) was obtained using a model that took into account the large difference in annual recapture probability between site-attached and transient adults (Model 2). The estimate of adult survival probability based on all adults pooled (Model 1) was biased because the recapture probability of summer residents was nearly 10 times that of transients (Table 1), which violates the assumption of homogeneity of recapture probabilities of the Cormack-Jolly-Seber model (Lebreton et al. 1992).

These results show that applying a criterion for defining summer residents based on recaptures of individuals within the breeding season can improve the accuracy of models of survival probability based on mist-net data. Such a criterion requires that mist nets be operated often enough to capture site-attached individuals more than once. Nur et al. (in press) found that survival estimates for adult Song Sparrows (*Melospiza melodia*) obtained from constant-effort mist netting closely matched estimates obtained from observations of color-banded individuals, provided a distinction was made between presumed transients (i.e. captured only once per breeding season) and presumed residents. Peach and Baillie (1998) also found that identifying transients reduced bias in estimating adult survival using constant-effort mist netting. A more accurate way to identify territorial breeders is by spot-mapping color-banded individuals breeding in the vicinity of the nets (e.g. Geupel and DeSante 1990, Martin et al. 1995). Mist-netting combined with observations of color-banded individuals allowed a more accurate estimation of adult survivorship in locally breeding Wrentits (*Chamaea fasciata*) at Palomarin (Nur and Geupel 1993a). Our survival estimate of 50.3% for summer residents still may be an underestimate, because we could not distinguish permanent dispersal out of the study area from mortality. We also may have underestimated survivorship because our summer-residence criterion is crude; i.e. some transients may have stayed in the area more than a week and been included as residents.

In this study, pooling males and females did not bias survival estimates because the recapture probability of males and females did not differ significantly (Table 1). Although our survival estimate was slightly higher for males than for females, the difference was not significant. Among birds, survival often is thought to be higher in males than in females, and summaries of existing data suggest that this pattern is common, but not universal, among species (Breitwisch 1989, Newton 1989, Promislow et al. 1992). Reports of differences in adult survival between males and females may be partly due to differences between the sexes in the propensity to disperse (Martin and Li 1992) or to be recaptured or resighted (Martin et al. 1995), but they also may reflect differences in reproductive effort and sexual selection (Promislow et al. 1992).

Our yearly samples of adult captures were too small to allow us to show that survival probability varied significantly among years, although inspection of the data in Table 2 shows that it did fluctuate markedly; i.e. in three years survival exceeded 60%, and in two years it was less than 25%. Apparently, the probability of adult Wilson's Warblers surviving from one breeding season to the next did not depend on abundance in the previous season. Although this result appears inconsistent with the hypothesis that the population is regulated by density-dependent adult mortality, density-dependent effects might result more from density in the wintering habitat than from abundance in the breeding habitat. Although there is evidence for competition among migrant birds on their wintering grounds (see Sherry and Holmes 1995), the few studies that have directly addressed the effect of population density on winter mortality in small passerines were conducted on resident species rather than migrants (Nilsson 1987, Arcese and Smith 1988, Peach et al.1995). We also found no evidence for a relationship between productivity in a given year and adult survival to the following year.

Annual survival of Wilson's Warblers was not positively related to abundance in the following year. However, results from two other studies comparing the relationship of productivity and survival to population size in migratory birds have suggested that survival is the major influence on annual variation in population size. Peach et al. (1991) estimated survival rates of Sedge Warblers (*Acrocephalus schoenobaenus*) from capture-recapture data, using within-season recapture criteria to distinguish residents from transients. They found that annual survival rates and annual indices of abundance were strongly correlated with indices of rainfall in the Sedge Warbler's African wintering quarters, while finding no relationship between productivity and population changes. Peach et al. (1995) also found a positive correlation between survival of adult Winter Wrens (*Troglodytes troglodytes*) and breeding density in the following year. Our results suggest that annual variation in abundance of adult Wilson's Warblers is influenced more by conditions on the breeding grounds than by factors affecting overwinter survival.

Methodological considerations.—Data from constant-effort mist netting have been used to assess abundance, productivity, and adult survivorship of landbirds (DeSante and Geupel 1987, DeSante et al. 1993). This technique also has been used to help determine which stage of a species' life history has the greatest influence on population trends (Peach et al. 1991, Peach and Baillie 1998). However, only a few recent studies have validated results derived from mist netting (Feu and McMeeking 1991; Nur and Geupel 1993a, b; Nur et al. in press; Silkey et al. unpubl. data). Admittedly, population studies based on mist-net data cannot answer many of the questions that can be addressed by more intensive methods such as spot-mapping and nest searching. For example, we cannot determine the exact size of the area sampled for Wilson's Warblers, absolute breeding density, or the factors that influenced nesting success. Also, Remsen and Good (1996) point out that variation in capture rates can be influenced by factors other than abundance, such as variation in spatial-movement patterns among species or among populations of a single species in different habitats. Although this is less of a problem for studies in a single location, we cannot rule out the possibility that warbler movement patterns were affected by successional changes in vegetation structure near the nets, thus obscuring a population trend. However, it is unlikely that the correspondence we observed between year-to-year variation in productivity and adult abundance was due to succession.

The use of adult capture rate as an index of abundance assumes that the number of adults captured is directly proportional to the abundance of breeding adults. Ideally, this assumption should be tested by comparing capture rate with an independent measure of abundance gathered from point counts or spot-mapping, and we hope that such studies will be forthcoming for migrant populations. However, Silkey et al. (unpubl. data) found that mist-net capture rates correlated positively with breeding density estimated by spot-mapping in three of four year-round resident bird species breeding at Palomarin; i.e. Song Sparrow, Wrentit, and Spotted Towhee (*Pipilo maculatus*). In our study, capture rates of transient and site-attached Wilson's Warblers were strongly correlated, indicating that both rates provide a similar index of adult abundance. However, if this were not the case, then recapture criteria distinguishing summer residents from transients could be used to obtain a better index of adult abundance (Johnson and Geupel 1996). Sex differences in "spacing systems" also may influence capture rates (Remsen and Good 1996). Although we captured more males than females, the significant correlation between male and female capture rates over the years of our study suggests that sex biases in capture probabilities did not affect our ability to detect long-term changes in abundance.

The use of mist-net data to monitor productivity assumes that the number of hatching-year birds captured is directly proportional to the number of young fledged in that year. However, this assumption is difficult to test because the spatial scale at which mist nets measure productivity varies among species (e.g. depending on dispersal tendencies of juveniles). For example, the number of hatching-year Song Sparrows captured in nets was strongly correlated with the number of fledglings produced at Palomarin (Nur and Geupel 1993a). However, the number of hatching-year Wrentits captured there was not significantly correlated with local productivity because many of the captured hatching-year birds came from outside the study area (Nur and Geupel 1993a). Similar differences among species in the ability of constant-effort mist netting to measure local productivity were found by Feu and McMeeking (1991) during a 12-year study of Eurasian Blackbirds (*Turdus merula*), Great Tits (*Parus major*), and Song Thrushes (*Turdus philomelos*). We note, however, that lack of a correspondence between estimates of local productivity from nest monitoring and mist-net captures of hatching-year birds does not necessarily mean that capture rate is not proportional to productivity. Another likely interpretation is that mist nets measure annual variation in productivity at a different spatial scale than does nest monitoring (Nur and Geupel 1993a). Further studies of productivity indices derived from mist netting are needed, especially for migratory species.

Whereas the number of hatching-year Wilson's Warblers captured in one year was correlated with the number of adults captured in the next, the ratio of hatching-year to after-hatching-year captures was not significantly correlated with adult captures in the next year. The absence of a relationship may be a consequence of a difference in the spatial scale of the catchment area of adults versus young, as demonstrated by Nur and Geupel (1993b) for Wrentits. For Wilson's Warblers, the ratio may be a less robust index of productivity than is the capture rate of hatching-year birds because it combines two variables, i.e. number of adults and number of young caught in the same year, that may be measured at different spatial scales.

As noted above, survival estimates from mist-net data can be biased by captures of transient adults. However, these estimates can be improved by using within-year recapture criteria to distinguish local breeders. Another potential problem is the tendency of birds to avoid mist nets after being captured once (MacArthur and MacArthur 1974, Karr 1981). Several factors suggest that our survival estimates were not biased by net-avoidance behavior. First, although summer residents would not meet our seven-day recapture criterion if they learned to completely avoid the nets after their first capture, this would only reduce the sample size of summer residents rather than bias survival estimates. Moreover, our method to identify summer residents required that an individual meet our recapture criterion only once in a single season in its lifetime. Second, although individuals may avoid nets some of the time, we found no compelling evidence that birds completely avoided nets after having been captured once. Many Wilson's Warblers (59% of summer residents) were captured three or more times during a breeding season. However, because some species are more likely than others to learn to avoid capture (MacArthur and MacArthur 1974), it is important to evaluate net avoidance on a species-specific basis. Finally, our estimates of annual recapture probability shed light on the probability that birds are avoiding the nets entirely in a given year. The annual recapture probability of summer residents indicates that approximately 31% of Wilson's Warblers surviving in a given year were not recaptured (Table 1). Because this figure includes birds that may have temporarily moved away from the study area and birds that were present but completely avoided capture, it appears that complete net avoidance between years was not widespread. Despite potential sources of bias, we believe that the cautious analysis of long-term mist-net data can provide valuable insight into population dynamics as well as identify species or demographic processes in need of more intensive study.

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