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### THE WHITE-CROWNED SPARROW: STABILITY, RECRUITMENT, AND POPULATION STRUCTURE IN THE NUTTALL SUBSPECIES (1975–1980)

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**ABSTRACT.**—We studied two banded populations of sedentary White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) over a 6-yr period. Most territory holders were identified (326 males and 286 females), all nestlings (1,052) were banded, and any unbanded birds that appeared were banded. Detailed analyses were based on only those territories that were occupied for at least 4 of the 6 yr. Of the males, 0.50 repeated as territory holders on any given year and of the females 0.35. Of those that stayed on the same territory, about one-quarter of the males had the same mate as compared to about one-half of the females. If there was a shift to a new territory on the succeeding year, both males and females had new mates. Females remained on a territory significantly fewer years (1.41) than did males (1.67). Divorce occurred in 0.31 of the possible instances, and there was one case of incest.

Among newly recruited territory holders, 0.17 of the male and 0.15 of the female recruits were nestlings of the area. The other recruits were post-dispersal birds: 0.14 were banded as fledglings, 0.26 as 1st-yr, brown-crowned birds, 0.32 as full-crowned adults (2 yr old or more), and 0.11 were unknown. Of the total number of nestlings banded in the course of the study 0.078 entered the breeding population.

In general: (1) territory size and density are stable across years. (2) One of the study regions was more variable in terms of reproductive success than the other across years, and the mean number of years that a bird held a territory was significantly less for the variable region. (3) A nonbreeding surplus of reproductively able males and females apparently is available throughout the breeding season. These results are discussed in relation to other data available. Some speculations are made regarding the significance of these findings to questions of natal dispersal. *Received 8 April 1981, accepted 1 July 1981.*

THE present report is part of a descriptive study of the population dynamics of the sedentary subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). This study has been conducted at two locations in the San Francisco Bay Area for a period of 6 yr. In this report we present data based on a banding program conducted with this territorial and monogamous species. In the course of this study most territory holders were identified and all nestlings were banded. An attempt was made to band all unbanded birds that appeared throughout the course of the study. Observers were present throughout the breed-

ing season either to retrap or to identify the bands of nonterritorial birds.

The data obtained allow us to determine the number of years individuals repeat in the breeding population, the site tenacity of males and females, the stability of pairs across years, the proportion of banded nestlings that enter into the breeding population, and the composition of the breeding population, both in terms of status at banding and age at entry into the population.

A companion report is being prepared (Patterson and Petrinovich in prep.) in which we present data on the reproductive success of the

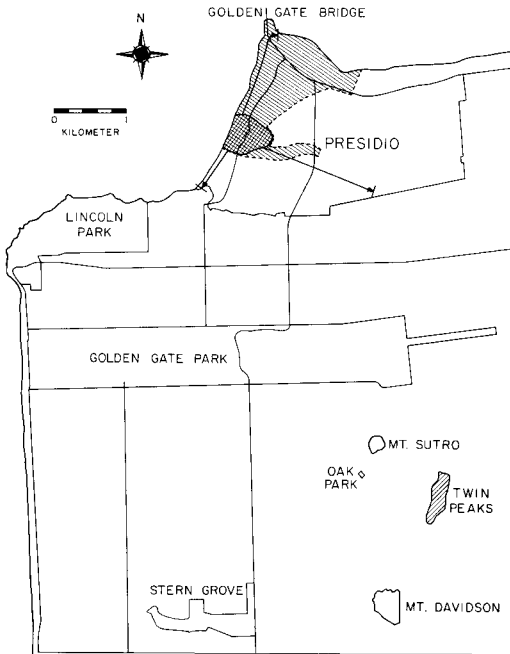


Fig. 1. Map of San Francisco illustrating the two study areas. The study area at Twin Peaks is indicated by cross-hatching. The Presidio study area is indicated by grid-lines.

birds in our study population as related to ecological factors. We also have recorded the song of most of the territorial males throughout the study. Analyses are underway to determine the stability of song across years, the cultural transmission of song from parent to son, and the relationship of song type to characteristics of the territory and to reproductive success.

Some of these birds were included as subjects in playback studies that have been reported elsewhere (Patterson and Petrinovich 1979; Petrinovich and Patterson 1979, 1980, 1981). We have also reported studies of the territory size and stability of this population (Patterson and Petrinovich 1978), polygyny (Petrinovich and Patterson 1978a), cowbird parasitism (Petrinovich and Patterson 1978b), and responses to predators (Patterson et al. 1980).

#### SUBJECTS

*Z. l. nuttalli* is sedentary and breeds in coastal California from about Cape Mendocino to Santa Barbara (Blanchard 1941, 1942). Blanchard (1936, 1941; see also De Wolfe 1968) has published information on the life history of both the sedentary and the migra-

tory subspecies, and the following descriptions are based both on her studies and on the studies we have conducted during six breeding seasons.

During the winter, adult and 1st-yr birds form feeding flocks of from 6 to 40 individuals. Prior to the breeding season, males establish territories and advertise for females. During these early stages of territory formation, the male sings a great deal, and occasional physical encounters and chases take place between a given territorial male and his neighbors as well as with foreign intruders. By the time the breeding season begins, the territorial conflicts consist mainly of bouts of singing and countersinging between neighboring males.

In early April the female builds a nest, the pair copulates, and the female lays a clutch of about three eggs, one per day, with the female beginning to incubate the eggs when the clutch is complete. Each pair attempts to build an average of about 3 nests each season, with a range of from 1 to 6. Unsuccessful nests usually are due to predation, but occasionally abandonment occurs (Patterson and Petrinovich in prep.). The breeding activities continue into July.

The young hatch after about 13 days, and the nestlings are fed insects and pill bugs (*Armadillium*), mainly by the female at first, with the male assisting more near the end of the nestling period, which is 9–12 days long. The predominant food of adults during the breeding season is vegetable material, mostly seeds.

When the young fledge, they stay in the region of the nest until they are about 36–40 days old, with the male assuming the major responsibility of feeding the young during the latter part of the period. A few days after the young of the early broods fledge, the female begins a new nest, and the whole cycle starts again, continuing until the pair has fledged 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 from both land and aerial predators, with only about 30% of the eggs produced resulting in fledglings (Patterson and Petrinovich in prep.).

Each male usually has one song that is about 2 s long and is repeated every 11 s during a bout of singing. There are pronounced regional dialect groups (Marler and Tamura 1962, Baptista 1975) that are stable from year to year. The songs of these groups are composed of similar elements, but they are combined in different orders.

#### STUDY AREA

We used two study regions in San Francisco, California: Twin Peaks (TP) and the Presidio (P) (see Fig. 1 for a map of the region).

*Twin Peaks (TP)*.—This region is composed of coastal soft chaparral and is located along the 740-m east face of a hill; it contains about 47 territories. The

TABLE 1. Total number of birds banded.

Year	Number of adults	Number of nestlings	Number of fledglings	Total
1975	137	98	29	264
1976	138	148	49	335
1977	140	150	70	360
1978	210	245	83	538
1979	93	166	31	290
1980	75	245	36	356
Total	793	1,052	298	2,143

vegetation is composed mainly of baccharis (*Baccharis pilularis*), berry brambles (*Rubus*), poison oak (*Toxicodendron diversiloba*), sage (*Artemisia*), and grasses.

*Presidio of San Francisco (P).*—This remnant dune region is located 5.6 km north of TP on the Pacific coast immediately south of the Golden Gate Bridge. The area is 1.5 km by 370 m and contains about 31 territories. The vegetation is composed of lupine (*Lupinus* sp.), chamise (*Adenostoma fasciculatum*), baccharis, poison oak, berry brambles, and grasses.

#### METHODS

The data reported in this paper are based on over 11,000 observer hours of field observation. A total of 2,143 birds was banded with U.S. Bureau of Fish and

Wildlife Service numbered aluminum bands and A. C. Hughes plastic color bands for identification. Adults were either trapped in Glenhaven Standby traps or were caught in mist nets. Nestlings were banded at approximately 8 days of age. Fledglings were trapped throughout the breeding season: all banded birds were noted and unbanded ones banded. The total number of birds banded in each age-class for each year is listed in Table 1. Included in this number are all of the adults, nestlings, and fledglings for the two study regions: 793 adults, 1,052 nestlings, and 298 fledglings, as well as birds banded in regions adjoining the study regions, for a total of 2,143 birds.

All nests of all pairs in each study region were located and monitored approximately every 3 days to the fledging stage. A nest was considered to have been fledged if the adults were seen feeding young a day or two after the nestlings had left the nest. If a nest bowl was built and not used, it was counted as a nest.

#### RESULTS

A total of 429 territories was studied for at least 1 yr over the 6-yr study period (Table 2A). In all, 326 male and 286 female territory holders were present, and 1,052 nestlings were banded on these territories. Several of these territories were studied for only 1 or 2 yr, because they

TABLE 2. Summary of results of banding program.

	1975	1976	1977	1978	1979	1980	Σ
<b>A. All territories studied at least 1 complete year</b>							
Number of territories	43	72	81	75	74	84	429
Number of banded ♂♂	18	42	66	64	60	76	326
Number of banded ♀♀	19	32	66	59	52	58	286
Number of repeat ♂♂	—	13	21	23	36	26	119
Number of repeat ♀♀	—	10	10	18	18	15	71
<b>B. 4-yr territories at TP (n = 37)</b>							
Number of territories	28	34	35	36	36	34	203
Number of banded ♂♂	15	23	31	32	32	32	165
Number of banded ♀♀	14	21	27	30	29	28	149
Number of repeat ♂♂	—	8	14	12	21	15	71
Number of repeat ♀♀	—	10	8	8	13	8	47
<b>C. 4-yr territories at P (n = 26)</b>							
Number of territories	9	20	25	23	24	23	124
Number of banded ♂♂	3	11	22	23	19	23	101
Number of banded ♀♀	3	6	22	20	19	19	89
Number of repeat ♂♂	—	1	9	8	11	6	35
Number of repeat ♀♀	—	1	1	6	5	7	20
<b>D. Combined 4-yr territories (n = 63)</b>							
Number of territories	37	54	60	59	60	57	327
Number of banded ♂♂	18	34	53	55	51	55	266
Number of banded ♀♀	17	27	49	50	48	47	238
Number of repeat ♂♂	—	9	23	20	32	21	105
Number of repeat ♀♀	—	11	9	14	18	15	67

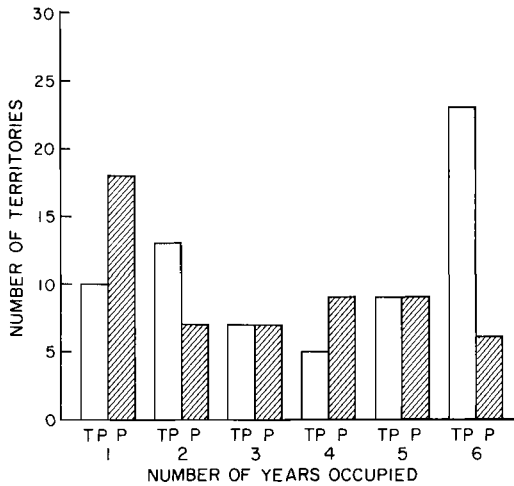


Fig. 2. The number of years each territory was occupied during the 6-yr study period at each of the study areas (TP = Twin Peaks; P = Presidio).

were located on the margins of the study area and were infrequently occupied. The number of years each of the territories was occupied is shown in Fig. 2. We detected a relatively greater number of occupied territories for the entire 6 yr at TP, because we made a more intensive effort there than at P in 1975. There are more territories at TP, as well as a more nearly constant use of the available territories.

Detailed analyses are done using only those territories that were occupied for at least 4 of the 6 yr to eliminate those marginal territories that would produce a bias in the estimates of turnover, dispersal, and recruitment. Although all territories were not included in the 4-yr study population, all nestlings were banded each year in every territory. This allowed us to identify them if they appeared as recruits in the breeding population. At TP, 37 territories were occupied for at least 4 yr (Table 2B), 26 at P (Table 2C). Examination of the table reveals that 0.76 (327/429) of the total number of all territories in which a nest was ever found were included in the 4-yr study population.

During the 6-yr period, 0.81 of the males at TP (165/203) and 0.81 at P (101/124) were banded, while 0.73 (149/203) of the TP females and 0.72 (89/124) of the P females were banded. The data for the two areas are combined in Table 2D: 0.81 (266/327) of the combined males and 0.73 (238/327) of the combined females were banded.

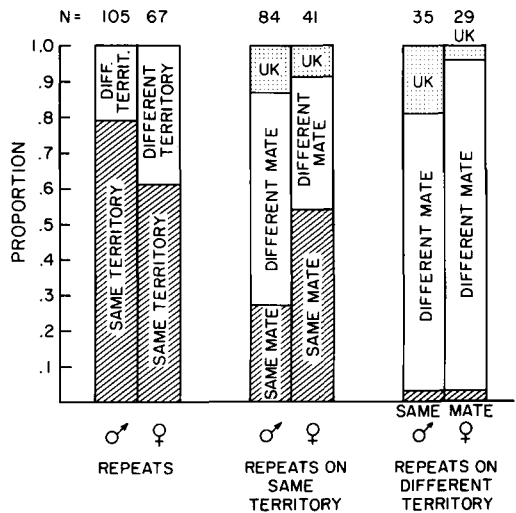


Fig. 3. The left pair of bars represents, for males and females, respectively, the proportion of repeat territory holders that retained the same territory and those that moved to a different territory. The middle pair of bars represents, for those repeats that remained on the same territory, those that retained the same mate and those that had a different mate. The right pair of bars represents, for those that had a different territory, those that retained the same mate and those that had a different mate.

*Repeat territory holders.*—The numbers of repeat males and females are also presented in Table 2A–D. The ratio of the number of males and females that were repeat territory holders on a given year is calculated using the number of banded birds the preceding year as a base, because only those that had been banded could be identified as repeats. For the 4-yr territories, the proportion of repeats was 0.50 (105/211) for the combined males, and 0.35 (67/191) for the combined females: the overall proportion of repeats was 0.43. Significantly more males repeated than did females ( $\chi^2 = 9.15$ ,  $P < 0.01$ , 1 df). Because the results for TP and P were similar in most respects, detailed results will not be presented for each of the areas. Instead, the results of combined analyses will be presented, and in only those instances in which the results were different for the two study regions will the results for each of the regions be discussed separately.

Of the males 0.79 (84/105) and of the females 0.61 (41/67) remained on the same territory (Fig. 3). Significantly more males that repeated

TABLE 3. The number of years birds were on the territory tabulated at the last year of their presence. (Only one of the years had to include a 4-yr study territory.)

Number of years on territory	♂						♀					
	1976	1977	1978	1979	1980	Σ	1976	1977	1978	1979	1980	Σ
<b>Area TP</b>												
1	8	9	4	7	19	47	8	13	7	9	26	63
2	2	4	4	9	7	26	5	5	5	8	4	27
3	x	4	3	5	5	17	x	2	2	1	2	7
4	x	x	0	1	0	1	x	x	2	1	1	4
5	x	x	x	1	0	1	x	x	x	0	0	0
6	x	x	x	x	1	1	x	x	x	x	0	0
<b>Area P</b>												
1	4	8	11	8	18	49	6	17	10	9	18	60
2	0	4	6	4	0	14	1	1	6	2	5	15
3	x	1	1	1	2	5	x	0	0	1	1	2
4	x	x	0	0	1	1	x	x	0	0	1	1
5	x	x	x	0	3	3	x	x	x	0	0	0
6	x	x	x	x	0	0	x	x	x	x	0	0

remained on the same territory (0.79) as compared to females (0.61) ( $\chi^2 = 5.93$ ,  $P < 0.02$ , 1 df). Of the birds that repeated on the same territory, 0.27 males (23/84) and 0.54 (22/41) females retained the same mate, while 0.59 (50/84) males and 0.37 (15/41) females had new mates [for 0.13 (11/84) of the males and 0.10 (4/41) of the females, the new mate was unknown]. The overall  $\chi^2$  was significant (8.39,  $P < 0.02$ , 2 df). Thus, of those birds that stayed on the same territory, about one-quarter of the males had the same mate as compared to about one-half of the females.

If there was a shift to a new territory in a succeeding year, both males and females had new mates. Only one of the 35 males and one of the 29 females that shifted territories had the same mate as before on the new territory: both members of only one pair shifted from one TP territory in 1977 to the adjoining one in 1978. In one other instance a male switched from one territory to an adjoining one upon the disappearance of the resident male in 1977. In 1978 his former mate joined him on the new territory, the resident female of 1977 having disappeared from the population.

The number of years male and female territory holders spent on a territory is indicated in Table 3. These data are for the 63 study territories. In cases where territory shift occurred of which only one territory was from the 4-yr study sample, the instance was included in this tabulation. Thus, if a bird moved from a 4-yr study territory to one that was not included in

that sample or to a 4-yr study territory from one not in that sample it is included in the table: only known movements, therefore, are considered. For the 1-yr birds, only the data for 1976–1979 were included, because it was possible neither to determine how many of the initial-year birds were repeats nor to know how many of the final-year birds would repeat. A sex difference also was present: more females were on territory for only 1 yr than was the case for males ( $\chi^2 = 3.91$ ,  $P < 0.05$ , 1 df). A larger proportion of birds at P were on the territory for only 1 yr [1 yr = 73 (0.64); greater than 1 yr = 41 (0.36)] than was the case for TP [1 yr = 65 (0.44); greater than 1 yr = 84 (0.56)] ( $\chi^2 = 10.50$ ,  $P < 0.01$ , 1 df).

The data can also be examined by subjecting the means for each sex at each area to a two-way analysis of variance. When this was done, there was a significant difference between regions ( $\bar{x}_P = 1.64$  and  $\bar{x}_{TP} = 1.41$ ;  $F = 4.95$ ;  $P < 0.05$ ;  $df = 1$  and 340) and between sexes ( $\bar{x}_\delta = 1.67$  and  $\bar{x}_\varphi = 1.41$ ;  $F = 4.95$ ;  $P < 0.05$ ;  $df = 1$  and 340) and no interaction ( $F = 0.0$ ). Thus, females remained on a territory for fewer years than did males, and birds at P remained on territory for fewer years than did those at TP.

*Divorce.*—Divorce, instances in which both members of a pair were present in a succeeding year but were paired with different mates, occurred in about one-third of the possible instances. There were 36 instances in which it was possible for the pair to remate, because

TABLE 4. Annual composition of banded adult population, indicating banding status of recruits.<sup>a</sup>

Status when banded		1975	1976	1977	1978	1979	1980	$\Sigma$ 1977-1980
Nestling	♂	—	2	2	5	10	8	25
	♀	—	2	7	4	12	3	26
Fledgling	♂	—	3	2	7	4	7	20
	♀	—	2	3	16	3	4	26
BC <sup>b</sup>	♂	6	7	7	7	3	9	26
	♀	7	14	9	12	15	23	59
FC <sup>b</sup>	♂	17	20	21	16	7	13	57
	♀	19	13	20	8	7	12	47
UK <sup>b</sup>	♂	13	11	8	1	5	1	15
	♀	12	12	10	2	5	3	20
Total recruit	♂	36	43	40	36	29	38	143
	♀	38	43	49	42	42	45	178
Repeat	♂	—	9	20	20	32	20	92
	♀	—	11	9	14	18	14	55
Total	♂	36	52	60	56	61	58	235
	♀	38	54	58	56	60	59	233

<sup>a</sup> Combined data for 4-yr territories.

<sup>b</sup> BC = brown-crowned 1st-yr adults; FC = full-crowned adults; UK = unknown.

both members were known to be again present in the breeding population. There were 25 rematings (0.69) and 11 divorces (0.31) in these 36 instances. Most of the divorced birds moved to the adjacent territory, but three moved a distance of 95–145 m. In one instance a male moved to a new territory in mid-season and was joined by his previous mate the next year. In another instance two birds that were banded in 1975 as an adult pair at an area 1.35 km from the study area occupied a study area territory in 1979: we presume they moved as a mated pair.

*Incest.*—There have been 10 cases in which a territorial female banded as a nestling entered the breeding population when the father was also present. In only one of these instances was the daughter mated with the father: a female born in 1976 mated with her father in both 1979 and 1980. This male held the same territory for the entire 6-yr study period.

We observed only three cases in which a territorial male banded as a nestling entered the breeding population when the mother was also present. In none of these instances was the son mated with the mother. In all three cases the mother had a new mate, two on a different territory and one on the same territory. There have been no observed instances of brother-sister matings. It appears, then, that incest is possible but that it occurs infrequently.

*Recruits.*—There were 286 identified recruits over the last 4 yr (1977–1980) located on a total

of 236 territories. Figure 4 is a graphical display of these data for each of the study years with a summary display of the years 1977–1980. It is possible to determine whether or not recruits were birds of the preceding season, because they have brown crowns (BC), while birds 2 yr and older have full black and white crowns: they are full-crowned (FC). Table 4 contains the combined data indicating the composition of the banded adult population for each year: the status of recruits refers to their status at the time of banding. (The number of identified birds in Fig. 4 is greater than the number of banded birds in Table 2, because some were sightings of unbanded territory holders whose crown color was determined.)

To obtain the most accurate estimate of the identity of the recruits, one should examine only the data of the last 4 yr. The banding effort was almost complete in 1976–1980, while it was not in 1975. Therefore, it is not possible to be certain of the origin of 1st-yr BC birds that entered the population in 1976. When only the data from 1977–1980 are considered, 0.17 (25/143) of the male recruits and 0.15 (26/178) of the female recruits originated as nestlings in the region. The other recruits were post-dispersal birds: 46 were banded as fledglings (0.14), 85 as 1st-yr BC's (0.26), and 104 as FC adults (0.32), with 35 unknowns (0.11). Thus, only 0.16 of the recruits were born in the area, while 0.40 dispersed into the study area in their natal year (as fledglings or BC's), and an additional

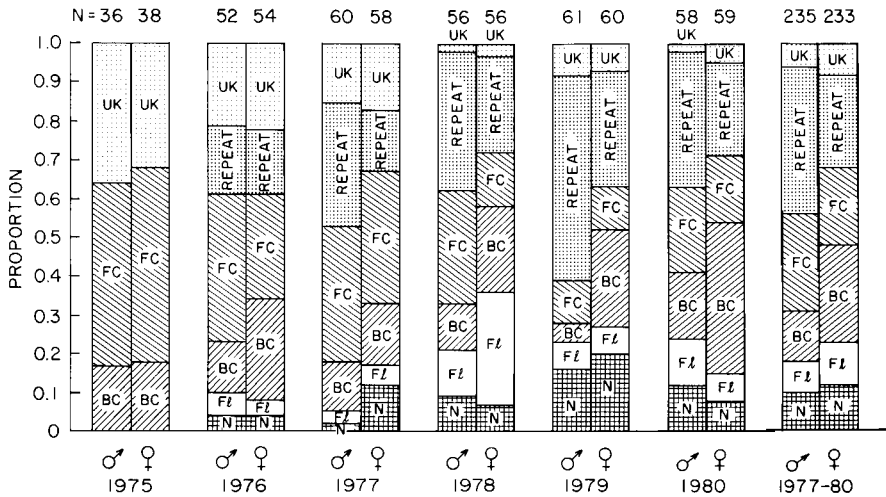


Fig. 4. The status of recruits at the time they were first banded for each of the years of the study. The final pair of bars is a representation of the data for the period 1977-1980.

0.32 appeared in the study area in their second year or later (with an unknown 0.11). The proportion of birds that were either born in the area or were repeats for 1977-1980 (excluding unknowns) was 0.53 males and 0.38 females. The proportion was 0.46 for the sexes combined.

When all territories studied for at least 1 complete year are considered, an average of about 60 territories was occupied in the study areas during each of the 6 yr: they yielded a total of 429 territory-years for examination (see Table 2A). When the recruits were categorized by sex and age status at the time of banding (nestling, fledgling, BC, FC, unknown) the calculated  $\chi^2$  was 11.99 ( $P < 0.02$ , 4 df). There was, therefore, a significant difference in the status of male and female territory holders in terms of their status at banding: there were fewer BC and more FC males than expected, while there were more BC and fewer FC females than expected.

The status of the recruits for the 4-yr study territories for the combined areas at the time they entered the population each year is shown in Table 5. A significant difference was obtained when the distribution of the frequencies was examined ( $\chi^2 = 30.71$ ,  $P < 0.01$ ,  $df = 12$ ). The three cells that made a large contribution to the  $\chi^2$  value were for the year 1977: among females there were fewer BC and more FC recruits than expected, and among males fewer

BC recruits than expected. Because 1977 was the second year of severe drought in the region, the 1977 results could mean that adults (especially females) moved from marginal territories outside the study area and successfully competed against the yearling birds for territories. On the other hand, this could mean that the drought had a greater adverse effect on the young than it did on adults, allowing subordinate adults to become territory holders who otherwise would have been unable to compete for territories even against young birds. The overall proportions indicate that the sex difference in the number of recruits is not significant ( $\chi^2 = 2.34$ ,  $P > 0.10$ , 1 df) but that significantly more of the recruits were FC as compared to BC adults ( $\chi^2 = 10.02$ ,  $P < 0.01$ , 1 df).

*Floaters.*—The results suggest that there was a floater population of birds available to enter as recruits. Although 0.39 (132/337) of the birds were banded the year they entered the population as territory holders, 0.37 (126/337) entered the year after banding, and 0.24 (74/337) did not become territory holders for 2-5 yr after their initial banding. There were no sex differences.

A number of birds were banded at least 2 yr before they acquired territories and also were sighted or recaptured in the study region during the intervening years. A considerable proportion of these birds (0.41; 41/102) were present on the study region during the time that

TABLE 5. Status of recruits at the time they enter the population (combined TP and P 4-yr study territories).

Recruits	1976	1977	1978	1979	1980	Σ
♂ BC	9	4	14	10	14	51
♀ BC	16	7	25	18	22	88
♂ FC	19	24	22	13	25	103
♀ FC	9	32	15	16	22	94
Total	53	67	76	57	83	336

intervened between bandings and territorial acquisition. (This figure excludes the nestlings discussed in the next section.) Again, there were no sex differences. One of the males was banded in 1975 at TP as a fledgling, was sighted at TP in 1976, and in 1977 assumed a territory in TP upon the disappearance of the territorial male. In this case, it appears that the male was part of a breeding surplus available to replace a male that disappeared. Six instances occurred in which a territory holder disappeared and was immediately replaced by another bird. These instances occurred early in the breeding season. All of these data suggest that there was a surplus breeding population available in the area.

*Nestlings.*—We banded 1,052 nestlings: 522 at TP, 412 at P, and 118 others at various locations throughout San Francisco. Fifty-five of the 706 (0.078) nestlings banded between 1975–1979 at TP and P have entered the breeding population as territory holders. There were no differences between sexes or study regions in the frequency with which nestlings became territory holders. There were no instances in which a nestling born at one region acquired a territory at the other. Most of the nestlings that acquired territories (0.74; 42/57) did so in the year after their birth. Eight birds acquired territories 2 yr after banding, five 3 yr after, one male 4 yr after, and one female 5 yr after. The median distance from the natal territory to the breeding territory was 110 m (the range is zero—the natal territory or the adjacent one—to 586 m). This distance involved moves from one extreme edge of the study region to the other extreme and occurred in both regions.

Few of the banded nestlings were either sighted or recaptured in the study regions: a total of 55 banded nestlings out of 522 at TP (0.11) and 53 of 412 at P (0.13), for a combined 108 of 934 (0.12). When all individual sightings and recaptures of banded nestlings were considered, there were 49 sightings or recaptures

during the natal year, 58 the next year, 25 2 yr after the natal year, 13 3 yr after, and 3 4 yr after. (These latter figures total to more than 108, because some birds were sighted on more than one year and were included each year they were sighted.)

*Dispersal.*—Most of the young of the year probably dispersed at the end of the natal breeding season, a time when flocks of unbanded fledglings began to appear in the study regions. These unbanded fledglings began to disperse into the study region in June and were prevalent until August. In Table 6 the number of birds banded each month is broken down by age category. (The number of birds in each category is slightly larger than in previous listings, as we have included a few birds that were banded in 1972 and 1974.)

The small number of BC's and FC's banded in January, February, and March occurred because little fieldwork was done at that time. Our fieldwork typically began at the end of March, when nesting behavior begins, and continued into August. We should have banded most post-dispersal fledglings from other areas, because the last fledgling ever banded in our study population was on 26 July. Almost all of the nestlings were banded during April, May, June, and July in this multiple-brooded subspecies. Unbanded fledglings began to appear in May; probably they were nestlings from nearby breeding areas that were driven from their natal territory by the parents. At about the same time that large numbers of unbanded fledglings began to appear (June and July), a number of unbanded BC's began to appear as well. These birds seemed to constitute a large floater population of predominantly 1st-yr and post-dispersal juveniles. The large number of FC and BC birds banded in April was the result of our efforts to band every bird in the study area at the beginning of the breeding season. The relatively constant number of BC and FC bandings throughout May, June, and July suggests that there was a surplus population of birds that did not have territories and appeared from time to time, only to be driven off by the territorial residents.

In October and November of 1978, 69 birds were trapped and banded: 64 were BC's and 5 were FC's. It is interesting that not many FC's were banded at that time: 0.93 of the birds were post-dispersal fledglings of the preceding season that had undergone their post-juvenile



TABLE 6. The number of birds of each age class banded during each month (1972–1980).

Age class	Month <sup>a</sup>												Σ
	1	2	3	4	5	6	7	8	9	10	11	12	
N	0	0	4	180	412	363	101	0	0	0	0	0	1,060
Fl	0	0	0	0	19	59	184	53	2	0	0	0	317
BC	0	1	3	59	24	32	36	9	0	50	14	9	237
FC	1	0	7	117	63	54	76	18	2	4	1	5	348
Total													1,962

<sup>a</sup> 1 = January . . . 12 = December.

molt and were now clear-breasted BC's. Thus, most of the young of the year disperse to other regions, and a large number of post-dispersal birds appear in the study region by the end of the breeding season.

#### DISCUSSION

*Stability of territories.*—Ten territories at one area on TP were studied systematically during the 1975 breeding season (Patterson and Petrinovich 1978), and the size of the territories was found to be 1,127 m and to be very stable within a season. There was a strong stability in both the size and the number of breeding territories across years as well. The number of territories occupied between 1976–1980 ranged between 54–60 in number, and a total of 63 was occupied for at least 4 of those years (Table 2).

We found no great changes in the density of territories or in the number of breeding pairs from year to year. Changes in density of territories and in the number of breeding pairs are typically found for hole-nesting species, such as the Great Tit (*Parus major*) that are provided with nesting boxes (e.g. Greenwood et al. 1979). Delius (1965) studied the population dynamics of Skylarks (*Alauda arvensis*) over a 6-yr period and found that the number of pairs in his study area hardly varied from year to year, a stability similar to that found for our territorial species.

*Stability of individuals.*—The proportion of repeat territory holders across the years was 0.43 overall: 0.50 for males and 0.35 for females. The comparable return estimates calculated from the 2-yr returns of Morton et al. (1972) are 0.46 for males and 0.24 for females of the migratory *Z. l. oriantha*. In general, return rates for most species are lower for females than for males (see Table 2, Knapton 1978), and the estimates for the return rate of territorial birds seem to range between 45–60% for males and

20–40% for females. Our rates are within the range of values reported for return to the breeding area in successive years [e.g. Song Sparrow (*Melospiza melodia*), Nice 1937; Clay-colored Sparrow (*Spizella pallida*), Knapton 1978; Great Tit, Bulmer 1973].

For the migratory White-crowned Sparrows found along the central California coast, Linsdale (1949) reported a 0.35 return on the wintering grounds the first year after banding and a 0.49 return of these the next year. Mewaldt (1964) reported a 0.26 return the first year and a 0.51 return of these the next year. Both of these studies support the idea that high mortality occurs in the first year and that the mortality rate is lower once adult age is reached (see Haartman 1971).

In our study, if the males repeated, 0.79 returned to the same territory and 0.27 had the same mate as the year before. If the females repeated, 0.61 returned to the same territory and 0.54 had the same mate. This could mean that the males had more site attachment, while the females were choosing both on the basis of territory and of mate. Harvey et al. (1979) found that male Great Tits normally reoccupied the same territory in the study area in consecutive years. They summarize the evidence on site tenacity and conclude that females tend to show less site attachment than males, especially in those species in which territory maintenance is the prerogative of one sex and in which the fitness of the territory defender is enhanced by retention of the same breeding area from year to year (Greenwood and Harvey 1976, 1977). Greenwood (1980) has surveyed the literature on mating systems and dispersal in birds and concludes that it is easier for a male to acquire the resources necessary to attract females in his natal area and also that familiarity with other males is valuable in intermale competition for territories.

Analyses of the quality of territories in terms

TABLE 7. Reproductive success of pairs on Twin Peaks (TP) and Presidio (P), 1975–1980.

	1975		1976		1977		1978		1979		1980	
	TP	P	TP	P	TP	P	TP	P	TP	P	TP	P
Number of nests	96	—	97	44	94	78	109	64	78	47	74	67
Proportion of nests with fledglings	0.49	—	0.44	0.57	0.31	0.62	0.33	0.57	0.40	0.62	0.82	0.63

of the reproductive success (RS) of the territory holders will help to resolve this question. Females should be more likely to move from unproductive territories to those that are better in quality and that have more successful males located on them.

When there was a shift to a new territory, birds of both sexes were almost always paired with a different mate. Divorce occurred in 11 instances out of a possible 36 (0.31) in our study. Harvey et al. (1979) reported that divorce occurred between at least 0.29 of Great Tits that had the possibility of remating.

Delius (1965) found strong site tenacity among Skylarks: they had a strong tendency to return to the same area from year to year and almost always tried to settle in the territory of the year before with the same mate. The distance between territories on successive years was smaller for males than for females.

*Regional differences.*—There were a few differences between the two major study regions. The pairs at P held a territory for fewer years than did those at TP (means of 1.64 and 1.41 yr, respectively). We have found that RS was significantly higher at P when considered over all years of the study than it was at TP (Patterson and Petrinovich in prep.). This suggests the need to make a fine-grained analysis of the RS of individual pairs to determine whether or not there is a tendency for successful birds, especially females, to have a lower likelihood of returning in the subsequent year. It has been suggested that the survival of females is often lower because of the strain imposed by reproductive activities (Ricklefs 1973). If so, those females that rear one or more successful broods might be expected to suffer more of the strains of parenthood than those that did not have to feed and nurture nestlings and fledglings. The data also can be examined in terms of the number of eggs produced in a season, as it has been estimated that egg production requires a relatively great amount of energy

expenditure: 13–16% above the daily energy requirement in small passeriforms (King 1973).

Although the TP region had a lower overall RS, it was more variable across years. Table 7 contains a summary of one measure of RS for each of the study regions for each year. It can be seen that the drought years of 1976 and 1977 had less impact on the P birds than it did on those at TP. The TP population, however, showed a dramatic and unexpected rise in RS in 1980. The reasons for this rise will be sought through the data obtained during the continuing study of these breeding populations.

Baker and Mewaldt (1981) compared the clutch sizes we obtained with those obtained by Blanchard (1941) and suggested that our study areas might be disturbed habitats. Blanchard reported an average clutch size of 3.25 for her Berkeley study, while Patterson reported a much smaller clutch size for the first 2 yr of the present study (Patterson 1977). The difference between Blanchard's figure and ours is due to a different method of calculation. Blanchard included in her calculations only those nests in which at least one egg had been laid, while we included all nests that had been started, whether or not an egg was ever laid in them. When we calculated the clutch size as Blanchard did, our average clutch size over the 6-yr study period is 3.13: a figure quite close to hers. Because the size of clutches was smaller on TP during the drought years, it might be expected that the average clutch size will continue to increase through the years.

*Composition of the breeding population.*—As indicated above, significantly more males (0.50) repeated across years than females (0.35). We found that only 0.16 of the recruits were nestlings born in the study regions, while 0.40 of the recruits entered the population as 1st-yr BC birds. We also found that 0.46 of the territory holders were either nestlings born in the region or repeats ("autochthonous"). From Fig. 3 (p. 145) in van Balen (1980), one can obtain

an estimate that 0.69 of Great Tits in the Netherlands study area were autochthonous. This figure seems meaningfully higher than ours.

Few of the total number of banded nestlings (0.079) ever obtained a territory in the study regions. In fact, few (0.12) were ever sighted or recaptured after they left the natal territory, even though the fledglings were trapped throughout the breeding season as well as at the end of the season. Johnston (1956) banded 241 nestling Song Sparrows in San Pablo Bay and recovered 34 (0.14), Nice (1937) recovered 0.126 of the nestling Song Sparrows she banded, and Nolan (1978) estimated that 0.11 of 272 nestling Prairie Warblers (*Dendroica discolor*) returned to the study area in the next year. All of these figures are comparable to our 0.12. A much lower figure was obtained by Knapton (1978), who banded 146 nestling and 305 juvenile Clay-colored Sparrows and recovered no nestlings and only four juveniles in subsequent years. Delius (1965) sighted only 0.09 of 171 banded nestlings in or near his study area. Six of these had territories in the study area and four had territories in adjoining areas ( $10/171 = 0.06$ ). All of these figures are comparable to ours: They all suggest that few of the nestlings of a study population become territory holders.

*Dispersal.*—The dispersal data available are not substantial enough at this time to support more than speculation. Several extensive transects have been done in all directions from the study areas in the last 2 yr, and all banded birds have been noted. These results will be reported in a later paper. We hope that the transect data will enable us to understand the patterns of dispersal better than we are able to at the present time.

We found that the natal to breeding territory dispersal of the 55 nestlings that became territory holders was 110 m. This is clearly an underestimate, because we confine ourselves to the immediate area of the study region (cf. Barrowclough 1978). We have documented several large movements of birds banded as nestlings, fledglings, and adults: several birds dispersed 500 m and some as far as 1.35–1.5 km. At the present time the number of recoveries are not sufficient to determine whether or not there are any sex differences in dispersal distance. Our results are comparable to those of Blanchard (1941), however, who found that 4 out of a total of 58 (0.069) banded nestlings bred 183–480 m

from the natal territory. In view of our larger sample size, the increase in range from that reported by Blanchard is to be expected.

Morton et al. (1972) reported that new adult White-crowned Sparrows of *Z. l. oriantha* began to appear near the end of the period of postnuptial molt, and he and his colleagues began to capture new immatures shortly after the fledging period. Three of these immatures had been banded as nestlings 6 km northwest of the Tioga Pass Meadow study area.

Hinde (1952) found that Great and Blue tit (*Parus caeruleus*) juveniles move greater distances than adults. Weise and Meyer (1979) studied a banded population of the nonmigratory Black-capped Chickadee (*Parus atricapillus*). They report that as soon as the family group dissolves, the young begin relatively immediate and long-distance movements away from their birthplaces. They conclude that their data are consistent with those of other studies of small songbirds in terms of median dispersal distance: Black-capped Chickadee, 204 m; Great Tit, 500 m; Blue Tit, 700 m; European Nuthatch (*Sitta europaea*), 900 m; Pied Flycatcher (*Ficedula hypoleuca*), 1,000 m; and Song Sparrow, 285 m in Ohio and 185 m in California. Our dispersal distances also seem to be consistent with these results. All of these results indicate that post-nesting dispersal is common and that this dispersal could include movements over great distances by fledglings from the natal site.

The only other detailed banding study of the sedentary *Z. l. nuttalli* was done by Baker and Mewaldt (1978, 1979). They reported that females dispersed an average of 614 m from the natal site while males dispersed only 555 m. Unfortunately, they assumed the earliest capture of a fledgling to be the best estimate of its hatching site. We have suggested elsewhere (Petrinovich et al. 1981) that this assumption may be erroneous. Our data suggest, and the above analysis of the literature supports, the conclusion that the movements of spotted juveniles should not be used to establish the dispersal distance from natal to breeding territory. We suggest that fledglings dispersed some distance from the natal area and that Baker and Mewaldt were dealing with many individuals that were already post-dispersal birds when banded. Thus, while Baker and Mewaldt's data will enable us to understand ranging patterns, they might not be germane to the question of

natal dispersal. It would be of great interest to study banded nestlings in their study region to determine whether or not there is, indeed, a different pattern of dispersal for their breeding population of the same subspecies we have studied. If such a pattern is found, it would suggest that the breeding biologies of the populations studied by us and by Blanchard might not be representative of the entire subspecies.

The pattern of natal dispersal we have found is consistent with the study of Weise and Meyer (1979) discussed above for the Black-capped Chickadee, in which they found an early dispersal from the natal territory and a post-dispersal site tenacity developing for the places the birds will subsequently breed. This is also the pattern reported by Jenkins (1978) for the Saddleback (*Philesturnus carunculatus*).

*Evidence for a nonbreeding surplus.*—There seemed to be a nonbreeding surplus available in our population. This is indicated by the fact that 0.24 of the territory holders entered the breeding population 2–5 yr after their initial banding, that 0.25 of the nestlings that acquired territories did so 2–5 yr after their birth, that 0.41 of territorial birds that acquired a territory more than 1 yr after they were banded were sighted on the study territories in an intervening year, and that birds that disappear during the breeding season were almost immediately replaced. It is, of course, never possible to be certain that many of the surplus birds seen in the territory during the breeding season did not have territories adjacent to the study areas. We think this unlikely because of their continued presence during the breeding season—a period when the territorial pairs spend their time almost exclusively on territory. As Mewaldt has suggested (pers. comm.), however, these data are not sufficient to rule out the alternative interpretation that territorial males from outlying territories move in with a female whose mate has disappeared. We know this almost never occurs within the study region but cannot rule out the possibility regarding birds from outside the study regions. In addition, the relatively constant number of BC and FC bandings that occurred throughout May, June, and July suggests that there was a surplus population of birds that did not have territories and that appeared from time to time, only to be driven off by the territorial residents.

Smith (1978) argued for the existence of an “underworld” in the Rufous-collared Sparrow (*Zonotrichia capensis*): when male territorial birds disappeared, they were replaced by marked birds within 4 days—often within a few hours. She argues that these “underworld” birds show site tenacity and tend to live in well-defined restricted home ranges within other birds’ territories. The sighting and recapture data that we have suggest that, with *Z. l. nuttalli*, the floaters tend to range within the different study areas of the region rather than show site tenacity for particular territories. Delius (1965) estimated that a nonbreeding surplus wandered about in his study area. Evidence exists for nonbreeding floater populations in the Great Tit (see Krebs 1971) and Blue Tit (Dhondt and Eyckerman 1980).

Stewart and Aldrich (1951) and Hensley and Cope (1951) removed as many breeding birds as they could from a study area and found large numbers of replacement males, but not of females. Their results suggest that there is a large and available surplus population of nonbreeders. Rappole et al. (1977) report a surplus of male White-throated Sparrows (*Z. albicollis*) in their study population. Haartman (1971) and Ricklefs (1973) conclude that many territorial populations apparently have available “reserves” of nonbreeding birds, probably 1st-yr birds, that survive to older ages but are reproductively “dead” because they cannot secure territories or attract mates.

It is not a simple task to ensure that a nonbreeding surplus exists, because it is always possible that the recruits are breeders that move in from suboptimal habitats, as Krebs (1971) has demonstrated for the Great Tit. The results obtained by Delius (1965), Smith (1978), and the present study document the existence of nonbreeders present throughout the breeding season and seem to provide evidence that such a nonbreeding surplus of reproductively able individuals does exist.

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