

MIGRATION IN PACIFIC COAST WHITE-CROWNED
SPARROWS

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THE PROBLEM

THE groundwork for the present paper was laid by five years' intensive study of the annual cycle of two extreme local populations of Pacific coast White-crowned Sparrows (*Zonotrichia leucophrys*), those of latitude 37–38° north and 49° north, that is, of Berkeley, California, and Friday Harbor, Washington. Owing to the false effect of the trinomial, which pretends to segregate a mass of creatures neither identical nor delimitable as a rigid geographic unit, it is nearly impossible in the course of the present discussion to keep clear of the vicious concept of two unified and unlike aggregates, represented by the subspecific names *nuttalli* and *pugetensis*. Actually most of the research referred not to two halves of the *nuttalli-pugetensis* population, but to the two extreme populations. The Berkeley population is permanently resident, the Friday Harbor population is strongly migratory, wintering probably in central or southern California. This work is discussed at length in a previous paper (Blanchard, 1941). The results are briefly summarized here.

Color-banding, watching, collecting, and histological studies of Berkeley residents and wintering migrants (the latter almost certainly represent breeding birds from the northern extreme of the range) revealed the sharpest contrasts between the two populations in behavior and in physiology. The adult Berkeley residents stay permanently paired on territories; the immatures flock in fall and winter but begin in January to mate and to carve out territories. Recrudescence of the gonads begins in late December and breeding condition is reached between early and late March, depending upon the year. The prenuptial molt is meager, and the birds never acquire more than a little fat. Migrants wintering on the same ground present the sharpest contrasts in all these respects. Both adults and immatures arrive in September in huge flocks, the unity of which is maintained up to departure the following spring. Recrudescence of the gonads begins later, and by mid-April, when migration occurs, the gonads average only about one-twentieth breeding size and are correspondingly undeveloped as to histologic condition. The prenuptial molt is extensive, and large amounts of fat are laid on prior

to spring migration. The song patterns of the two aggregates are quite distinct.

Behavior of the migrants on their breeding grounds at Friday Harbor offered further contrasts to that of the resident Berkeley population. The battle for territory and mates began on the day of arrival and was waged fiercely for three weeks, up to the beginning of incubation. Among the southern residents territorial disputes, while occupying about the same interval of time, are begun much earlier in relation to the stage of the gonad cycle, and stop some 6.5 to 8.5 weeks before incubation.

The whole breeding period of the northern birds, from day of arrival until fledging of the third brood, occupied less than four months, whereas the Berkeley birds consumed 6 to 6.5 months to achieve the same fraction of the cycle. The average clutch size in the northern population was 4.09 eggs, that of the southern, 3.25.

As to morphology, on the other hand, migrants and residents are so closely similar as to be indistinguishable on the basis of quantitative characters. The only difference, perceptible only in individuals at the extremes of large series, is a slightly darker tone in the rump patch of the southern breeding birds.

Between these two extremes, then, migration of a thousand miles changes to permanent residence. The time of breeding changes by six weeks. The length of the breeding period changes by nine weeks. The average clutch size changes by one-fourth to one-fifth. The manner, as well as the time, of molt, change radically; sudden and heavy seasonal assumption of fat appears and disappears. The song pattern changes in a variety of ways. Least important of all, probably wholly without practical application to the birds' lives, a faint change in color takes place. Finally, these several transitions occur, not *pari passu*, but more or less independently.

To establish, over 1500 miles of coastline, and stage by stage, the nature of each of these changes, would be the work of a lifetime for many investigators and is of course out of the question for the present. Yet, if the picture which the data tempt us to draw, of the modification of all these habits in correlation with the Recent cycle of the environment, is to be substantiated, then it is necessary to understand to some degree the nature of the transition from one set of habits to the other: whether, for instance, there exists any abrupt break, such as might suggest the present interface of two independently established and only recently confluent populations, or whether the transition is so gradual as to occur parallel with the

very gradual present, or the undoubtedly less-gradual Pleistocene, transformation of the environment from north to south.

A few fragments of information were available for an intermediate segment of the White-crown range, that between latitudes 41° north and 45° north (between Eureka, California, and Tillamook, Oregon). From banding data and previous field work, I knew the birds to be absent from Tillamook in winter and present the year round at Eureka and therefore that somewhere within this four-hundred miles of coast, migration must stop and residence begin. In December 1937, Dr. Mary Erickson and I spent three weeks in this intermediate zone, and established Myrtle Point, Oregon, as the northern limit of the winter range. North of this point White-crowns were totally absent; south from Myrtle Point to Crescent City we found only small scattered flocks. As we continued south these gradually increased in size and numbers until in the Eureka region we found large flocks of thirty to fifty birds, which congregated in roadside brush along the edges of open fields while suitable adjacent breeding ground, where two years before I had collected nesting birds, stood empty. Whether these flocks were composed solely of migrants from more-northern breeding grounds, or of residents which had left their local territories, or of both, was the next problem which had to be solved, and for which there was almost no concrete evidence available. From purely theoretical considerations, however, it seemed likely that in this intermediate area close to the northern limit of year-round residence, the migratory instinct would be weaker, less regular, than at the northern extreme of the range, and therefore that these marginal birds, if migrants, would have bred in latitudes not far north of Eureka. That is to say, in these intermediate populations the habit of migration would pass very gradually into permanent residence, as a shade might pass into white, with no hint of an abrupt change from one fully developed set of habits to the other.

Since the migratory habit is the most spectacular of all the various changes, most of which appear to be more or less subservient to it, and since I had ventured, in my first paper, to hypothecate the nature of this transition, it seemed most important to work in the area where migration and residence appeared and disappeared, respectively, to find out whether this was abrupt or gradual, regular or irregular, and whether a uniform change of all these major habits took place on the same ground.

Of broader application than the mere light which might be thrown upon the differentiation in habits and physiology of the two races in

question, lay the possibility that in working out, stage by stage, from zero to one hundred per cent, the nature of the appearance, strengthening and regularizing of the habit of migration in successive fractions of this one species, one might unconsciously be working out the history of migration itself. Furthermore, if such a phenomenon is visibly coming into being or disappearing today, and if its correlation with obvious factors in the environment is evident, then such factors and circumstances may reasonably be considered as at least among those responsible for the rise of migration among birds.

HUMBOLDT COUNTY

It was for the reasons just stated that I returned to the northwest coast this spring (1939) at certain points intermediate between Eureka, California, and Tillamook, Oregon, color-banding, watching, and collecting. From banding data and previous field work I knew the birds to be absent from Tillamook in winter and present the year round at Eureka. Furthermore, I was shortly to prove that some members of the wintering Eureka flocks were resident and therefore that somewhere within this four hundred miles of coast, migration must stop and residence begin.

On my arrival in the Eureka region on March 15, I found a few birds already established on territories, but the vast majority were still integral parts of huge winter flocks. Both groups had undoubtedly spent the winter there, since spring migration, as recorded by departure dates at Berkeley and arrival dates at Tillamook and Friday Harbor, was not to begin until two or three weeks later. I spent ten days in the field, banded 55 birds, collected and preserved for microtechnical analysis 55 specimens, and spent 100 hours watching both banded and unbanded birds.

This brought to light the general fact that, instead of the two clearly defined groups, each with its great uniformity of behavior, song pattern, gonad condition, and fat, that I had left at Berkeley, or the single very uniform group I had watched arrive at Friday Harbor, there existed at this middle point the utmost confusion in all these respects. The transition was intergradational and gradual indeed,—certainly there was no question of one population ending abruptly and another beginning, as if divided by a wall. But the intergradation was not passing smoothly and uniformly from stage to stage with population after population, as a shadow might pass gradually into white, but by an irregular jumbling of marginal individuals which showed one tendency or the other in highly variable degrees.

That is to say, instead of two cleanly divided populations typical of resident or migrant condition and behavior, one paired on territories, with large gonads and no fat (like Berkeley *nutalli* at this date), the other flocking, approaching migration, with small gonads and large amounts of fat (like Berkeley *pugetensis*), a single flock contained fat birds and thin birds with all gradations between; a continuous series from birds with small gonads, just beginning recrudescence, to those with rapidly enlarging gonads with spermatids already formed; birds with a song pattern identical with that previously recorded for the local breeding population and birds with song patterns of more northern populations; fat birds, undoubtedly at least submigrants on their wintering grounds (checked over a month) with gonads three times the size reached by wintering migrants at Berkeley; thin birds, which were to leave the flock, take local territory and begin nesting before I returned three weeks later, in other words acting precisely like the wintering *pugetensis* of the south but omitting the migration. Others which, as will be shown, were to breed locally remained flocking up to a gonad enlargement of 40–50 mm.³, a situation perfectly unparalleled in either extreme population.

I spent nine days following March 15, watching, color-banding and collecting, at six stations within about a twenty-square-mile area. Three weeks later I returned, followed up as many of the banded birds as I could find, collected additional specimens and further checked by field observations on the stage of the reproductive cycle reached by the population as a whole.

On my first arrival, I had found the vast majority of White-crowns in flocks of 50 to 75 birds, a few in smaller flocks of 10 to 20, and only rare individuals, alone or paired, already established on territories. With the exception of these last few, the scene was identical with that in mid-winter of 1937, when I had visited the same region. Practically all the suitable breeding ground stood empty, while the birds congregated by roadsides and open fields in large, apparently completely unified flocks, with no trace of territorial jealousy or sexual interest between flock-mates.

It is beyond question that these flocks, as well as the isolated individuals, were not migrants passing through from some more southern wintering ground, but birds which had spent the winter on the spot. The spring migration, watched by Dr. Mary M. Erickson and Mr. T. T. McCabe, at Berkeley, California, by Mr. Alex. Walker, Mr. Reed Ferris and myself at Tillamook, Oregon, and by Mrs. Forrest Fuller at Friday Harbor, Washington, was not to occur until two or three weeks later. Close watching and collecting at

Berkeley revealed most wintering *pugetensis* not fully prepared, physiologically, to migrate until March 31, and no appreciable decrease in numbers until April 7. With the exception of two birds collected by Mr. Alex. Walker on March 18 and 23, respectively, no White-crowns were seen in the Tillamook region by Mr. Walker, Mr. Ferris or myself, working at points 25 miles apart, until March 28; no appreciable increase in numbers occurred until about April 5. No White-crowns were seen at Friday Harbor until April 4.

Since, during my previous visit to the Eureka region in mid-winter, I had found no White-crowns whatsoever established on territories, it seemed highly probable that the isolated pairs and lone males I found there in March had been members of a flock, perhaps up until only a short time before my arrival. This was made more probable by the histories of other birds, to be discussed below, color-banded while still within a flock, which later settled on local territories to breed. That the isolated birds were destined to breed on the spot seemed certain from their behavior toward the ground and toward neighboring landowners, as well as from the identity of their song pattern with that previously recorded for the local breeding population. As will be shown later, this was proved beyond question by the fact that some of them which had been color-banded in mid-March were found beginning to nest at the same spots a month later.

There were no such clues to the identity of the birds still within the flocks. Were they local residents which had quit their territories in fall and not yet returned to them, or sojourning migrants from more northern breeding grounds, or were they a mixture of both? That is to say, were the flocks homogeneous units, composed of breeding populations from a single latitude, that of the Eureka region or of one farther north, or were they heterogeneous, made up of birds from breeding grounds of different latitudes perhaps several hundred miles apart?

Intensive study of a single flock, combined with sampling from other flocks in the same area, seemed most likely to yield an answer. I chose a large flock of about 75 birds near Waddington, 18 miles south of Eureka, color-banded 23 of its members, banded with a single Biological Survey band 16 more, collected and preserved for microtechnical analysis 37 others, and spent the greater part of six days watching the movements of the flock as a whole. In addition, I watched several other smaller flocks and took a few specimens from each.

The Waddington flock was a homogeneous unit: the birds sang,

foraged, perched, and moved about together in perfect unison. But here the uniformity stopped. Analysis of the specimens revealed the utmost confusion as to physiological condition: this single flock contained birds with testes ranging from 2.8 mm.³ in volume to 17.2 mm.³, or from the histologic stage of first appearance of primary spermatocytes in synapsis to that of fully formed spermatids; birds with large amounts of fat, with moderate amounts, and with little or none; birds barely beginning the prenuptial molt, birds molting heavily, and birds which had finished. Nor did the factors of gonad size, amount of fat and stage of molt vary together with any constancy. There were thin birds with small gonads, fat birds with small gonads, both fat and thin birds beginning the molt, and thin birds which had completed it.

This diversity in physiologic condition was accompanied by a like diversity in song: some used the pattern of the local breeding population, a few used one identical with that of the Berkeley wintering, and the Friday Harbor breeding, birds; others used patterns which, a few weeks later, I was to hear on the breeding grounds of the Tillamook region.

Birds collected from other, smaller, flocks varied even more widely as to gonad size, from 5.1 mm.³ to 61.0 mm.³ (or an average of 25.9 mm.³ for nine adults), and from 4.6 mm.³ to 25.7 mm.³ (or an average of 11.4 mm.³ for seven immatures). They also varied widely as to stage of molt, but, unlike the Waddington flock, were uniform as to amount of fat and song pattern. None had more than a little fat, and the only song pattern I heard while hunting or watching these flocks was that of the local breeding population. Two birds, using this pattern at the time I shot them, had gonads of 13.5 mm.³ and 25.7 mm.³, respectively. Another, trapped where a bird had sung the local song a few minutes before, had gonads of only 8.3 mm.³ One other, already paired on a territory, had gonads of 40.0 mm.³ Even within a single population, then, if we are justified in using identity of song pattern as a criterion, the individual variation as to stage of reproductive cycle was exceedingly high.

Here was confusion twice confounded. Not only did a single flock contain individuals in all stages of gonad development, molt and fat assumption, but those birds which, for reasons already discussed, presumably belonged to a single breeding population, also showed a remarkably high degree of individual variation. Nor was there any obvious differentiating factor of behavior or physiology which set apart one section from another of this heterogeneous, conglomerate mass which the White-crown population or populations of the Eureka

region presented at this season. This situation contrasted strongly with that I had left at Berkeley, where two sharply sundered populations, set apart by distinct sets of behavioristic and physiologic characters, with no trace of overlap, existed side by side, as effectively separated as if by a space of a thousand miles, but where the condition of the birds within the wintering flocks was extremely uniform, even just before migration.

In spite of this confusion, however, there were a few slender clues to the identity of the birds in the Waddington flock, and, indirectly, to the identity of the wintering population as a whole. The fact that some of the flock used the local song pattern, that the adult males with little or no fat had testes averaging larger (from 3.9 mm.³ to 17.2 mm.³ or an average of 13.3 mm.³ for ten birds) than adult males which were moderately fat or fat (from 2.8 to 6.1 mm.³ or an average of 4.8 mm.³ for nine birds) and that these thin birds had gonads approaching in size those of the four individuals, already discussed, which were almost certainly local residents, led me to hypothesize that at least that fraction of the Waddington flock were local residents, or at least not true migrants, which had not yet segregated into pairs on territories. Conversely, the fact that some of the flock used song patterns of more northern populations, and that some individuals (the nine adults referred to above) had reached a stage of fat and gonad size almost identical with that reached by Berkeley migrants on the verge of departure, pointed to the presence of sojourning migrants from more northern breeding grounds. That the latter represented breeding populations from several, rather than a single, more northern latitude, seemed probable both from the diversity of song pattern and from the diversity of physiologic conditions present in the single flock. The presence of local residents in the Waddington flock was proved beyond question when, in mid-April, I returned to follow up the birds I had color-banded a month before. The presence of migrants from more northern breeding grounds was also substantiated, by evidence only slightly less direct. When I returned to Waddington in mid-April I found practically all available breeding ground within 400 yards of the flock headquarters occupied by pairs of White-crowns, several of which were color-banded members of the previous flocks, while at the headquarters itself was still a group of 10 to 20 birds, including several color-banded individuals, apparently all that remained of the original flock.

I found 15 of the 24 birds I had color-banded within the flock a month before. Seven were mated and settled on territories within

350 yards of where I had trapped them; eight were nesting at or close by the flock headquarters. One of the males in the first group was mated to a female engaged in nest-building. I collected him and found that he had no fat and that his gonads had reached full breeding size (163 mm.³). The day after I took this male, another, also color-banded, was following this same female about, as if he were mated to her. Another banded bird in this same group, a female mated to an unbanded male, was seen carrying nest material to a point about 250 yards away from where I had trapped her. In addition to these fifteen already mentioned, I found three other birds, banded with only the numbered metal band, within a few hundred yards of the flock area. One was mated to a color-banded bird; two were alone, singing loudly the song of the local population.

In addition to the color-banded male already mentioned, I collected four other adult males from the same places I had previously taken the nine adults, discussed earlier, with testes averaging 25.9 mm.³, which, because of their song pattern, I had judged to be local residents. These four were all thin, with testis volume of 18.1, 58.1, 64.5, and 129.9 mm.³, respectively. This brings the average to 86.9 mm.³, if the color-banded male is included, which is over three times as large as that for the nine thin adults taken at the same spots three weeks earlier.

As for the birds still at the Waddington flock headquarters, I collected three males, and found that they were much fatter, and had testes averaging much smaller than the birds just discussed. One was 'fat' and had gonads only 4.1 mm.³ in volume, another was 'very fat,' with gonads 7.4 mm.³ in volume, and the third, a color-banded bird, was 'moderately fat,' with gonads 33.5 mm.³ in volume. The stage of fat and gonad development reached by the first two coincides almost exactly with that reached by the Berkeley *pugetensis* on the verge of departure. The physiologic condition of the banded male, on the other hand, has no counterpart in migrants wintering at Berkeley, for although it was fat, it was not so fat as the average Puget Sound sparrow about to leave Berkeley, and yet its testes were *over six times as large* as the average for Berkeley *pugetensis* (4.8 mm.³) just prior to spring migration. Nor was it at all likely that this bird was going to breed at Waddington, for it was far behind the average of the local population, both as to behavior with respect to territory and as to gonad development, and furthermore was considerably fatter. The most probable prediction as to the destiny of this bird would be that before settling on a territory it was preparing to make a flight north, but a much shorter flight than that which either of

the two fatter birds with much smaller gonads would make. As in March, I heard several distinct song patterns at Waddington, but now the local pattern was restricted to birds spaced out on territories, the patterns of more northern breeding populations, to individuals still in flocks. It is highly probable, therefore, that most of the latter were not to breed on the spot, and that others of the color-banded birds still at the headquarters, had I collected them, would have turned out to be fat with small gonads.

It is hardly necessary to state that the color-banded birds already established on territories in mid-March were still in precisely the same spots and mated to the same individuals three weeks later. During a few minutes' search I found six out of ten, all within a few yards of where I had trapped them. The four which were paired in March were still with the same mates.

Here on the same spot, then, were birds representing all degrees of development of the migratory instinct, from those which flew less than five hundred yards to those which, I believe, on the basis of fat, gonad size and song pattern, were to fly far north. This contrasts strongly with the situation at Berkeley, where only the two extremes, of year-round residence on territories and migration of a thousand miles or more, are represented. Here, among the local population at Waddington, was 'migration' reduced to its logical minimum,—one might, rather literally, follow up the migratory instinct to its source, a shift of a few yards in the centering of the activities of daily life. Here, at the northern extreme of residence, were the very beginnings, or the last remnants, of the instinct, no longer of life-and-death value, to forsake the breeding ground in fall.

Here also, close to the northern extreme of year-round residence, the local population bridges the transition from flocking to paired isolation at a much later stage in the sexual cycle (at an average gonad size of about 25 mm.³, during the three weeks before nesting) than does the local *nuttalli* population at Berkeley. They form indiscriminate parts of the flocks in winter, while in the southern Nuttall's Sparrows the adults never leave their territories, even in mid-winter, and the first-year birds begin to segregate into pairs on territories at an average gonad size of only 3 mm.³, some eight to twelve weeks before nesting. The only vestige in the Eureka population of the once essential instinct to migrate is flocking for a part of the year.

TILLAMOOK

The nature of the intergradation was fairly evident at Eureka, but this told me nothing very definite as to the relative distances

of the migration. It was obviously cogent that birds geographically nearest to the margin of year-round residence and showing a general breaking down of the uniform cycle of factors associated with migration in the extreme populations, would possess a weaker migratory instinct and might migrate shorter distances. But this remained an hypothesis. As I had already written, barring the evidence from marked birds caught or seen before and after migration, which was impossible to obtain unless by an occasional stroke of amazing luck, I felt that gonad size on arrival at the breeding ground would be the key to the problem. Migrants to Friday Harbor or southern Vancouver Island arrived with male gonads from half to full breeding size. Would the birds arriving at a southern station, such as Tillamook, Oregon, arrive with much smaller gonads, suggesting evidence that, if they had started at the usual range of size, which is so narrow at Berkeley, and only a little wider at Eureka, they had flown a much shorter distance and therefore belonged to the northern wintering populations? This hypothesis found abundant support.

Nine years' banding records of Mr. Reed Ferris of Beaver, Oregon, as well as many years' observations and collecting by Mr. Alex. Walker of Tillamook, Oregon, indicate the absence, with a few rare exceptions, of wintering White-crowns in the Tillamook region. The winter of 1938-39 was no exception. Although both Mr. Ferris and Mr. Walker had kept almost constant watch for White-crowns, they had seen none, with the exception of two lone males, up to my own arrival on March 26. On March 18, Mr. Walker had collected one male, which was in the process of molting, with gonads only 6.8 mm.³ in volume, scarcely larger than the average gonad volume (4.88 mm.³) for Berkeley *pugetensis* on the verge of departure. On March 23, he had collected another, also molting, with gonads 6.1 mm.³ in volume.

The day of my arrival I searched over about twelve square miles of suitable White-crown country, soon to be populated, but neither saw nor heard a single bird. I selected a dozen stations scattered throughout the area, visited these on the average of once each day during the ensuing two weeks, and, as soon as the influx of White-crowns began, recorded the number of birds at each station and the precise location of their singing posts. So gradual and unspectacular was the influx at this latitude, so widely scattered and inconspicuous the individual birds, that had I not followed some such system I could scarcely have measured the almost imperceptible increase in numbers of breeding birds. It would be difficult to imagine a greater contrast with the spectacular and noisy inrush farther north, at Friday Harbor.

A day's search on March 27 revealed only two lone birds singing

weakly about five miles apart. The next morning I found about six to ten males at a third point, spaced out, singing from conspicuous posts. They were not yet ready to settle on and defend any definite areas, however, for when I frightened them they flew as one bird to a spot several hundred yards away, and did not return the rest of that day. I collected one male from this group, an adult without fat which had completed the prenuptial molt and had gonads 52.9 mm.³ in volume, the largest of any I was to collect in the ensuing two weeks. At a fourth station I found a group of about ten White-crowns singing sporadically, not as isolated individuals, but as members of a loosely knit flock. As soon as they spied me, they, too, became silent and sought cover. I found no others that day. The following morning I found this second group in the same spot. None was singing, and all behaved as integral parts of a flock. I collected three males, all of which were molting, and found that all had the brown or partially brown heads of first-year birds, were without fat, and had gonads ranging from only 2.7 mm.³ to 14.0 mm.³ Four others taken at different points that same day were also molting, had brown crown-feathers, no fat, and gonads ranging from only 2.3 mm.³ to 23.2 mm.³ A survey of the remaining stations revealed no further increase in numbers of individuals that day.

For the rest of the two weeks the birds continued to straggle in little by little, either alone or in small, loosely knit flocks, until by April 7, I estimated that from half to two-thirds the area of suitable breeding ground had been carved into territories by birds intending to breed there.

During this two-weeks period I collected twenty-one males from stations unoccupied only the day or two previous to the date of capture,—birds which were, therefore, unquestionably new arrivals. I spent about thirty hours watching others whose arrival time I knew within the same narrow limits. That these new arrivals were prospective breeding birds, if not on the spots they first settled, at least on closely adjacent ground, and not birds of passage sojourning *en route* to far-northern breeding grounds, is almost certain. In the first place, all twenty-one males had little or no fat and therefore, if we may judge from the uniformly fat condition reached by all migrants before departure from Berkeley, were not physiologically ready for further flight. Only one 'fat' male, not included in the averages, was collected at Tillamook. Secondly, I color-banded a male on March 31 and, although he shifted his headquarters and singing posts to a point several hundred yards away from where I trapped him, I was able to find him on several occasions in the new area until by April

8 he was singing strongly, pursuing other White-crowns, and giving every indication of intention to establish breeding territory. In the third place there was no hint of a wave of migrants suddenly appearing, passing through for a few days and then disappearing, such as is familiar, to choose a closely allied bird, in *Zonotrichia coronata*.

The two-weeks' watching and collecting at Tillamook brought to light the following contrasts between the nature of the influx there and that at Friday Harbor some 300 miles farther north:

1. The gradualness of the influx at Tillamook as opposed to its suddenness at Friday Harbor.

2. The small average size of the gonads at Tillamook as opposed to the large size at Friday Harbor.

3. The wide individual variation as to gonad size and histologic stage at Tillamook as opposed to the greater uniformity of size and stage at Friday Harbor.

4. The relatively large proportion of birds still in the process of molt at Tillamook in contrast to the absence of molting birds at Friday Harbor.

5. The weakness of the territorial instinct in new arrivals at Tillamook as opposed to its high development in the Friday Harbor birds at the moment of arrival.

6. The identity of the Tillamook song patterns with certain of those in the Eureka region, as opposed to the identity of certain Friday Harbor song patterns with those of wintering birds at Berkeley and points farther south.

Nature of the influx.—At Tillamook the birds straggled in over a period of more than two weeks, by which time only about one-half to two-thirds the available breeding ground was occupied. At Friday Harbor the bulk of the population arrived on the same day.

Average gonad size.—The gonads of twenty-one newly arrived Tillamook males collected from March 28 to April 6 averaged only 19 mm.³ in volume. Those of nine new arrivals at Friday Harbor averaged 55 mm.³

Range of individual variation in gonad size.—Birds belonging to the breeding population of Tillamook ranged from 2.3 mm.³ to 52.9 mm.³ as to gonad volume; or from that stage of histological development where a few primary spermatocytes in synapsis are beginning to appear to that where all cell generations, including a few mature sperms, are present. The gonad volumes of new arrivals at Friday Harbor ranged from 33 mm.³ to 78 mm.³, representing only two consecutive and very similar stages of histologi-

cal development which differ only in the presence or absence of a few mature sperms.

Proportion of molting birds.—Eight of the twenty-one Tillamook males, as well as many others seen in the field, were still molting. None of the Friday Harbor males I collected, to say nothing of the hundreds I watched in the field, showed any sign of molt.

Strength of territorial instinct.—During the first few days after arrival the Tillamook birds showed little or no attachment to any particular piece of ground. Many came in small flocks, which traversed relatively large areas in their daily foraging, and did not break up at least for several days after arrival. Even the males which had spaced out and were singing at frequent intervals would become silent as soon as they saw me, quit their posts with no hint of reluctance, fly straight away for distances of several hundred yards, and never, as long as I followed, try to turn back. Even when I could detect no external cause for fright, they shifted singing posts frequently, and flew distances far exceeding those contained within the average-sized White-crown territory. This shifting was not the orderly patrol of definite points on the periphery of a limited area, but merely the haphazard, seemingly purposeless, movement of a restless animal. I saw very few pursuits and no fights. The only hint of territorial jealousy was the tendency for neighboring males to alternate in song.

On the day of arrival in Friday Harbor, on the other hand, I had been able to find no trace of a flock or fragment of a flock. All males were spaced out, either alone or paired, singing strongly, ready to chase off intruders. Pursuits and fights were common, and the battle for land was fierce and brief. Birds banded a day or so after arrival stayed throughout the summer on the spot where they first settled.

The arrival I watched at Tillamook, then, less than 150 miles from the northern limit of year-round residence, was extremely irregular and haphazard compared with that which I had watched at Friday Harbor, 450 miles from the limit of year-round residence. The competition for territory was far less severe, perhaps partly owing to the smaller numbers of birds to come on any one day, but unquestionably also in correlation with the undeveloped condition of the gonads. The settlement of the land at Tillamook was a much more leisurely affair. The birds, arriving at a relatively early stage of gonad development, had time and to spare to find mates, carve out territories, and learn their boundaries before they would be physiologically ready to breed. The Friday Harbor birds, arriving little more than a week before copulation was to take place, had to settle all these matters in a few days.

Song pattern.—The predominant song pattern at Tillamook was identical with one I had just recorded at Eureka,—not with that of the breeding population but with one used by a small number of individuals, some of which still frequented the flock headquarters when I returned to Waddington in mid-April. As I have already said in the section on Humboldt County, the behavior of these flocking birds indicated they were not destined to breed at Waddington, and were certainly, therefore, going to make at least a short flight north. The predominant song pattern at Friday Harbor, on the other hand, resembled most closely that of wintering flocks at Berkeley and points farther south, although rare individuals at Waddington were heard using a similar song pattern.

If the birds using the Tillamook song pattern left their wintering grounds at approximately the same stage of gonad development as did the Friday Harbor birds, it is obvious that the former must have spent less time in flight. The facts that the gonads of the Tillamook arrivals averaged little larger than the maximum gonad size for Berkeley *pugetensis* on the verge of spring migration, and that a fair proportion arrived before the molt was finished, point to a relatively short flight from wintering to breeding grounds.

The irregularity of arrival time, the wide range of individual variation in gonad size and the rudimentary nature of the territorial instinct, all point to a far less uniform and precise cycle than that of the breeding birds at the northern limit of the range. The identity of song pattern of the Tillamook population with that of birds wintering at Eureka is further evidence of the relative proximity of wintering to breeding grounds.

This is what we should expect to find from purely theoretical considerations, and is what I have hypothecated in the longer paper on the Coast White-crowns now in press. In the birds breeding nearest to the region of transition from year-round residence to migration, the migratory instinct would almost certainly be less highly developed, less regular, than in birds breeding at the northern limit of the range, farthest from the transition area.

CONCLUSION

At Tillamook, 400 miles north of Eureka, the breeding population has become almost completely migratory. Judging from the observations made during the winter of 1937–38 by Dr. Erickson and myself, practically every member must fly at least 150 miles south each fall. Nonetheless, the behavior of the breeding population offers the sharpest contrasts to that of the more northern populations and in

directions which suggest its kinship with and proximity to the marginal flocks of Humboldt County. Thus, while the Eureka birds, as compared with those at Berkeley, are irregular in time of detachment from the flocks or occupation of territory, so the Tillamook birds are irregular in time of arrival and occupation of territory. Just as the Eureka birds tend to linger in stable flocks until their gonads reach several times the size of departing migrants from Berkeley, so the Tillamook birds, even after their brief migratory flight, linger with enlarged gonads and with a wide variation of individual gonad size in flocks before segregating into pairs on their individual territories.

Tillamook birds loiter for days or weeks on their breeding grounds in a condition of slight sexual development. They differ from the Eureka birds in this respect only by the interpolation of a probably brief northern flight. In general, one has the feeling of dealing once more with a section of the Eureka population which has been selected out by the rather unimportant factor of a brief movement but which possesses no other distinction.

In the transition from the constitution of the Eureka flocks and their response to the onset of the reproductive period, to those of the breeding population of Tillamook we see a rather complete picture either of the growth or the subsidence of a single example of bird migration. It is probably impossible, from the evidence of morphology or physiology, to support the contention that such behavior is vestigial rather than incipient. Such support as may be forthcoming must be derived from our slowly growing knowledge of the late Pleistocene environment. That at the northern confines of the range vast environmental changes, in the direction of amelioration, have taken place within, at the most, the biologically brief period of from ten to fifteen thousand years seems beyond question. That during this period the front of permanent residence may have crept northward and is now passing Eureka is a cogent, but not a necessary, supposition. We know little of the Pleistocene environment of the central and northern California coast, but what evidence there is inclines to minimize post-Pleistocene change. The essential concept is that northern California or southern Oregon, at the center of the range of the species, and lying between the area of comparative Recent uniformity of climate of central California and the great changes of the latitude of the international boundary, is, from an adaptive standpoint, the logical region for the point of equilibrium between migratory and non-migratory behavior, with their many physiological correlates.

ACKNOWLEDGMENTS

Research for this paper was carried on under the Alice Freeman Palmer Fellowship for 1938-39 from Wellesley College.

I should like to thank Mr. Thomas T. McCabe for invaluable advice and suggestions for a plan of attack on this problem, and for criticism of the manuscript.

I should like to thank the Department of Zoology of the University of California for laboratory and library privileges, and the following persons for assistance of the utmost value in the collection of specimens and field data: Dr. Mary M. Erickson, Mr. Reed Ferris, Mrs. Forrest Fuller, and Mr. Alex. Walker.

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