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CONTINUITY OF BEHAVIOR IN THE NUTTALL WHITE-CROWNED SPARROW

WITH ONE CHART

By BARBARA D. BLANCHARD

For the past three years I have studied the behavior of the Nuttall White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) on the University of California campus at Berkeley. In the spring of 1934, when I began intensive study, the population on the campus comprised about sixteen pairs. Since it would have taken too much time to follow up so many birds, I restricted myself to seven pairs on territories in the center of the campus. These I trapped and banded recognizably with colored bands.

The springs of 1934 and 1935 were devoted to the phases of breeding behavior: copulation, nest-building, incubation, hatching and development of the nestlings and fledging of the young. Thereafter I followed the same birds through the interval between breeding seasons, from the post-nuptial molt in autumn to the beginning of nesting the next spring.

During the interbreeding periods I was aware of many familiar elements, scattered manifestations of behavior we are too apt to consider as purely a product of the physiology of the breeding time. Consciously or unconsciously, we stress the discontinuity of breeding and winter behavior. We emphasize changes and beginnings and look on song, territorialism and mutual attraction of opposite sexes as exclusive manifestations of the reproductive period—strictly limited phases which begin and end abruptly. Actually, perhaps, effective breeding behavior is less something new than a coordination of many elements already present, some permanently, some, as far as we can perceive, for short preceding periods.

Copulation, nest-building and patrol of territory ceased at or before the fledging of my birds' last brood. On the other hand, the special and continuous interest in the *mate* as opposed to all others, the observance of territorial boundaries, and the occasional use of full song by the male during every month of the interbreeding period constituted permanent elements of behavior.

Each pair remained on its breeding area throughout fall and winter. Mates foraged and perched together and followed each other about. In some cases the pair remained alone, in others, they were joined by a flock of immature or mateless birds which the male tolerated. Unquestionably, even in the latter cases, when the pair seemed for long periods to be undifferentiated parts of the flock, a definite liaison must have persisted, for with the coming of spring, the male drove out the sojourning strangers, and the pair remated. It is unthinkable that this represented a revived memory of the previous year.

As an example of the tenacity of the bond between mates, I have a definite case in which the second mate of a polygamous male remained with him through the winter and bred with him again, disregarding a young male (mateless in winter and quickly losing a mate acquired in early February) with adjacent territory; the latter sang strongly, especially from March 3 to April 18, shortly after which he acquired a mate from elsewhere. The facts were as follows. In the spring of 1934, two Nuttalls, designated as male I and female III, both had other mates and lived on adjacent territories. Female III lost her mate after she fledged her first brood. Male I then entered her territory, incorporated it in his patrol and mated with her for her second brood. Female III mated with male I again the following year, although an unmated male, already mentioned, was available. That this represented a continued interest of female III in her mate rather than in her previous breeding area is suggested by her behavior during the winter. After her second brood had become independent, she retained no interest in her old area but followed male I into his own where he already had one mate, spent the winter with him there, and the following spring nested in a fraction of it.

As to both permanent occupation of territory, and permanent mating, through the year and from year to year, there seems to be no doubt. Male I has stayed in about the same area for almost four years. He was banded on May 20, 1932, by Dr. Seth B. Benson, at the southwest corner of the Life Sciences Building. At this time, according to Dr. Benson's notes, the bird had partly immature plumage and was probably a bird of the year, hatched in 1931. Dr. Benson states that the bird owned the narrow lawn on the south side of the Life Sciences Building and that on June 3, 1932, he saw it with its mate, feeding a family. I first noticed this male singing in a tree by the same strip of lawn on February 6, 1934. He had apparently remained in about the same area since 1932. The mate of 1932 had probably died, since a few days later I saw him with an unbanded, brown-headed, bird with which he subsequently mated. Up to the present time the pair has stayed in the same area, throughout fall and winter as well as breeding time.

A third permanent element was the use of full song by the male. The song was, to be sure, sporadic and often weaker than during breeding time, but, like interest in mates and restriction to the breeding area, never disappeared.

Before the studies of environmental and physiological changes in which I was interested could be of the slightest value, it was necessary to be sure of the time and manner of the coming of the less permanent behavior elements. I had come to suspect, from the winter behavior itself and from scattered hints in the literature, that these elements would appear gradually, with early and almost imperceptible manifestations. I still suspect as much, but I realize better the difficulty of sufficiently close observation. Actually, the beginnings of change as I detected them were relatively abrupt, so that the apparent cycle, up to egg-laying, lies within about nine weeks.

The behavior of the birds during January, February and March suggested to me the accompanying diagram (fig. 28), which attempts to analyze three principal subdivisions of consummate reproductive behavior, copulation, territorialism, and nest building, and to show the emergence and synchronization of their elements.

Copulation takes place in this way: the female crouches with wings spread and quivering, tail slightly raised and head pointed upward at a sharp angle to the back. She utters a prolonged trill while maintaining this position. When the male approaches, she stops trilling and raises her tail still higher until it is perpendicular to her body. Then the male mounts and copulates with her. The substratum of interest of each bird for its mate is permanent. The other elements appear *seriatim*. Trilling and posturing are not necessarily linked. As early as January 9, and by February 1 at the latest, the

females begin to trill. For the first few weeks trilling is sporadic and may or may not be accompanied by fluttering of the wings. As the season progresses, trilling and posturing occur together more and more often, and both actions increase in frequency and intensity until the peak is reached in early or middle March.

During January and February the male appears indifferent to the trilling and posturing of his mate. He pays no special attention to her other than to forage with

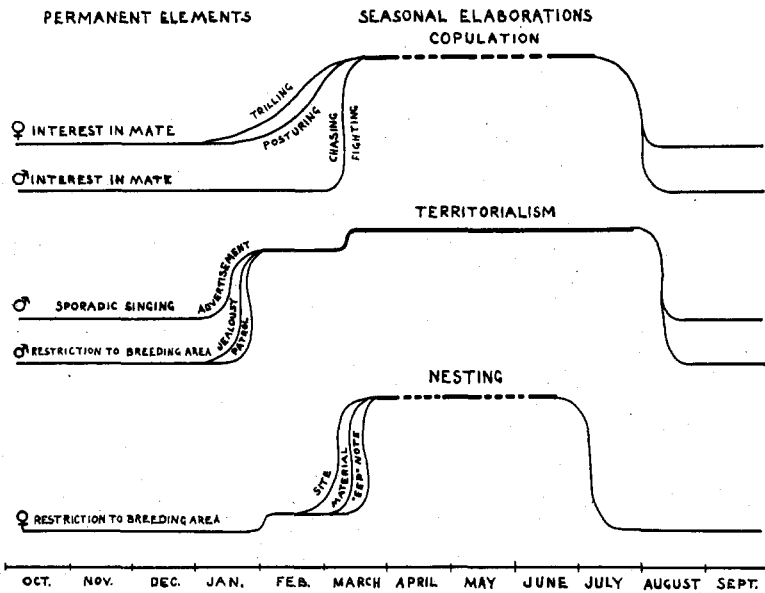


Fig. 28. Relation of permanent and seasonal elements of behavior.

her and utter location notes as he has done throughout fall and winter. From early March on, however, the male punctuates long periods of indifference by what I interpret as unsuccessful attempts to copulate. Quite suddenly, without any warning that I can detect, his attitude of indifference changes to one of aggression. He chases his mate and, on catching up with her, apparently attempts to mount her. She repulses him and the two birds jab each other with their beaks. After a few moments they separate and the male resumes his air of indifference. Apparently the female is not yet ready to mate, although she may trill and posture both before and after the "fight." By mid-March, some six or eight weeks after the beginning of trilling, the instincts of both birds synchronize. The female follows her mate persistently, trilling and posturing vigorously. He responds by flying to her with crown raised and tail lowered and slightly spread. She permits him to mount and copulation takes place.

The highest development of territorialism is expressed normally only in the male. He makes himself conspicuous by loud, persistent singing. He patrols his area, that is, he flies from one tree to another on the periphery and stops at each perch to sing. If a neighboring male attempts to come in, which happens rarely during actual breeding time, the owner flies toward the intruder and chases it to the boundary. Here he stops, perches in a conspicuous place and sings several loud songs. The intruder may also perch in full view and alternate with the defending male in loud singing. The permanent substrata of territorial behavior are restriction to the breeding area and

song. The less permanent elements are increased and seemingly purposeful song or "advertisement," territorial jealousy, and patrol. Hints of these can be detected early in spring. The climax is reached about nine weeks later, usually on the first day the female begins to incubate.

I had an exceptionally good chance to watch the coming of these elements in January, 1936. On the morning of January 4, I heard one of my banded birds, male VIII, singing every few seconds. I found him perched conspicuously in a bare tree on the east side of his territory. He showed no fear of me even when I stopped within six feet of him, but faced me and continued to sing for several seconds. The singing itself was not new. During winter I had often heard Nuttalls sing as loudly if not as many times in succession. It was the fact that this male perched in a conspicuous place and continued to sing while I stood so near, that foreshadowed a change. On January 7, I heard him sing again several times in rapid succession. This time I found him perched on top of a low hedge in the western part of his area. He flew a few yards to a cotoneaster by the lawn where the day before he had tolerated, and foraged with, two immatures. Today, however, when an immature tried to perch in the same bush, male VIII immediately drove it out. This set him off to sing again, alternating in utterance with male I, his neighbor on the north.

Two days later I watched male I go through the same performance in an even more striking way. All winter he had tolerated within his area a group of eight to ten immature Nuttalls. On the morning of January 9, I saw him perched on a bare sycamore with about seven of the immatures. He sang loudly several times, then stopped to preen the feathers of his breast and flanks. Suddenly he started to chase two of the immatures which had been perched within a few inches of him. I soon lost sight of all three, but I heard a cry as if male I had caught up with one of the immatures and attacked it. A few moments later the whole flock, including male I and his mate, were foraging peaceably on the lawn. Then I heard a weak quavering song from a Nuttall perched in a tall pyracantha several yards north. Immediately male I flew to this tree, displaced the singer, and himself sang, loudly. The displaced bird continued to perch on another branch of the same tree only a foot away from male I. As the latter shifted his position from one twig to another, the other bird always gave way before him, although male I never actually chased it. Then suddenly male I flew straight toward me across a wide lawn and over to a tall cedar, where he sang again. As he continued to sing I heard several immature Nuttalls sing fragments of songs, but he did not chase any of them again that morning as long as I watched.

These actions exhibited hints of all the elements of territorial behavior: advertisement by loud singing, territorial jealousy by chasing other birds, and patrol by flying to three conspicuous perches many yards apart and singing loudly from each one. For some time after, these instincts came and went. Fits of territorial jealousy were interspersed with periods of apparent indifference, when male I foraged peaceably with the flock, or even permitted another male to perch near him in the same tree and sing. After January 26 the instincts of territorial behavior remained on a "plateau," as is usual at about this time. There was little chasing, since the immatures had segregated into pairs each on its own area. There was also less loud singing. On the first day of incubation, the territorial behavior suddenly rose to a new climax. Male I sang loudly every few seconds, and patrolled his area. The instinct to chase was present but rarely exercised because encroachments upon the boundaries were rare.

It must not be understood that territorial behavior is peculiar to the male. The same instincts are latent in the female, but are overtly expressed only in cases of polygamy, which are common. The development of the territorial sense in the female

independently of the male is illustrated in the behavior of females I and III, simultaneous mates of male I. In winter both females made free of their common mate's territory, though with some tendency to localization, as discussed below. With the approach of reproduction, however, each female created for herself a subdivision of the main territory which she defended *against the other female* by loud singing and fighting, and in which she finally chose her nest-site. From February 1 until late March, by which time both had nests, each female sang frequently from a favorite perch within her section. The two alternated in utterance, as do neighboring males. Twice, when female III followed the male toward the section which belonged to female I, a fight ensued between the two females. They locked feet and jabbed each other on the breast. Then they separated, and female III flew back to her section, while female I sang. Had they not been banded, I should have thought I was watching a boundary dispute between two males.

Nest-building, like copulation and the highest development of territorialism, involves synchronization of successively emergent elements. I watched female I closely during February and March, 1935, to see how early she would begin to pick up straws, utter notes associated with nest-building, or visit the future nest-site. It may have been merely a coincidence that on February 10, as I passed by the oriental thuja which was later to serve as her nest-site, I saw female I fly out from this tree. But her subsequent behavior attracted my attention. She acted as she had so often the previous spring, when I visited her nest to examine and weigh the young birds. She flew only five or six feet away from the thuja, perched in full view on a cotoneaster twig, and uttered a series of strident alarm notes. This was not the typical reaction of a startled bird, which seeks refuge in dense foliage and rarely utters more than one or two "eep's." Female I distinctly registered protest rather than fright. The suggestion is strong that she had special interest in the thuja as early as February 10.

On March 10, I saw her pick up nest material for the first time. She was hopping about on the ground underneath the same tree. She pecked at dried leaves, picked one up, dropped it. On March 13, I heard her utter a series of sharp "eep's." This note is ordinarily given by the female Nuttall as she approaches the nest-site with nest-material in her beak. On this day, however, female I, while giving the note, merely perched near the thuja without any nest-material in her beak. Again she protested as she saw me approach the thuja. On March 15, I watched her pick up a small piece of paper and a strand of dead grass, fly with these to a perch on a twig of cotoneaster within a foot of the thuja, and there utter a series of "eep's." Again she failed to enter the tree, but remained perched on the cotoneaster holding the straw and paper in her beak. Within a few minutes she flew to the ground and dropped the material. The instincts to pick up nest-material, fly toward the nest-site, and utter notes associated with nest-building were all present, but apparently had not yet been synchronized into an effective procedure.

Two days later, on March 17, I saw her approach the thuja with straws in her beak, uttering loud "eep's" just before she entered. But even on this day she did not work continuously. She made a few visits to the nest-site, and then ceased working altogether. Twice on March 18 I saw her approach the thuja with straws in her beak, only to drop the material without entering the tree. On the following day, March 19, the instincts related to nesting became synchronized at last into coördinated activity, and she began continuous work on the nest. By March 25 the nest appeared complete, although it is possible that female I added more material to the lining after this date. On March 31, forty-nine days after female I had first showed concern at my approach to the thuja, the first egg was laid.

We can only speculate as to whether nest-building, like copulation and territorial behavior, has a permanent substratum. The case already mentioned where females I and III showed a cumulative interest in small sections of their mate's territory in which the nest-sites were finally chosen, suggests the possibility. In 1934 the breeding area of male I included the lawns and shrubbery between the Life Sciences Building and California Hall, as well as the narrow lawns on the south sides of both buildings. During fall and winter each female was seen occasionally in almost every part of this area, but female I was found more often in the northeastern part, by the flag-pole in front of California Hall, while female III was seen more frequently in the southeast part, by the lawn south and southwest of California Hall. The broad lawn in front of the Life Sciences Building which comprised the west half of the territory was only rarely visited by either female. A certain amount of restriction within the male's area was apparent, then, even in winter. This became more marked from early February on, when I noticed that female I stayed almost entirely within an area surrounding the flag-pole about 30 yards square, near the center of which stood the small thuja where she had built a nest the year before. Female III, on the other hand, stayed in an adjacent part, the southern corner of the lawn south of California Hall. At the edge of this lawn was a clump of raphiolepis bushes and a small tree in which female III frequently perched. In mid-March, when female I started to build her nest, she chose the thuja as the nest-site. Female III started to build in late March, and put her nest in the clump of raphiolepis bushes.

I do not mean to imply that as early as February 1, the birds had begun to take interest in possible nesting places conceived as such. I simply want to point out that from the beginning there was substantial segregation of the two females to subdivisions, that with the advance of the season each female restricted her activities more and more, and that later when she started to build her nest, she chose a tree or bush within this section.

I have described a few outstanding elements of breeding behavior. There are undoubtedly many others, shading back no one can say how far, emerging or intensifying no one can say how gradually or in response to how distant threshold conditions. A great deal has been discovered or rediscovered and emphasized in the last twenty years in the field of behavior, yet in minute and coherent observation we are merely beginning. Adequate observation, unfortunately, demands an almost prohibitive amount of time, not only in numbers of hours but in numbers of seasons and years, with small assurance of significant results.

Museum of Vertebrate Zoology, Berkeley, California, April 4, 1936.

STEPS IN THE DEVELOPMENT OF THE BIRD-FLOWER

By A. L. PICKENS

Again red leads, with purple as a lagging second, in this the second list of bird-visited flowers (see Condor, vol. 33, 1931, pp. 23-28). Pink, orange, blue, yellow, white, green and maroon follow in descending order of avian choice as indicated by this and preceding investigations. Figworts, mints, peas, lilies, and composites are in order the five favorite families of flowers as so far indicated.

While assembling the new list of avian flowers, over seven hundred associations between flowers and insects have been recorded. Maroon or brownish flowers show the highest proportion of associations with insects of primitive or unspecialized mouth-