# THE WHITE-CROWNED SPARROW:
# REPRODUCTIVE SUCCESS (1975–1980)

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ABSTRACT.—We report the results of a 6-yr study of two banded populations of sedentary White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). All birds were banded and territory holders identified each year. We determined the outcome of 1,264 nests and located all nests of 186 pairs during a breeding season. Each pair produced an average of 2.5 fledglings in a season. Given the fact that a territorial bird has an expectancy of remaining on territory about 1.5 yr, the population seems to be at a stable level. The birds at one of the study locations, Twin Peaks, were less successful overall and more variable year to year than at the other, the Presidio. The differences between the two areas could be the result of severe weather changes that altered the characteristics of the vegetation.

Only 0.34 of the total number of nests (978) were successful, predation being the greatest cause of nest failure. Of the total nests, 0.39 were lost to predation (0.13 to egg predation and 0.26 to nestling predation). Survival rates indicate that nest mortality is 0.0197 per day for the incubation stage, 0.0450 per day for the nestling stage, and 0.0366 per day for the total nesting period. Although it is possible that observer disturbance biased the results, the increased understanding of these birds that is derived from establishing natal sites, parentage, and kinship is of greater benefit than the probable cost of any such disturbance. *Received 1 March 1983, accepted 4 July 1983.*

THIS report is the second part of a study of the population dynamics of the sedentary subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) that resides in the San Francisco Bay area. The first part (Petrinovich and Patterson 1982) concerned the population structure of the birds at the same two study locations during the same time period covered by this report. Here, we consider reproductive success, the relative importance of different causes of mortality at different stages of the nesting cycle, and day-to-day nest-survival rates.

The Nuttall subspecies is sedentary and breeds in coastal California from about Cape Mendocino to Santa Barbara (Blanchard 1941, 1942). Detailed information on the life history of the Nuttall subspecies of the White-crowned Sparrow is available (Blanchard 1936, 1941, 1942; De Wolfe 1968).

Briefly, the breeding season begins in early April, the female builds a nest, the pair copulates, and the female lays a clutch of about three eggs, one per day. The breeding activities con-

tinue into July. During the years of our study the first egg was laid between 16 March (1980) and 27 March (1975 and 1979), and the last nestling fledged between 1 July (1977 and 1980) and 26 July (1975).

The young hatch after about 13 days, and the nestling period is about 10 days long. When the young fledge, they stay in the region of the nest for 20–30 days. A few days after the young of the early broods fledge, the female begins a new nest, and the whole cycle starts again. It continues until the pair has two broods or until sometime in July, when feeding flocks of juveniles and adults can be seen foraging through the territories and the territories begin breaking down. The young suffer heavy predation both from land and aerial predators. Each pair attempts to build an average of about 3 nests in each season, with a range from 1 to 7.

Considerable information on readily observable aspects of avian demography such as clutch size, nesting success, and survival rates is available for several species (e.g. Nice 1957, Ricklefs 1969). There is little information, however, on the annual productivity of young for identified individuals, i.e. the number of young fledged by individual pairs throughout one or more breeding seasons. In this paper analyses are made for each year at each of the study locations of the mean number of eggs laid in each

clutch and in each nesting during the breeding season, the mean number of nestlings hatched per nest and in each nesting, and the mean number of fledglings produced per nest and in each nesting. In addition, the stage of the nesting cycle at which losses occur, the causes of nest failure for all nests located, the number of attempted and successful nests, and nest survival rates are presented.

## STUDY LOCATIONS

There were two main study locations in San Francisco, California: Twin Peaks and the Presidio [see fig. 1 in Petrinovich and Patterson (1982) for a map of the region].

*Twin Peaks.*—This location, composed of coastal soft chaparral, was located along the 740-m east face of a hill. The vegetation consisted mainly of baccharis (*Baccharis pilularis*), berry brambles (*Rubus*), poison oak (*Toxicodendron diversiloba*), sage (*Artemisia*), and grasses. This location contained about 47 territories.

*Presidio of San Francisco.*—This remnant dune location was 5.6 km north of Twin Peaks on the Pacific coast immediately south of the Golden Gate Bridge. The vegetation consisted of shrubby lupine (*Lupinus arborens*), chamise (*Adenostoma fasciculatum*), baccharis, poison oak, berry brambles, and grasses. The area was 1.5 km by 370 m and contained about 31 territories.

In addition to these primary study locations, in which most nests were located throughout the breeding season, a few birds were studied at several other locations in San Francisco: the west slope of Twin Peaks; the north slope of Mt. Sutro above the University of California Medical Center; Fort Mason; the Arguello Gate entrance to the Presidio; Mt. Davidson; O'Shaughnessy Blvd.; and Golden Gate Park.

## METHODS

The data reported in this paper are based on 11,888 h of field observation over the 6-yr period, 1975–1980. Over 2,100 birds were banded with U.S. Fish and Wildlife Service numbered aluminum bands and A. C. Hughes plastic color bands for identification. Most adults were trapped in Glenhaven Standby traps, and a few were caught in mist nets. Nestlings were banded at a mean age of 7.14 days ($s = 1.52$; number of nests = 383; range = 4–10). Fledglings were trapped at the end of the breeding season: all banded birds were noted, and unbanded ones were banded. The number of birds banded in each age class for each year is listed in Table 1 in Petrinovich and Patterson (1982). Included in the total number of 2,143 are adults (793), fledglings (298), and nestlings (1,052).

All nests of all pairs in each study location were found and then were monitored approximately every 3 days to the fledgling stage. If a nest bowl or complete nest was built and not used, it was counted as a nest. A nest was considered to be successful (i.e. at least one nestling fledged) if it was found to be empty and untorn on the 9th or 10th day of the nestling stage and if fledglings were directly observed, the adults emitted fledgling warning calls, or the adults were observed carrying arthropods to feed fledglings. All instances of predation were noted throughout the study, as well as the type of predator when it could be determined.

## RESULTS

*Mean number of eggs in the two locations across years.*—For all 1,264 nests located during the study period, there was little variation between years in the mean number of eggs laid in each nest. The mean number of eggs per nest over the 6 yr was 2.66 ($s = 1.28$), a value that is lower than that reported by Blanchard (1941), who found a mean of 3.25 ($s = 0.55$) for 147 nests. The difference in mean values occurs because the data of the two studies are expressed to a different base. Blanchard did not count nests that were completed but in which no eggs were laid. When we omitted those nests from our calculations, the mean number of eggs per nest was 3.15 ($s = 0.70$) for 1,062 nests. A $t$-test between these two means revealed no significant difference in clutch size ($t = 1.43$; df = 1,208; $P > 0.10$). Our findings, then, agree quite well with Blanchard's when the data are expressed to the same base.

Clutch size was significantly larger at the Presidio ($\bar{x} = 2.86$; $s = 1.14$; $n = 378$) than at Twin Peaks ($\bar{x} = 2.60$; $s = 1.33$; $n = 690$) during the 6-yr study period (Table 1). A two-way analysis of variance (ANOVA) of clutch size was done using the GLM procedure of SAS79 (Helwig and Council 1979) with the two main effects of location (Twin Peaks and Presidio) and year (1975–1980). Location main effect was significant ($F = 9.34$; df = 1/1,048; $P = 0.0015$), but neither the Year main effect ($F = 1.06$; df = 5/1,048; $P = 0.38$) nor the Interaction ($F = 2.20$; df = 5/1,048; $P = 0.0521$) was significant. The variance in the number of eggs was significantly greater at Twin Peaks than at the Presidio (Bartlett's test; $\chi^2 = 10.88$; df = 1; $P < 0.001$).

Sampling error might have produced the difference between locations. The Presidio had more dense vegetation, and nests were more difficult to locate. Therefore, nests could have been located later in the incubation cycle, and

TABLE 1.   Mean number of eggs ($\bar{x}_E$), nestlings ($\bar{x}_N$), and fledglings ($\bar{x}_F$) and standard deviation of eggs (SD$_E$), nestlings (SD$_D$), and fledglings (SD$_F$) in 1975–1980 for all nests located, for those at Twin Peaks, and for those at the Presidio.

|  | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | Totals |
|---|---|---|---|---|---|---|---|
| | | | | **All nests** | | | |
| $N$ | 144 | 234 | 257 | 226 | 166 | 237 | 1,264 |
| $\bar{x}_E$ | 2.66 | 2.47 | 2.72 | 2.69 | 2.82 | 2.66 | 2.66 |
| SD$_E$ | 1.23 | 1.35 | 1.27 | 1.34 | 1.11 | 1.32 | 1.28 |
| $\bar{x}_N$ | 1.56 | 1.27 | 1.54 | 1.73 | 1.74 | 1.75 | 1.59 |
| SD$_N$ | 1.36 | 1.46 | 1.51 | 1.49 | 1.45 | 1.49 | 1.48 |
| $\bar{x}_F$ | 0.82 | 0.60 | 0.75 | 0.71 | 0.87 | 1.18 | 0.82 |
| SD$_F$ | 1.23 | 1.11 | 1.25 | 1.24 | 1.25 | 1.43 | 1.27 |
| | | | | **Twin Peaks** | | | |
| $N$ | 112 | 136 | 129 | 134 | 89 | 90 | 690 |
| $\bar{x}_E$ | 2.68 | 2.37 | 2.69 | 2.54 | 2.57 | 2.84 | 2.60 |
| SD$_E$ | 1.89 | 1.41 | 1.34 | 1.41 | 1.29 | 1.22 | 1.33 |
| $\bar{x}_N$ | 1.63 | 1.13 | 1.57 | 1.55 | 1.54 | 2.11 | 1.56 |
| SD$_N$ | 1.34 | 1.47 | 1.55 | 1.46 | 1.48 | 1.38 | 1.47 |
| $\bar{x}_F$ | 0.74 | 0.39 | 0.68 | 0.49 | 0.73 | 1.61 | 0.72 |
| SD$_F$ | 1.19 | 0.89 | 1.24 | 1.05 | 1.18 | 1.47 | 1.21 |
| | | | | **Presidio** | | | |
| $N$ | 17 | 56 | 95 | 74 | 62 | 74 | 378 |
| $\bar{x}_E$ | 2.88 | 2.80 | 2.70 | 3.03 | 3.12 | 2.63 | 2.86 |
| SD$_E$ | 1.22 | 1.09 | 1.24 | 1.09 | 0.80 | 1.26 | 1.14 |
| $\bar{x}_N$ | 1.82 | 1.73 | 1.59 | 2.07 | 1.90 | 1.70 | 1.79 |
| SD$_N$ | 1.51 | 1.41 | 1.51 | 1.49 | 1.41 | 1.51 | 1.48 |
| $\bar{x}_F$ | 1.47 | 1.04 | 0.87 | 1.11 | 1.03 | 1.14 | 1.05 |
| SD$_F$ | 1.46 | 1.36 | 1.28 | 1.48 | 1.33 | 1.42 | 1.37 |

nests that were abandoned with eggs during the first few days of incubation could have been overlooked. The possibility that the difference was due to sampling error was evaluated by considering only the nests of those pairs at Twin Peaks for which every nest was located throughout a season. The 542 nests of these pairs had a mean of 2.60 eggs ($s = 1.33$) (Table 2). The mean number of eggs for the 148 nests of pairs at Twin Peaks for which all nests were not found was 2.61 ($s = 1.30$). The fact that there was no difference between these two samples suggests that there was not a sampling bias at Twin Peaks.

The same conclusion is supported by a comparison of the mean clutch size at the Presidio of those pairs for which all nests were found ($\bar{x} = 2.88$; $s = 1.16$; $n = 255$) (Table 3) with that of those pairs for which all nests were not found ($\bar{x} = 2.78$; $s = 1.11$; $n = 123$). Again, these results indicate there was no sampling bias at the Presidio. (There were no significant differences in either the number of nestlings or fledglings between complete pairs and incomplete ones.)

*Number of eggs in the different nestings within a*

*year.*—For the first three nestings of those 183 pairs that had three nestings, the only significant difference between sites was that there were more eggs at the Presidio ($\bar{x} = 2.89$; $s = 1.23$; $n = 59$; for 2 of the 61 cases the value was unknown) than at Twin Peaks ($\bar{x} = 2.57$; $s = 1.53$; $n = 124$; for 1 of the 125 cases the value was unknown) ($F = 5.95$; df $= 1/181$; $P < 0.02$). Thus, there was no difference in the clutch size between the two sites when the nests were classified by order, but, again, the clutches resulting from these nestings were significantly larger at the Presidio (Table 3) than at Twin Peaks (Table 2).

*Mean number of nestlings in the two locations across years.*—The mean number of nestlings hatched per nest over the 6 yr was 1.59 ($s = 1.48$; $n = 1,264$; Table 1). A two way ANOVA of the number of nestlings hatched at each area for each year revealed that the Location main effect was significant (Twin Peaks, $\bar{x} = 1.56$, $s = 1.47$; Presidio, $\bar{x} = 1.79$, $s = 1.48$; $F = 5.94$; df $= 1/1,062$; $P = 0.01$); the Year main effect ($F = 3.26$; df $= 5/1,056$; $P < 0.01$) and the Interaction ($F = 2.71$; df $= 5/1,056$; $P < 0.02$) also are

TABLE 2. For those pairs at Twin Peaks for which all nests were located, the mean number of eggs ($\bar{x}_E$), nestlings ($\bar{x}_N$), and fledglings ($\bar{x}_F$) and standard deviation of eggs (SD$_E$), nestlings (SD$_N$), and fledglings (SD$_F$) for each nest by nesting attempt in 1975 through 1980.

| | Nesting attempt | | | | |
| | 1 | 2 | 3 | 4–7 | Totals |
|---|---|---|---|---|---|
| **1975** | | | | | |
| $N$ | 28 | 28 | 27 | 13 | 96 |
| $\bar{x}_E$ | 2.86 | 2.96 | 2.63 | 1.92 | 2.70 |
| SD$_E$ | 0.76 | 1.07 | 1.28 | 1.80 | 1.21 |
| $\bar{x}_N$ | 1.82 | 1.25 | 1.96 | 1.42 | 1.64 |
| SD$_N$ | 1.31 | 1.35 | 1.37 | 1.38 | 1.36 |
| $\bar{x}_F$ | 0.89 | 0.54 | 0.96 | 0.58 | 0.77 |
| SD$_F$ | 1.29 | 1.00 | 1.37 | 1.08 | 1.21 |
| **1976** | | | | | |
| $N$ | 33 | 33 | 20 | 12 | 98 |
| $\bar{x}_E$ | 2.70 | 2.55 | 2.05 | 2.00 | 2.40 |
| SD$_E$ | 1.19 | 1.42 | 1.58 | 1.41 | 1.38 |
| $\bar{x}_N$ | 1.70 | 1.03 | 1.05 | 1.17 | 1.28 |
| SD$_N$ | 1.53 | 1.47 | 1.54 | 1.59 | 1.53 |
| $\bar{x}_F$ | 0.21 | 0.39 | 0.58 | 0.67 | 0.40 |
| SD$_F$ | 0.65 | 0.97 | 1.07 | 1.07 | 0.91 |
| **1977** | | | | | |
| $N$ | 30 | 30 | 25 | 19 | 104 |
| $\bar{x}_E$ | 2.77 | 3.00 | 2.44 | 2.37 | 2.68 |
| SD$_E$ | 1.33 | 1.31 | 1.50 | 1.34 | 1.37 |
| $\bar{x}_N$ | 1.47 | 1.83 | 1.56 | 1.32 | 1.57 |
| SD$_N$ | 1.46 | 1.66 | 1.64 | 1.45 | 1.55 |
| $\bar{x}_F$ | 0.50 | 0.50 | 1.04 | 0.74 | 0.67 |
| SD$_F$ | 1.07 | 1.20 | 1.46 | 1.19 | 1.23 |
| **1978** | | | | | |
| $N$ | 31 | 31 | 30 | 19 | 111 |
| $\bar{x}_E$ | 2.00 | 2.68 | 2.60 | 2.37 | 2.41 |
| SD$_E$ | 1.41 | 1.42 | 1.54 | 1.42 | 1.46 |
| $\bar{x}_N$ | 1.19 | 1.19 | 1.93 | 1.58 | 1.46 |
| SD$_N$ | 1.25 | 1.47 | 1.48 | 1.46 | 1.43 |
| $\bar{x}_F$ | 0.55 | 0.39 | 0.57 | 0.16 | 0.44 |
| SD$_F$ | 1.03 | 0.95 | 1.22 | 0.50 | 1.00 |
| **1979** | | | | | |
| $N$ | 25 | 25 | 13 | 5 | 68 |
| $\bar{x}_E$ | 1.88 | 2.88 | 3.08 | 3.20 | 2.57 |
| SD$_E$ | 1.39 | 1.13 | 1.12 | 0.84 | 1.31 |
| $\bar{x}_N$ | 0.76 | 1.76 | 2.08 | 2.80 | 1.53 |
| SD$_N$ | 1.16 | 1.59 | 1.44 | 1.30 | 1.51 |
| $\bar{x}_F$ | 0.44 | 0.88 | 0.38 | 2.00 | 0.71 |
| SD$_F$ | 0.92 | 1.27 | 0.96 | 1.58 | 1.17 |
| **1980** | | | | | |
| $N$ | 27 | 27 | 10 | 1 | 65 |
| $\bar{x}_E$ | 2.70 | 3.22 | 2.50 | 3.0 | 2.89 |
| SD$_E$ | 1.30 | 0.58 | 1.58 | — | 1.12 |
| $\bar{x}_N$ | 1.67 | 2.74 | 2.20 | 3.0 | 2.22 |
| SD$_N$ | 1.44 | 0.71 | 1.62 | — | 1.29 |
| $\bar{x}_F$ | 1.22 | 2.26 | 2.20 | 3.0 | 1.83 |
| SD$_F$ | 1.42 | 1.10 | 1.62 | — | 1.40 |
| **Total** | | | | | |
| $N$ | 174 | 174 | 125 | 69 | 542 |
| $\bar{x}_E$ | 2.49 | 2.86 | 2.53 | 2.29 | 2.60 |

TABLE 2. Continued.

| | Nesting attempt | | | | |
| | 1 | 2 | 3 | 4–7 | Totals |
|---|---|---|---|---|---|
| SD$_E$ | 1.29 | 1.21 | 1.45 | 1.44 | 1.33 |
| $\bar{x}_N$ | 1.45 | 1.60 | 1.77 | 1.51 | 1.58 |
| SD$_N$ | 1.40 | 1.51 | 1.52 | 1.47 | 1.47 |
| $\bar{x}_F$ | 0.62 | 0.79 | 0.86 | 0.66 | 0.74 |
| SD$_F$ | 1.11 | 1.25 | 1.35 | 1.13 | 1.22 |

significant. The Year main effect is due to a large drop in the number of nestlings in 1976 and an increase in 1980. The Interaction is due to a gradual increase in the number of nestlings across years at Twin Peaks as compared to a constant number at the Presidio. In 1976 there was a drought (the first of two drought years in the region), which appears to have influenced the birds at Twin Peaks more strongly than those at the Presidio. There was an increase in the number of nestlings found at Twin Peaks in 1980 ($\bar{x} = 2.11$; $s = 1.38$, $n = 90$) and in 1981 ($\bar{x} = 2.45$; $s = 1.03$; $n = 86$). There was no overall difference in the variance of the total number of nestlings (Bartlett's test; $P > 0.05$).

*Mean number of nestlings hatched in the different nestings within a year.*—There were no significant differences between sites ($P > 0.05$) for Location, Nesting, or Interaction (see Table 1).

*Mean number of fledglings produced in the two locations across years.*—The mean number of fledglings per nest over the 6 yr was 0.82 ($s = 1.27$; Table 1). A two-way ANOVA on the number of fledglings at each area for each year revealed that the Location main effect was significant ($F = 12.79$; df = 1/1,056; $P < 0.001$), as was that of Year ($F = 6.45$; df = 5/1,062; $P < 0.001$) and Interaction ($F = 4.87$; df = 5/1,056; $P < 0.001$). More fledglings were produced at the Presidio ($\bar{x} = 1.05$; $s = 1.37$) than at Twin Peaks ($\bar{x} = 0.72$; $s = 1.21$). The overall pattern was much the same as for nestlings: an increase across years at Twin Peaks and a relatively constant level at the Presidio, a drop at both the Presidio and Twin Peaks in 1976, and a large increase at Twin Peaks in 1980. The number of fledglings produced at Twin Peaks (range = 0.39–1.61) was more variable than at the Presidio (range = 0.87–1.47): the variance at Twin Peaks was significantly greater than that at Presidio (Bartlett's test; $\chi^2 = 9.00$; df = 1; $P < 0.005$).

TABLE 3. For those pairs at the Presidio for which all nests were located, the mean number of eggs ($\bar{x}_E$), nestlings ($\bar{x}_N$), and fledglings ($\bar{x}_F$) and standard deviation of eggs ($SD_E$), nestlings ($SD_N$), and fledglings ($SD_F$) for each nest by nesting attempt in 1976 through 1980.

| | Nesting attempt | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4–6 | Totals |
| **1976** | | | | | |
| N | 14 | 14 | 6 | 0 | 34 |
| $\bar{x}_E$ | 2.57 | 3.29 | 3.17 | 0.00 | 2.97 |
| $SD_E$ | 1.09 | 0.99 | 0.75 | — | 1.03 |
| $\bar{x}_N$ | 1.79 | 1.57 | 2.33 | 0.00 | 1.79 |
| $SD_N$ | 1.42 | 1.60 | 0.82 | — | 1.41 |
| $\bar{x}_F$ | 0.71 | 0.86 | 1.67 | 0.00 | 0.94 |
| $SD_F$ | 1.20 | 1.41 | 1.51 | — | 1.35 |
| **1977** | | | | | |
| N | 20 | 20 | 19 | 6 | 65 |
| $\bar{x}_E$ | 3.35 | 2.65 | 2.89 | 2.17 | 2.89 |
| $SD_E$ | 0.49 | 1.46 | 1.45 | 1.33 | 1.25 |
| $\bar{x}_N$ | 2.00 | 1.10 | 1.42 | 1.83 | 1.54 |
| $SD_N$ | 1.52 | 1.55 | 1.61 | 1.47 | 1.56 |
| $\bar{x}_F$ | 1.15 | 0.20 | 1.00 | 1.50 | 0.85 |
| $SD_F$ | 1.42 | 0.70 | 1.37 | 1.64 | 1.30 |
| **1978** | | | | | |
| N | 19 | 19 | 13 | 10 | 61 |
| $\bar{x}_E$ | 3.05 | 3.47 | 2.62 | 2.70 | 3.03 |
| $SD_E$ | 0.97 | 0.51 | 1.26 | 1.49 | 1.06 |
| $\bar{x}_N$ | 1.79 | 2.37 | 2.00 | 1.90 | 2.03 |
| $SD_N$ | 1.40 | 1.38 | 1.73 | 1.37 | 1.45 |
| $\bar{x}_F$ | 0.47 | 1.79 | 1.23 | 0.70 | 1.08 |
| $SD_F$ | 0.90 | 1.58 | 1.69 | 1.06 | 1.43 |
| **1979** | | | | | |
| N | 15 | 15 | 10 | 1 | 41 |
| $\bar{x}_E$ | 3.27 | 3.29 | 2.70 | 3.00 | 3.13 |
| $SD_E$ | 0.46 | 1.07 | 1.06 | — | 0.88 |
| $\bar{x}_N$ | 2.00 | 2.21 | 2.20 | 2.00 | 2.13 |
| $SD_N$ | 1.51 | 1.25 | 1.03 | — | 1.26 |
| $\bar{x}_F$ | 1.40 | 0.86 | 1.30 | 2.00 | 1.20 |
| $SD_F$ | 1.55 | 1.23 | 1.25 | — | 1.34 |
| **1980** | | | | | |
| N | 18 | 18 | 13 | 5 | 54 |
| $\bar{x}_E$ | 2.72 | 2.11 | 2.67 | 2.40 | 2.47 |
| $SD_E$ | 0.89 | 1.60 | 1.37 | 1.52 | 1.32 |
| $\bar{x}_N$ | 2.11 | 0.83 | 1.77 | 1.60 | 1.56 |
| $SD_N$ | 1.23 | 1.42 | 1.48 | 1.67 | 1.46 |
| $\bar{x}_F$ | 1.83 | 0.39 | 1.23 | 1.20 | 1.15 |
| $SD_F$ | 1.34 | 0.92 | 1.59 | 1.79 | 1.42 |
| **Total** | | | | | |
| N | 86 | 86 | 61 | 22 | 255 |
| $\bar{x}_E$ | 3.01 | 2.93 | 2.78 | 2.50 | 2.88 |
| $SD_E$ | 0.85 | 1.29 | 1.25 | 1.37 | 1.16 |
| $\bar{x}_N$ | 1.94 | 1.59 | 1.84 | 1.82 | 1.79 |
| $SD_N$ | 1.39 | 1.55 | 1.46 | 1.37 | 1.46 |
| $\bar{x}_F$ | 1.12 | 0.81 | 1.21 | 1.09 | 1.04 |
| $SD_F$ | 1.36 | 1.30 | 1.45 | 1.38 | 1.37 |

*Number of fledglings produced in the different nestings within a year.*—For those pairs that had at least three nestings, more fledglings were produced at Presidio ($\bar{x} = 0.92$; $s = 1.25$; $n = 59$; Table 3) than at Twin Peaks ($\bar{x} = 0.63$; $s = 1.32$; $n = 124$; Table 2) ($F = 5.90$; df = 1/181; $P = < 0.02$). There were significantly more fledglings produced from the third nesting ($\bar{x} = 0.99$; $s = 1.39$) than from the first ($\bar{x} = 0.61$; $s = 1.09$) or second ($\bar{x} = 0.58$; $s = 1.15$) ($F = 7.28$; df = 2/362; $P < 0.001$).

*Stage of nesting cycle where losses occurred.*— When all nests found at the two locations were considered, significantly more nests did not have eggs laid in them at Twin Peaks ($115/690 = 0.17$) than at the Presidio ($41/376 = 0.11$) ($\chi^2 = 7.13$; df = 1; $P < 0.01$ with Yates' correction). The proportion of nests that were built and had eggs laid in them was not significantly different across nestings or across years for either location (see Tables 4 and 5). (None of the calculated $\chi^2$ values was significant; all $P$ values $> 0.05$.) It appears, then, that nests were more likely to be abandoned at Twin Peaks before any eggs were laid in them.

With the exception of Twin Peaks in 1976, a high and relatively constant proportion of the eggs hatched once they were laid in a nest (Tables 4 and 5). When the totals over all nestings and years were considered at Twin Peaks, 0.69 of the nests with eggs had nestlings; the proportion at the Presidio was 0.72 (corrected $\chi^2 = 0.68$; df = 1; $P > 0.70$). Thus, the difference in fledgling success between the two study locations was not due to failure of eggs to hatch.

At Twin Peaks, 0.51 of those nests with nestlings later produced fledglings (Table 4). At the Presidio, 0.65 of those nests with nestlings later produced fledglings (Table 5). When nests with nestlings at each location were classified according to whether they produced fledglings or not, the difference between areas was significant (corrected $\chi^2 = 10.94$; df = 1; $P < 0.001$). This indicates that the difference in reproductive success between Twin Peaks and the Presidio was due both to a greater loss (usually due to predation) of nestlings and to abandonment of nests at Twin Peaks.

*Major causes of nest failure.*—For the 978 nests studied, 846 (0.87) had at least one egg, 603 (0.62) had at least one hatched nestling, and 337 (0.34) produced at least one fledgling (Table 6). For the 641 nests that were not success-

TABLE 4.   Reproductive success of pairs at Twin Peaks, 1975–1980.

| | Nesting attempt number and year | | | | | | | | | | | |
| | 1 | | | | | | 2 | | | | | |
| | 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A. Number of nests | 34 | 44 | 49 | 42 | 39 | 48 | 32 | 53 | 36 | 36 | 32 | 31 |
| B. Number with eggs | 33 | 38 | 42 | 33 | 29 | 39 | 28 | 42 | 33 | 30 | 29 | 31 |
| Proportion of (A) with eggs | 0.97 | 0.86 | 0.86 | 0.79 | 0.74 | 0.81 | 0.88 | 0.79 | 0.92 | 0.83 | 0.91 | 1.0 |
| C. Number with nestlings | 26 | 23 | 27 | 26 | 18 | 30 | 16 | 17 | 22 | 17 | 18 | 30 |
| Proportion of (A) with nestlings | 0.76 | 0.52 | 0.55 | 0.62 | 0.46 | 0.62 | 0.50 | 0.32 | 0.61 | 0.47 | 0.56 | 0.97 |
| Proportion of (B) with nestlings | 0.79 | 0.61 | 0.64 | 0.79 | 0.62 | 0.77 | 0.57 | 0.40 | 0.67 | 0.57 | 0.62 | 0.97 |
| D. Number with fledglings | 11 | 4 | 11 | 14 | 10 | 19 | 7 | 9 | 7 | 6 | 12 | 27 |
| Proportion of (A) with fledglings | 0.32 | 0.09 | 0.22 | 0.33 | 0.26 | 0.40 | 0.22 | 0.17 | 0.19 | 0.17 | 0.38 | 0.87 |
| Proportion of (C) with fledglings | 0.42 | 0.17 | 0.41 | 0.54 | 0.56 | 0.63 | 0.44 | 0.53 | 0.32 | 0.35 | 0.67 | 0.87 |

ful (did not produce at least one fledgling), 257 (0.40) suffered predation during the nestling stage, and this was the major cause of all nest failures. The most common causes of loss of nests with eggs were predation (132/846 = 0.16) and abandonment (111/846 = 0.13), and the most common cause of loss of nests with nestlings was predation (257/603 = 0.43).

The data in Table 6 can be categorized by location and outcome (nests abandoned, eggs abandoned, egg predation, nestlings abandoned, nestling predation, successful) (Table 7A). A $\chi^2$ was calculated, and the value was 26.4 (df = 5; $P < 0.0001$). We found that at Twin Peaks significantly more nests with eggs were abandoned ($\chi^2 = 7.13$; 1 df; $P < 0.01$) and there was more predation on nests with nestlings than at the Presidio ($\chi^2 = 16.06$; df = 1; $P < 0.001$). There were more successful nests at the Presidio ($\chi^2 = 10.94$; df = 1; $P < 0.001$). The differences between years occurred because in 1976 there were significantly more losses early in the nesting cycle (nests abandoned, eggs abandoned, egg predation) and fewer losses later in the cycle (nestling predation), as well as fewer successes ($\chi^2 = 14.36$; df = 5; $P < 0.001$). Table 7B contains the data from Table 6 categorized by year (1975–1980) and by outcome (nests abandoned, eggs abandoned, egg predation, nestlings abandoned, nestling predation, successful). The $\chi^2$ calculated on outcome was 72.1 (df = 25; $P < 0.0001$). As mentioned earlier, this was the first year of a severe drought that was accompanied by very high temperatures. In 1980, there was significantly less egg and nestling predation and more success ($\chi^2 = 24.34$; df = 5; $P < 0.001$).

The causes of failure can also be examined by considering the outcome of the total num-

ber of eggs rather than the nest as the basic unit (Table 8). The results for the total number of eggs were so similar to those obtained when nests were used as the basic unit that no further analysis of these data will be presented.

*Attempted and successful nests.*—Table 9 contains the number of attempted nestings and the number of successful nests for every pair at Twin Peaks for which all nests were located for an entire breeding season for combined years 1975–1980 (no pairs with only one attempted nesting were included as complete). Of these pairs, 0.39 did not have a successful nest, while 0.61 produced at least one fledgling each year. At the Presidio only 0.16 did not have a successful nest, while 0.84 of the pairs produced at least one fledgling (Table 10).

When the data were categorized by pairs that attempted 2, 3, or 4+ nests and by location, there was no significant difference between the areas in number of attempted nests ($\chi^2 = 1.65$; df = 2; $P > 0.30$). For the two locations combined, 0.29 of the pairs attempted 2 nestings, 0.44 attempted 3, 0.22 attempted 4, and only 0.06 attempted 5 or more nestings. For the 178 successful pairs, the most frequent situation was 3 attempts with 1 success (48/178 = 0.27), followed by 2 attempts with 1 success (33/178 = 0.19), and 3 attempts with 2 successes (23/178 = 0.13). The most frequent outcome was one successful nesting (107/178 = 0.60), and the second most frequent outcome was two successful nestings (69/178 = 0.39).

*Survival rates.*—To determine the hatch rate of eggs, exposure days were counted from the time when the first egg was laid, even though the nest might have been found before that time. Thus, for a four-egg clutch represented in Table 11, the day the first egg was laid would

TABLE 4. Continued.

| | | 3 | | | | | | 4–7 | | | | | | Total | | | | Total all years |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 | |
| 32 | 27 | 25 | 36 | 13 | 10 | 14 | 12 | 19 | 20 | 5 | 1 | 112 | 136 | 129 | 134 | 89 | 90 | 690 |
| 28 | 17 | 19 | 29 | 12 | 8 | 9 | 9 | 15 | 16 | 5 | 1 | 98 | 106 | 109 | 108 | 75 | 79 | 575 |
| 0.88 | 0.63 | 0.76 | 0.81 | 0.92 | 0.80 | 0.64 | 0.75 | 0.79 | 0.80 | 1.0 | 1.0 | 0.88 | 0.78 | 0.84 | 0.81 | 0.84 | 0.88 | 0.83 |
| 23 | 9 | 13 | 24 | 10 | 7 | 8 | 5 | 10 | 13 | 5 | 1 | 73 | 54 | 72 | 80 | 51 | 68 | 398 |
| 0.72 | 0.33 | 0.52 | 0.67 | 0.77 | 0.70 | 0.57 | 0.42 | 0.53 | 0.65 | 1.0 | 1.0 | 0.65 | 0.40 | 0.56 | 0.60 | 0.57 | 0.76 | 0.58 |
| 0.82 | 0.53 | 0.68 | 0.83 | 0.83 | 0.88 | 0.89 | 0.56 | 0.67 | 0.81 | 1.0 | 1.0 | 0.74 | 0.51 | 0.66 | 0.74 | 0.68 | 0.86 | 0.69 |
| 12 | 7 | 10 | 7 | 2 | 7 | 4 | 4 | 6 | 2 | 4 | 1 | 34 | 24 | 34 | 29 | 28 | 54 | 203 |
| 0.38 | 0.26 | 0.40 | 0.19 | 0.15 | 0.70 | 0.29 | 0.33 | 0.32 | 0.10 | 0.80 | 1.0 | 0.30 | 0.18 | 0.26 | 0.22 | 0.31 | 0.60 | 0.29 |
| 0.52 | 0.78 | 0.77 | 0.24 | 0.20 | 1.0 | 0.50 | 0.80 | 0.60 | 0.15 | 0.80 | 1.0 | 0.47 | 0.44 | 0.47 | 0.36 | 0.55 | 0.79 | 0.51 |

be −4, with day +1 being the first day after the clutch was complete. The normal incubation time is 12 days. The number of nests at exposure and the number of losses are listed for each day.

Following the recommendations of Klett and Johnson (1982), the Product Method variant of the Mayfield (1961) method was used to estimate survival rates, because the daily mortality rate of nestlings varied by age. With this method, a daily mortality rate ($m$) is calculated for each day by dividing the number of clutches that were lost on that day by the total number of nests under observation (and hence exposed to loss) on that day. The probability of survival is the product of one minus the loss rate on each day. Thus, for the data from Twin Peaks (Table 11), the egg survival rate is $(1 − 0.0133)$ $(1 − 0.0170) \ldots (1 − 0.0229) = 0.7732$. This indicates that the probability of a nest surviving the entire incubation stage is 0.7732. If the date a nesting attempt failed was unknown, the exposure period was calculated using half the interval between the last two visits added to the known survival period.

There was an artifactual increase in $m$ on egg day 12 due to our method: any nest that was last seen with eggs and that then was checked and found to have dead eggs after they could have hatched was terminated as a day 12 egg mortality. This was done to assure that our estimates of nestling loss would be as conservative as possible. This decision rule caused both an elevated day 12 egg value and a decreased day 1 nestling value. The data for egg day 12 presented in Table 11 and those for nestling day 1 in Table 12 were obtained by assigning the value observed on egg day 11 in the former case and that on nestling day 2 in the latter.

The obtained data for those two days are enclosed in parentheses.

No mortality occurred during the 4 days before hatching (no eggs being lost during that time). These last 4 days were not included in further analysis. The total egg-mortality rate was calculated for each location (Table 11A: Twin Peaks; Table 11B: Presidio) and the combined areas (Table 11C). The mortality rate at Twin Peaks was 0.0199, at the Presidio it was 0.0191, and for the combined areas it was 0.0197. A trend analysis of mortality rate was done on Egg Days and Location. There was no overall Day effect ($t = 0.24$; df = 21; $P = 0.44$) or Location effect ($t = 0.24$; df = 21; $P = 0.81$). The Interaction was significant, however ($t = 2.15$; df = 21; $P < 0.05$). The interaction accounted for 0.18 of the total variance and was the result of an increase over days in mortality rate at Twin Peaks and a decrease over days at the Presidio (see Table 11).

The mortality rates for nestlings were calculated beginning with the hatching day and continuing for 10 days, at which time birds fledge from the nest. The results are presented in Table 12. A linear trend analysis of mortality rate was done on nestling days and location. There was a significant Day effect ($t = 4.24$; df = 18; $P = 0.0005$) and Location effect ($t = 2.30$; df = 17; $P < 0.04$), while the Interaction was not significant ($t = 1.16$; df = 16; $P > 0.26$). The Day effect was due to a decrease in $m$ from day 4 to 10, and it accounted for 0.50 of the total variance. The Location effect was due to a higher $m$ at Twin Peaks, and it accounted for 0.12, and the complete model accounted for 0.62.

Although the linear trend accounted for a sizeable proportion of the variance during the

TABLE 5. Reproductive success of pairs at the Presidio, 1975–1980.

| | Nesting attempt number and year | | | | | | | | | | | |
| | 1 | | | | | | 2 | | | | | |
| | 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A. Number of nests | 6 | 24 | 45 | 31 | 30 | 34 | 6 | 22 | 25 | 20 | 21 | 20 |
| B. Number with eggs | 6 | 22 | 42 | 30 | 19 | 31 | 4 | 19 | 19 | 19 | 19 | 14 |
| Proportion of (A) with eggs | 1.0 | 0.92 | 0.93 | 0.97 | 0.97 | 0.91 | 0.67 | 0.86 | 0.76 | 0.95 | 0.90 | 0.70 |
| C. Number with nestlings | 4 | 17 | 30 | 22 | 16 | 27 | 4 | 12 | 11 | 16 | 15 | 6 |
| Proportion of (A) with nestlings | 0.67 | 0.71 | 0.67 | 0.71 | 0.53 | 0.79 | 0.67 | 0.55 | 0.44 | 0.80 | 0.71 | 0.30 |
| Proportion of (B) with nestlings | 0.67 | 0.77 | 0.71 | 0.73 | 0.55 | 0.87 | 1.0 | 0.63 | 0.58 | 0.84 | 0.79 | 0.43 |
| D. Number with fledglings | 4 | 10 | 18 | 10 | 11 | 20 | 4 | 8 | 5 | 12 | 7 | 4 |
| Proportion of (A) with fledglings | 0.67 | 0.42 | 0.40 | 0.32 | 0.37 | 0.59 | 0.67 | 0.22 | 0.25 | 0.60 | 0.33 | 0.20 |
| Proportion of (C) with fledglings | 1.0 | 0.59 | 0.60 | 0.45 | 0.69 | 0.74 | 1.0 | 0.67 | 0.45 | 0.75 | 0.47 | 0.67 |

nestling period, the trend for both locations had an early curvilinear component: the mortality rates increase to day 4, especially at Twin Peaks, and then describe a linear decrease (see Table 12). A log transformation was done of the $m$ value for each day, followed by a transformation taking the log of the logs to fit the curvilinearity. The linear log values accounted for a significant proportion of the total variance ($t = 2.42$; df = 8; $P < 0.05$), and the curvilinear log values also accounted for a significant proportion of variance ($t = 3.6022$; df = 7; $P < 0.01$). The complete model accounted for 0.80 of the total variance, with the linear component accounting for 0.42 and the curvilinear component for an additional 0.38.

## DISCUSSION

This study was conducted over a sufficient period of time to detect year-to-year variation in the reproductive success of individual territory holders. Two study locations were used to detect any differences between local populations. Such differences have been reported for the Great Tit (*Parus major*) (e.g. van Balen 1973). The studies of the Great Tit indicate the value of studying more than one population to identify any systematic biases influencing the generality of conclusions derived from intensive research on one local population.

*General findings regarding reproductive success.*—The overall reproductive success of the birds in these study areas perhaps can best be estimated by calculating the annual productivity value after Pinkowski (1979), where: $P =$ (young fledged/successful nest)(proportion nest success)(nests/season). An estimate of the first term would be the mean of 2.46 for the 418 successful nests of all 1,264 nests located. The proportion of success, then, is 0.33. An estimate of nests/season would be the value for those birds in the two study locations for which all nests were found during a breeding season. For the 174 pairs at Twin Peaks the mean was 3.11, and for the 86 pairs at the Presidio it was 2.97: The combined mean was 3.06. Thus, $P = (2.46)(0.33)(3.06) = 2.48$, indicating that, on the average, about 2.5 fledglings were produced by each pair in a season.

The only estimate of fledgling survival for this subspecies is the value of about 0.5 calculated by Baker et al. (1981) from January retraps of fledglings banded between June and August at their Pt. Reyes study site. This value seems appropriate, because territorial establishment begins in about January (Blanchard 1941).

An estimate of the longevity of territory holders on a territory can be obtained from Petrinovich and Patterson (1982). We reported, for the same birds under consideration here, that for 63 territories studied for at least 4 yr (number of territory years = 327), the mean time a territory holder was on territory was about 1.5 yr (1.67 for males and 1.41 for females). Given an average repeat rate for adults of 0.43/yr, 1.14 adults must be added to the breeding population each year. Each pair produces about 2.5 fledglings each year. Thus, over the 1.5 yr on the breeding territory, each pair would produce 3.75 fledglings. If the probability of survival from fledgling to adult is about 0.5, this would provide about 0.9 birds each year, almost the 1.4 replacement required.

The fledgling survival value of 0.5 is higher than that usually estimated for small passerines: Ricklefs (1977) estimates it to be about one quarter of adult survival. The increased surviv-

TABLE 5.  Continued.

| | | 3 | | | | | | 4–6 | | | | | | Total | | | | Total all years |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 | 75 | 76 | 77 | 78 | 79 | 80 | |
| 5 | 10 | 19 | 13 | 10 | 15 | 0 | 0 | 6 | 10 | 1 | 5 | 17 | 56 | 95 | 74 | 62 | 74 | 376 |
| 5 | 10 | 15 | 12 | 9 | 12 | 0 | 0 | 5 | 8 | 1 | 4 | 15 | 51 | 81 | 69 | 58 | 61 | 335 |
| 1.0 | 1.0 | 0.79 | 0.92 | 0.90 | 0.80 | 0 | 0 | 0.83 | 0.80 | 1.0 | 0.80 | 0.88 | 0.91 | 0.85 | 0.93 | 0.94 | 0.82 | 0.89 |
| 3 | 7 | 9 | 8 | 9 | 10 | 0 | 0 | 4 | 6 | 1 | 3 | 11 | 36 | 54 | 53 | 41 | 46 | 241 |
| 0.60 | 0.70 | 0.47 | 0.62 | 0.90 | 0.67 | 0 | 0 | 0.67 | 0.60 | 1.0 | 0.60 | 0.65 | 0.55 | 0.57 | 0.72 | 0.66 | 0.62 | 0.64 |
| 0.60 | 0.70 | 0.60 | 0.67 | 1.0 | 0.83 | 0 | 0 | 0.80 | 0.75 | 1.0 | 0.75 | 0.73 | 0.71 | 0.67 | 0.77 | 0.71 | 0.75 | 0.72 |
| 2 | 5 | 8 | 5 | 6 | 7 | 0 | 0 | 3 | 4 | 1 | 2 | 10 | 23 | 34 | 31 | 25 | 33 | 156 |
| 0.40 | 0.50 | 0.42 | 0.38 | 0.60 | 0.47 | 0 | 0 | 0.50 | 0.40 | 1.0 | 0.40 | 0.59 | 0.41 | 0.36 | 0.42 | 0.40 | 0.45 | 0.41 |
| 0.67 | 0.71 | 0.89 | 0.62 | 0.67 | 0.58 | 0 | 0 | 0.75 | 0.67 | 1.0 | 0.67 | 0.91 | 0.64 | 0.63 | 0.58 | 0.61 | 0.72 | 0.65 |

al rate found by Baker et al. (1981) might well occur, because the subspecies *nuttalli* does not migrate, and the weather along the Northern California coast is not extremely variable, being neither very warm in the summer nor harsh in the winter.

Another way to estimate the population level is to base it on the number of adult territory holders that repeat each year. Using the Baker et al. (1981) estimate of 0.5 for fledgling survival gives an estimate of 0.5 multiplied by the adult repeat rate of 0.43 = 0.22. This would lead to an estimate of 0.22 × 5 fledglings = 1.08, or just below the 1.14 required every 2 yr to maintain a stable population.

The estimate of 0.43 on which these calculations are based is lower than the true survival rate, because some territory holders that did not repeat have been sighted in the breeding area during the breeding season. Also, there is a non-breeding surplus available from year to year: 0.24 of territory holders entered the breeding population 2–5 yr after their initial banding, 0.25 of nestlings that required territories did so 2–5 yr after their birth, 0.41 of territorial birds that acquired a territory more than one yr after they were banded were sighted on a study territory in an intervening year, and birds that disappeared during the breeding season were almost immediately replaced. Although it is likely that the fledgling survival rate is lower than the 0.5 reported by Baker et al. because their estimates were based on fledgling recoveries while ours are based on the presence of fledged young in the natal territory it seems safe to conclude that the population is at a stable level.

Reproductive success can also be expressed as the ratio of the number of nests that resulted in at least one fledgling to the number of nests that had at least one egg. This expression indicated that 0.40 (337/846) of the nests for the combined locations were successful (Table 7B). This result is the same as that reported by Oakeson (1954), who found a value of 0.40 (12/30) for a Berkeley population of the same subspecies.

Ralph and Pearson (1971) reported that 0.60 (9) of the 15 nests of *nuttalli* found at Pt. Reyes, California had at least one fledgling. This value could be higher than our 0.40, because the small number of cases on which this estimate is based provided an unrepresentative value. It could also be spuriously high, because they did not locate the nests. Rather, they used parental behavior as an indication of nesting success, and this could have produced the overestimation due to an inability to detect some early losses of nests with eggs. On the other hand, by not locating the nests there was less disturbance, which could have resulted in the higher value (see discussion below, however.)

Nice (1937), in her study of Song Sparrows (*Melospiza melodia*), found that 0.47 of nests with eggs were successful. Nice (1957) summarized 24 studies of the nesting success of altricial birds that build open nests in the north temperate zone. She reported that, for the 7,788 nests surveyed, success ranged from 0.38 to 0.77, with a mean of 0.49, the latter value being a bit higher than our 0.40. Ricklefs (1977) reported that, for passerines in temperate regions, 0.30–0.80 of eggs became fledglings. In Nice's (1937) study of Song Sparrows, 0.36 of eggs became fledglings, as compared to our 0.32 (839/2,667; Table 8). Nice did report that in a bad year 0.25 of the eggs resulted in fledglings, while in a good year 0.42 did. In the present study, we found a

range of 0.24–0.54, again indicating that the data for this study population are comparable to those usually found.

*Differences between locations.*—There were some pronounced differences in reproductive success between the two study locations. Birds at Twin Peaks were, overall, less successful than those at the Presidio in all regards: significantly fewer eggs were laid, they resulted in fewer nestlings, and there were fewer fledglings and successful nests. Egg mortality was the same for the two areas, and the hatch rate for eggs was the same. In addition to fewer eggs per clutch at Twin Peaks, more nests were abandoned before an egg was laid, and there was a greater loss of nestlings to predation. Finally, there was significantly higher variability in the mean number of eggs and fledglings at Twin Peaks over the entire study period, and the year-to-year variability in the number of nestlings was greater. For 1976–1980 (1975 is not included because there were only 17 nests observed at the Presidio that year) Twin Peaks had both the highest and lowest proportion of the number of nests with nestlings to those with eggs (1976: 0.51; 1980: 0.86) and proportions of the number of nests with fledglings to those with nestlings (1978: 0.36; 1980: 0.79) (Tables 4 and 5).

The major physical difference between the two areas is that Twin Peaks is located along a steep, leeward hillside with considerable open space between available nest bushes. As a result of the steepness, the hill is seldom frequented by casual visitors. The vegetation at the Presidio is more uniform, and the terrain is more gradually pitched from the beach to the top of a slope. The temperature variation is more extreme at Twin Peaks after the fog burns off, and the fog is denser and stays longer at the Presidio, which is by the Pacific Ocean. The characteristics of the environments of these two locations were studied during 1975–1979, and the relationship between ecological variables and reproductive success will be the subject of a forthcoming paper.

The causes of nest mortality were roughly comparable for the two locations, except for the aforementioned increase in predation of nestlings and the greater abandonment of nests at Twin Peaks. The variability in reproductive success at Twin Peaks seems to be related to the weather: 1976 and 1977 were both years of severe drought and this was coupled with unusually high temperatures. The vegetation became more sparse and less dense and was still recovering in 1979.

*Difference between years.*—There were no year-to-year differences in number of eggs produced, but there were in number of nestlings and fledglings (1976 being low and 1980 high). The differences between years were due to more losses early in the nesting cycle in 1976, which resulted in fewer successful nests. In 1980, the reproductive success was the highest of any year, and this was due to less predation on eggs and nestlings.

TABLE 6. Outcome of nests located during the 6-yr study period for the combined locations.

| | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | Total | Proportion of total |
|---|---|---|---|---|---|---|---|---|
| Total number of nests | 123 | 188 | 193 | 185 | 140 | 149 | 978 | 1.00 |
| Nests abandoned with no eggs | 15 | 33 | 28 | 24 | 11 | 21 | 132 | 0.14 |
| Nests with eggs | 108 | 155 | 165 · | 161 | 129 | 128 | 846 | 0.87 |
| All hatched | 51 | 62 | 63 | 71 | 55 | 69 | 371 | 0.38 |
| Predation | 13 | 32 | 36 | 21 | 23 | 7 | 132 | 0.14 |
| Abandoned | 9 | 30 | 23 | 20 | 16 | 13 | 111 | 0.11 |
| Partial failure | 35 | 31 | 43 | 49 | 35 | 39 | 232 | 0.24 |
| Nests with nestlings | 86 | 93 | 106 | 120 | 90 | 108 | 603 | 0.62 |
| Fledged | 44 | 47 | 55 | 56 | 53 | 82 | 337 | 0.34 |
| Predation | 42 | 44 | 48 | 62 | 37 | 24 | 257 | 0.26 |
| Abandoned | 0 | 2 | 3 | 2 | 0 | 2 | 9 | 0.01 |
| Nests with fledglings | 44 | 47 | 55 | 56 | 53 | 82 | 337 | 0.34 |

TABLE 7.  Outcome of nests (A) located at each of the sites during all years combined and (B) during each year at the combined sites.

| | | Nests with eggs | | Nests with nestlings | | | |
|---|---|---|---|---|---|---|---|
| | Abandoned | Abandoned | Predation | Abandoned | Predation | Successful | Total |
| **A. Sites** | | | | | | | |
| Twin Peaks | 99 | 70 | 87 | 3 | 186 | 191 | 636 |
| Presidio | 33 | 41 | 45 | 6 | 71 | 146 | 342 |
| Total | 132 | 111 | 132 | 9 | 257 | 337 | 978 |
| **B. Years** | | | | | | | |
| 1975 | 15 | 9 | 13 | 0 | 42 | 44 | 123 |
| 1976 | 33 | 30 | 32 | 2 | 44 | 47 | 188 |
| 1977 | 28 | 23 | 36 | 3 | 48 | 55 | 193 |
| 1978 | 24 | 20 | 21 | 2 | 62 | 56 | 185 |
| 1979 | 11 | 16 | 23 | 0 | 37 | 53 | 140 |
| 1980 | 21 | 13 | 7 | 2 | 24 | 82 | 149 |
| Total | 132 | 111 | 132 | 9 | 257 | 337 | 978 |
| Proportion of total | 0.14 | 0.11 | 0.14 | 0.01 | 0.26 | 0.34 | 1.00 |

(Header spanning "Outcome" over all outcome columns)

We pointed out above that there was considerable variability across years, especially at Twin Peaks. The extreme variability in reproductive success at Twin Peaks seemed to be related to extremes in weather conditions, especially in 1976 and 1977, which were severe drought years at the study locations. The effects of the drought were most pronounced at Twin Peaks, perhaps because of the decreased prevalence of drought-resistant vegetation at Twin Peaks and because of the heavier concentration of fog at the Presidio, which compensated for the lack of rain.

*Causes of nesting failure.*—When all nests at the two study locations were considered, the greatest cause of nest failure (381/978 = 0.39) was predation (0.13 to egg predation and 0.26 to nestling predation; see Table 6). For 185 nests of four species of sparrows (Vesper Sparrow, *Pooecetes gramineus*; Grasshopper Sparrow, *Ammodramus savannarum*; Savannah Sparrow, *Passerculus sandwichensis*; and Field Sparrow, *Spizella pusilla*), Wray et al. (1982) reported that 90 (0.49) were presumed lost to predators (0.30 to egg predation and 0.19 to nestling predation).

TABLE 8.  Outcome of eggs at the combined locations for 1975–1980.

| | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | Total | Proportion of total |
|---|---|---|---|---|---|---|---|---|
| **Total number of eggs** | 343 | 452 | 529 | 513 | 404 | 406 | 2,667 | 1.00 |
| Hatched | 215 | 260 | 300 | 327 | 245 | 299 | 1,646 | 0.62 |
| Predation | 49 | 82 | 110 | 82 | 89 | 17 | 429 | 0.16 |
| Abandoned | 79 | 130 | 119 | 104 | 70 | 90 | 592 | 0.22 |
| **Total number of nestlings** | 215 | 260 | 300 | 327 | 245 | 299 | 1,646 | 0.62 |
| Fledged | 107 | 110 | 137 | 138 | 128 | 219 | 839 | 0.31 |
| Predation | 104 | 133 | 151 | 180 | 112 | 67 | 747 | 0.28 |
| Abandoned | 4 | 17 | 12 | 9 | 5 | 13 | 60 | 0.02 |
| **Total number of fledglings** | 107 | 110 | 137 | 138 | 128 | 219 | 839 | 0.31 |

(Header spanning "Outcome" over columns 1975–Total)

TABLE 9. Number of attempted nestings and number of successful nestings at Twin Peaks for those pairs for which all nests were found (1975-1980).

| Attempted nestings | Successful nestings | | | | | Proportion of total |
|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | Total | |
| 2 | 16 | 17 | 17 | — | 50 | 0.29 |
| 3 | 29 | 23 | 19 | 1 | 72 | 0.41 |
| 4 | 15 | 16 | 7 | 1 | 39 | 0.22 |
| 5 | 6 | 2 | 2 | — | 10 | 0.06 |
| 6 | 1 | 1 | — | — | 2 | 0.01 |
| 7 | 1 | — | — | — | 1 | 0.01 |
| Total | 68 | 59 | 45 | 2 | 174 | |
| Proportion of total | 0.39 | 0.34 | 0.26 | 0.01 | | 1.00 |

Ricklefs (1969) used eggs rather than nests as the base for analysis in his survey of 5,131 eggs laid by six passerine species. He reported that there were 1,859 (0.36) losses to predators (0.23 to egg predation and 0.13 to nestling predation). In the present study, of the 2,667 eggs produced, 1,176 (0.44) were lost to predators (0.16 to egg predation and 0.28 to nestling predation).

It appears that the overall rates of predation found here are roughly comparable to those reported by others and that the proportion of egg predation is lower or at about the same level. A higher proportion of nestlings suffered predation, however, than is usually reported.

It can be argued that the higher level of nestling predation is the result of intense predation by the western terrestrial garter snake (*Thamnophis elegans*). Although there are mammalian and avian predators that take both eggs and nestlings at our study locations, snakes have been found to be a major predator at the San Francisco locations (James et al. 1983). Snakes have never been observed to take eggs, even though they have been observed in or beside nests with eggs 11 times. There have been 39 instances observed in which snakes took nestlings, and, when snakes were trapped and forced to regurgitate, several were found to contain White-crowned Sparrow nestlings.

Nests from which snakes took nestlings were significantly lower in height than those of the general population (James et al. 1983). Nests with nestlings that suffered predation were significantly lower than those with eggs that suffered predation, again suggesting that different predators might be responsible for losses at different stages of the nesting cycle. That nestling losses occurred predominantly in lower nests supports the idea that snakes were the major cause of nestling loss. It is reasonable to suppose that our population was subject to more intensive snake predation than is usual for small passerines and that this accounts for the higher level of nestling predation.

*Survival rates.*—For the combined locations,

TABLE 10. Number of attempted nestings and number of successful nestings at the Presidio for those pairs for which all nests were found (1976-1980).

| Attempted nestings | Successful nestings | | | | | Proportion of total |
|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | Total | |
| 2 | 3 | 16 | 6 | — | 25 | 0.29 |
| 3 | 6 | 25 | 11 | — | 42 | 0.49 |
| 4 | 5 | 6 | 6 | — | 17 | 0.20 |
| 5 | 0 | 1 | 0 | — | 1 | 0.01 |
| 6 | 0 | 0 | 1 | — | 1 | 0.01 |
| Total | 14 | 48 | 24 | 0 | 86 | |
| Proportion of total | 0.16 | 0.56 | 0.28 | 0 | | 1.00 |

TABLE 11. Nest mortality rates ($m$) for nests with eggs calculated by the Mayfield method for each day. See text for explanation.

| Day | A. Twin Peaks | | | B. Presidio | | | C. Combined data | | |
|-----|----------|--------|----------|----------|--------|----------|----------|--------|----------|
|     | Exposure | Losses | $m$      | Exposure | Losses | $m$      | Exposure | Losses | $m$      |
| −4  | 1        | 0      | 0        | 1        | 0      | 0        | 2        | 0      | 0        |
| −3  | 31       | 0      | 0        | 13       | 0      | 0        | 44       | 0      | 0        |
| −2  | 104      | 0      | 0        | 33       | 0      | 0        | 137      | 0      | 0        |
| −1  | 126      | 0      | 0        | 43       | 0      | 0        | 169      | 0      | 0        |
| 1   | 150      | 2      | 0.0133   | 53       | 2      | 0.0377   | 203      | 4      | 0.0197   |
| 2   | 176      | 3      | 0.0170   | 68       | 1      | 0.0147   | 244      | 4      | 0.0164   |
| 3   | 192      | 3      | 0.0156   | 78       | 4      | 0.0513   | 270      | 7      | 0.0259   |
| 4   | 216      | 5      | 0.0231   | 95       | 1      | 0.0105   | 311      | 6      | 0.0193   |
| 5   | 232      | 7      | 0.0302   | 105      | 3      | 0.0286   | 337      | 10     | 0.0297   |
| 6   | 257      | 5      | 0.0195   | 115      | 2      | 0.0174   | 372      | 7      | 0.0188   |
| 7   | 262      | 6      | 0.0229   | 133      | 2      | 0.0150   | 395      | 8      | 0.0203   |
| 8   | 272      | 6      | 0.0221   | 144      | 3      | 0.0208   | 416      | 9      | 0.0216   |
| 9   | 288      | 6      | 0.0208   | 152      | 2      | 0.0132   | 440      | 8      | 0.0182   |
| 10  | 291      | 7      | 0.0241   | 160      | 3      | 0.0188   | 451      | 10     | 0.0222   |
| 11  | 306      | 7      | 0.0229   | 162      | 3      | 0.0185   | 468      | 10     | 0.0214   |
| 12  | (310)    | (12)   | (0.0387) | (163)    | (9)    | (0.0552) | (473)    | (21)   | (0.0444) |
|     | 306      | 7      | 0.0229   | 162      | 3      | 0.0185   | 468      | 10     | 0.0214   |
| Total | 3,210  | 64     | 0.0199   | 1,517    | 29     | 0.0191   | 4,727    | 93     | 0.0197   |

nest mortality calculated for eggs was estimated to be 0.0197 per day for the incubation stage, 0.0766 per day for the nestling stage, and 0.0450 per day for the total nesting period. The values for the Song Sparrows studied by Nice (see Ricklefs 1969) were: eggs, 0.0234; nestlings, 0.0386; total, 0.0293. Our results were, once again, lower for the egg period and enough higher for the nestling period that the total mortality rate was higher.

A trend analysis indicated that mortality rates did not vary across days during the egg stage. There were strong linear and curvilinear components during the nestling stage, however. The nestling mortality rate increased to day 4 after hatching and then decreased linearly to day 10. Thus, nestlings were increasingly at risk until day 4, and the probability of their survival to fledging increased quite rapidly after that time.

These results might have been influenced by the disturbance created by activities of observers. It is conceivable that locating nests, following them every few days, and banding the nestlings could enhance mortality rates. This has often been suggested as a general concern (e.g. Skutch 1976) and has been suggested specifically in regard to the present species (e.g. Baker et al. 1982, Baker 1983). Baker et al. (1982: 134) present the argument that the method of choice when studying population dynamics

should be to "... use trapping as the primary method of obtaining first captures for banding, with a few supplementary bandings of nestlings, rather than focusing on location and banding nestlings only." They suggest that human-caused depression of reproductive success might easily give a misleading picture of population dynamics. Baker and Mewaldt (1981) reported that birds at their Pt. Reyes study site had larger clutches ($\bar{x} = 3.47$; $s = 0.66$) than we found. The difference between the mean of 3.15 for San Francisco and that of 3.47 for Pt. Reyes is not significant, however ($t = 1.78$; df $= 1,077$; $P > 0.05$).

An examination of evidence in the literature offers little support for the disturbance hypothesis. Bart (1977) used data on five species from the Nest Record Cards Program and found that there was an increase in daily mortality rate of nests on the day following a visit to the nest as compared to the rate on subsequent days. Two experimental studies that have been conducted, however, found no effect of human visitation on survival rates. Willis (1973) studied Bicolored Antbirds (*Gymnopithys leucaspis*) and found a high mortality rate early in the nesting cycle for watched nests, followed by a rise for both watched and unwatched, with a large increase for unwatched nests with hatched nestlings. He concluded that "At watched nests it seemed that my visits accelerated the destruc-

TABLE 12.   Nest mortality rates ($m$) for nests with nestlings calculated by the Mayfield method for each day. See text for explanation.

| Day | A. Twin Peaks | | | B. Presidio | | | C. Combined data | | |
|---|---|---|---|---|---|---|---|---|---|
| | Exposure | Losses | $m$ | Exposure | Losses | $m$ | Exposure | Losses | $m$ |
| 1 | (309) | (14) | (0.0453) | (177) | (0) | (0) | (486) | (14) | (0.0288) |
| | 291 | 32 | 0.1100 | 174 | 11 | 0.0632 | 465 | 43 | 0.0295 |
| 2 | 291 | 32 | 0.1100 | 174 | 11 | 0.0632 | 465 | 43 | 0.0295 |
| 3 | 264 | 33 | 0.1250 | 163 | 18 | 0.1104 | 427 | 51 | 0.1194 |
| 4 | 228 | 41 | 0.1798 | 154 | 15 | 0.0974 | 382 | 56 | 0.1466 |
| 5 | 217 | 18 | 0.0829 | 150 | 8 | 0.0533 | 367 | 26 | 0.0708 |
| 6 | 207 | 15 | 0.0724 | 146 | 7 | 0.0479 | 353 | 22 | 0.0623 |
| 7 | 197 | 13 | 0.0660 | 140 | 10 | 0.0714 | 337 | 23 | 0.0682 |
| 8 | 189 | 12 | 0.0635 | 142 | 2 | 0.0141 | 331 | 14 | 0.0423 |
| 9 | 186 | 5 | 0.0269 | 141 | 3 | 0.0213 | 327 | 8 | 0.0245 |
| 10 | 187 | 2 | 0.0107 | 143 | 2 | 0.0140 | 330 | 4 | 0.0121 |
| Total | 2,257 | 203 | 0.0899 | 1,527 | 87 | 0.0570 | 3,784 | 290 | 0.0766 |
| Grand total | 5,467 | 267 | 0.4880 | 3,044 | 116 | 0.0381 | 8,511 | 383 | 0.0450 |

tion of easily discovered nests, but had little or no effect on the final percentage of nests surviving" (pp. 265–266). Gottfried and Thompson (1978) set out experimental nests with eggs for 1-week periods and then visited some every day and some not until the end of a 6-day period. There were no differences in the success rate of the visited and the nonvisited nests.

Baker et al. (1982) cite Lenington (1979) as support for their belief that nests located while active are lost to predators. Lenington considered the effect of human activity on predation of the Red-winged Blackbird (*Agelaius phoeniceus*) in marsh and upland study sites in successive years. Any decrease in success rate in a second year she attributed to the predator's having learned and retained the ability to follow human scent from nest to nest. Although in the marsh sites nests were less successful in a second year, in the upland sites there was a decrease in the proportion of successful nests in three studies and an increase in two, resulting in no clear differences.

Clearly, the existing evidence provides little support for the view that the harmful effects of human visitation are sufficient to override the benefits of establishing natal site, parentage, and kinship. It also seems unlikely that banding nestlings led to increased predation. Nestlings were banded at a mean age of 7.14 days; yet the mortality rates for nestlings reach a maximum at day 4 and show a linear decrease to day 10.

It seems safe to conclude that the results obtained here provide an accurate picture of the patterns of reproductive success for these two study locations. The next task is to relate individual patterns and differences between locations and between years to proximate factors. Data have been recorded concerning nest-site characteristics, insect abundance, characteristics of vegetation, and weather during the 1975–1979 breeding seasons. These data will be brought to bear in the next paper of this series in an attempt to understand the variations in reproductive success.

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