CORRELATION OF AGE, SIZE OF TERRITORY, PLUMAGE, AND BREEDING SUCCESS IN WHITE-CROWNED SPARROWS

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This study presents observations on 15 pairs of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) breeding near Point Reyes Bird Observatory, Marin County, California, in the spring of 1969.

Z. l. nuttalli is the only non-migratory race of this widespread North American species and is confined to the coastal fog belt of California from Santa Barbara to Mendocino Counties. Another unique feature of this population is the variation in extent of the first prenuptial molt (Grinnell 1928) manifested by the varying degree of black and white in the four black and three white post- and supraorbital stripes on the crown. At the time of the first prenuptial molt the year-old birds may replace none, some, or all of the brown and gray juvenal crown feathers with the black and white ones of the adults. Adult crown patterns are acquired by all birds by September of their second year during the first postnuptial molt. A few individuals may retain a few (less than two per cent) of the brown juvenal feathers through their first postnuptial molt into their second year. Mewaldt et al. (1968) have suggested that hormone activity of the early breeding *nuttalli* may prevent the completion of the prenuptial molt.

The study described below offered the opportunity in a marked population to investigate the correlations among age, territory size, breeding success, and plumage, and to speculate on the possible mechanisms involved in the regulation of the population.

METHODS

The study area is located at an elevation of about 80 m on a gentle south-facing slope in disturbed coastal chaparral about 400 m from the ocean. This 5.5 hectare (13.5 acre) plot is an "island" of favorable *Zonotrichia* habitat; i.e., a mixture of grass, shrubs (mostly *Baccharis* and *Artemisia*), and bare ground of fire trails. These three elements are always present in the nesting territory of this species (DeWolfe *in* Bent 1968:1295). The plot is delimited by areas of less favorable habitat including fir, oak woodlands, and weedy fields.

Our observations began 26 March with the onset of nest construction and terminated 10 May after the fledging of the first broods of all the successful birds. Of the 18 males studied, 15 successfully paired and are included with their mates in our calculations (table 1). As a consequence of the regular trapping program at the Observatory, 28 of these 30 individuals had been banded as young birds, and their ages were known. The remaining two were originally banded as adults and were known to be more than two and four years old, respectively, at the time of the study. In addition, 17 birds in breeding condition (brood patch or cloacal protuberance present) were trapped on the study area. We could not determine if they were surplus individuals of the "Level 3" of Brown (1969) or were merely birds wandering from nearby breeding areas.

We utilized nonparametric statistics to calculate the significance of differences. These statistical treatments, based on Siegel (1956), included the Mann-Whitney *U* test, the Fisher exact probability test, and the Spearman rank correlation coefficient.

Territory size was determined with a method adapted from Odum and Kuenzler (1955) in which utilized territory is the unit measured rather than the classical "any defended area" of Noble (1939). We feel that this is a more logical concept of territory, especially from a trophic point of view. In the 15 territories studied, an average of 32.6 per cent of the area of each was utilized periodically by one or more of the adjoining pairs.

Observations of each pair were made at various times during the day, usually for one-half hour periods, and each change of location of members of the pair was charted on field sheets. An average of more than 40 observations of location was made of each pair of birds. The territory size was determined by drawing a polygon about the limits of the series of locations recorded for the pair.

A pair was considered successful if it fledged any young from the nest. The specific location of most nests was not determined; instead, parental behavior was used as an indication of nesting success. The behavior of a pair which has lost its nestlings differs markedly from that of a pair which is feeding successfully fledged young (Blanchard 1941).

The per cent of black feathers in the crown stripe was estimated, with 100 per cent being the usual amount in a bird two years of age or older. Since the many estimates of each individual by several persons usually differed by no more than five per cent, the mean of these estimates was used. Adventitious molt

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TABLE 1. Age, per cent black in crown, territory size, and breeding success of White-crowned Sparrows.

Pair	Age ♂	Age ♀	% black ♂	% black ♀	Territory size (m^2)	Successful
A	1	1	30	25	980	Yes
B	1	1	48	20	1530	Yes
C	1	2	60	100	1620	Yes
D	1	1	96	40	710	No
E	2	1	100	8	1840	Yes
F	2	1	100	4	1260	Yes
G	1	2	96	100	1760	No
H	1	1	10	40	2600	No
I	2	2	100	100	4540	Yes
J	4+	1	100	73	4480	Yes
K	2	1	99	20	2820	Yes
L	2	1	100	5	5850	Yes
M	1	1	88	5	1890	No
N	1	2+	90	98	2160	No
O	1	1	99	40	1500	No
X[a]	3	?	100	?	600(?)	?
Y[b]	1	2+	50	98	2900	–
Z[c]	1	–	80	–	860	–
$\bar{x}$	1.5	1.3	81.1	45.2	2360	60%

[a] Not included in calculations because not enough information was obtained.

[b] Not included in calculations because the male paired with the female of N after the loss of her mate and first brood; therefore this was essentially a second nesting attempt.

[c] Not included in calculations because this male remained unmated after establishing himself in favorable habitat among three successful pairs during the fledging period.

due to trapping or handling rarely results in the replacement of more than those feathers comprising the anterior ten per cent of the crown stripes and is assumed to be equal for all ages and sexes.

RESULTS

DENSITY AND TERRITORIALITY

The density in the study area was one pair per 0.37 hectares (0.9 acres). In our opinion this is perhaps 50 per cent above the average density for the subspecies in the Point Reyes area, a condition probably due to the favorable juxtaposition of habitat requirements described above. Another contributing factor may have been the high winter density maintained by artificial feeding at the Observatory headquarters about 100 m from the study area. Most of the birds that subsequently bred in the study area were members of this winter flock of approximately 75 birds. When these birds moved onto breeding territories they may have been either less inclined to range from their winter flock territory or more tolerant of crowding, because of the unusually large winter flock size. That the latter may have been the case is indicated by the mutual breakdown in territoriality exhibited by pairs N and O, as follows:

Many times pairs N and O were seen foraging together with no apparent preference for any particular arrangement of individuals.

TABLE 2. Average territory size (m^2) of breeding White-crowned Sparrows.

Age class	Males	*n*	Females	*n*
First-year	1640	7	2220	11
Older	3460	6	2520	4
P	$\leqslant 0.04$		n.s.	

Additionally, there was mutual use of approximately 80 per cent of the two territories. Following periods of mutual feeding the pairs would move into the cores of their respective territories, where the males typically sang from prominent perches. Copulation was observed three times, twice in pair N and once in pair O. Normal pair bonds were maintained even though the male of one pair was on two occasions closer to the female of the other pair just prior to copulation with his mate. Pair O was unsuccessful in the first nesting attempt and, after the dissolution of pair N when the male died, incorporated and defended the N territory. Such aberrant territorial behavior was not observed between any other pairs.

AGE AND TERRITORY SIZE

First-year males had significantly smaller territories than did older males (table 2). However, the difference between the territory size of first-year females and older females was not significant. These data suggest that the male determines the size of the territory, and that the older males maintain larger ones. Dhondt and Hublé (1968) found that in Great Tits (*Parus m. major*) the young males have the smaller territories.

AGE AND BREEDING SUCCESS

Pairs containing a first-year male were less successful in fledging young than those pairs with older males (table 3). Although the first-year females tended to be slightly more successful than older females, the difference was not significant. When the ages of both members of a pair are combined (in other words, their experience is summed), successful pairs tend to have a mean combined age of 3.0 years and unsuccessful pairs, 2.3 years;

TABLE 3. Per cent of each age-sex class of White-crowned Sparrows successfully fledging young.

Age class	Males	*n*	Females	*n*
First-year	33.3	9	63.5	11
Older	100.0	6	50.0	4
P	$\leqslant 0.03$		n.s.	

TABLE 4. Percentage of black in the crowns of breeding *Zonotrichia leucophrys nuttalli*.

Age	Males	Females	*P*
First-year			
$\bar{x}$	68.6	25.5	$\leqslant 0.005$
range	10–99	4–73	
n	9	11	
Older			
$\bar{x}$	99.8	99.5	n.s.
range	99–100	99–100	
n	6	4	

the difference is significant ($P \leq 0.05$). Previous studies showing a correlation between age and breeding success have concerned either colonial species (Nelson 1966) or birds in captivity (Lehrman and Wortis 1967).

TERRITORY SIZE AND BREEDING SUCCESS

Although the average territory size of successful pairs was 2760 m^2 and that of unsuccessful pairs was 1770 m^2, the variation in size was so great that the difference was not significant. We feel, however, that further work might indeed show that large territories are correlated with greater breeding success.

SEXUAL DICHROMATISM

Blanchard (1941) felt that first-year male *nuttalli* had a greater amount of black in their crowns than did first year females. In her study, 27 breeding first-year birds showed such a trend. Banks (1964), however, determined that no sex-related plumage dichromatism existed in this subspecies. Our data (table 4) show a significant difference between the amount of black in the crowns of first-year males and females. Banks' data differs critically from that of Blanchard and of this study in that Banks' birds were taken at random and undoubtedly included nonbreeding individuals. The birds in Blanchard's study and in this study, however, were known to be breeding. This would suggest a greater degree of sexual dichromatism in the breeding population of first-year birds than in the total population of birds that age.

PLUMAGE AND TERRITORY SIZE

If the color of the crown plumage is an important factor in some aspect of territorial defense, then the percentage of black in the crown might be expected to correlate with territory size. A coefficient of correlation was determined for these factors, but no significant correlation was found. Nor was a correlation apparent when only the first-year birds of either sex were considered.

TABLE 5. Mean per cent of black in crowns of successful and unsuccessful breeders among first-year White-crowned Sparrows.

Sex	Successful	*n*	Unsuccessful	*n*	*P*
Males	46.0	3	70.5	6	$\leqslant 0.09$
Females	22.1	7	31.3	4	n.s.
			Total (Weighted)[a]		$\leqslant 0.05$

[a] Mann-Whitney *U* test.

PLUMAGE AND BREEDING SUCCESS

The average percentage of black in the crown of all successful individuals did not differ significantly from that of all unsuccessful individuals. However, among first-year birds (table 5), in which all the variation in crown pattern occurs, successful individuals had less black in their crowns than unsuccessful individuals. A weighted Mann-Whitney *U* test was used to offset the greater amount of black in the crowns of males, and it revealed that the difference in the amount of black in the crowns of successful and unsuccessful individuals of both sexes were significant ($P \leq 0.05$). Although these results are perhaps not as clear-cut as desired, we suggest the problem is one of sample size. Therefore we conclude that a first-year bird with more black in its crown will be less successful, although, as we discuss below, we do not necessarily imply a direct relationship.

DISCUSSION

An older bird would be expected to have more experience in breeding and hence to be more effective in courtship, nest construction, and raising young. We found that older males had significantly larger territories than first-year birds, and that pairs with older males were more successful than were pairs with first-year males. The obvious correlate to be derived from this is that those birds with large territories would most often be successful. While this is suggested by our results, the difference is not significant ($P \leq 0.13$). Although Stenger (1958) showed that territory size in Ovenbirds (*Seiurus aurocapillus*) is inversely proportional to the amount of food available, her study was of 12 territories in four markedly different habitats. We would suggest that in a single species in a relatively uniform habitat, the more vigorous and experienced birds tend to have the larger territories, the situation shown by our results. The lower breeding success and smaller territory size of young birds indicate that age and territory size are important factors in the regula-

tion of the White-crowned Sparrow population.

The incomplete first prenuptial molt, with its resultant partial acquisition of the typical adult plumage occurs primarily in the resident race *nuttalli*. Possibly the migratory races have need of feathers in better condition during migration. However, since the flight feathers are not involved in this molt, perhaps other factors are important. Our data suggest that there is selective pressure for brown crowns in the first-year birds. It is tempting to think that the more cryptically colored brown crowns might be evolutionarily favored through reduced predation, although other phenomena could be involved. If increased levels of those hormones associated with the breeding state do inhibit the molt, as suggested by Mewaldt et al. (1968), then those birds achieving such levels earlier in spring would tend to have reduced prenuptial molt. Such individuals might very well have increased sexual and territorial drives, resulting in more successful breeding. Banks' (1964) data, in conjunction with ours, support this alternative, showing that the degree of molt of breeding first-year birds, as indicated by the degree of sexual dichromatism, differs from that of this age class as a whole.

SUMMARY

Observations of 15 breeding pairs of the nonmigratory race of the White-crowned Sparrow at Point Reyes, California, indicated that the unusually dense breeding population of one pair per 0.37 hectare (0.9 acre) is probably due to the exceptionally suitable habitat and the high density of winter flocks maintained by a nearby feeding station.

Among breeding first-year birds, many of which only partially acquire the adult plumage, males have more black in their crowns than females. The population of first-year birds as a whole does not show this. Also, among first-year birds, successful individuals have less black in their crowns than unsuccessful birds. Perhaps increased levels of reproductive hormones earlier in the spring inhibit the prenuptial molt and stimulate breeding activity.

Older males occupy larger territories and are more often successful in breeding than younger males. These data indicate that age and territory size are important correlates with breeding success and therefore important in the regulation of this population.

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LITERATURE CITED

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrows *Zonotrichia leucophrys*. Univ. California Publ. Zool. 70:1–123.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. California Publ. Zool. 46:1–178.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

DEWOLFE, B. B. 1968. Nuttall's White-crowned Sparrow. *In* Bent, A. C., Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus., Bull. 237.

DHONDT, A. A., AND J. HUBLÉ. 1968. Age and territory in the Great Tit (*Parus m. major* L.). Angew. Ornithol. 3:20–24.

GRINNELL, J. 1928. Notes on the systematics of West American birds, III. Condor 30:185–189.

LEHRMAN, D. S., AND R. P. WORTIS. 1967. Breeding experience and breeding efficiency in the Ring Dove. Anim. Behav. 15:223–228.

MEWALDT, L. R., S. S. KIBBY, AND M. L. MORTON. 1968. Comparative biology of Pacific coastal White-crowned Sparrows. Condor 70:14–30.

NELSON, J. B. 1966. The breeding biology of the Gannet (*Sula bassana*) on the Bass Rock, Scotland. Ibis 108:584–626.

NOBLE, G. K. 1939. Dominance in the social life of birds. Auk 56:263–273.

ODUM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72:128–137.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335–346.

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