BREEDING BEHAVIOR AND LIFE HISTORY OF THE WILSON'S WARBLER[1]

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BENT (1953) summarizes most of the information available on the biology of the Wilson's Warbler (*Wilsonia pusilla*). Dawson (1923), Grinnell and Storer (1924), and Grinnell, Dixon, and Linsdale (1930) described aspects of Wilson's Warbler behavior. Dwight (1902) described plumages and molt cycles, but his descriptions reliably apply only to the eastern race (*W. p. pusilla*). An observation of one nest of *pusilla* not included in Bent was described by Harrison (1951). I observed Wilson's Warbler for two years on a breeding area in Marin County, California.

METHODS AND STUDY AREAS

I spent approximately 500 hours in the field from March to August 1969–1970 observing or looking for Wilson's Warblers. Daily observations were made during the period of spring arrival on individuals that remained to breed. Observations of banded singing males were plotted on the maps of the study areas made from aerial photographs. Lines were drawn connecting the outermost observations for each male and the area on the map was measured resulting in the size and location of the maximum defended territory.

In 1969 the study was limited to Area 1, 4.9 hectares in size, which included Arroyo Hondo Creek and a small tributary. The Arroyo Hondo Creek is a perennial stream cutting into an old marine terrace. The relative density of the cover vegetation based on the point quarter method of vegetation analysis (Cottam, 1956) was: California bay (*Umbellularia californica*) 41 percent; coast live oak (*Quercus agrifolia*) 24 percent; California buckeye (*Aesculus californica*) 19 percent; canyon oak (*Quercus chrysolepis*) 9 percent and five other species 7 percent. The mean height of the cover vegetation was estimated to be 15 m. The predominant understory plants in order of abundance consisted of California blackberry (*Rubus ursinus*), nettle (*Urtica* sp.), sword fern (*Polystichum munitum*), lady fern (*Athyrium felix-femina*), and poison oak (*Rhus diversiloba*).

In 1970 I made observations in a second study area which was 0.8 km northwest of the Arroyo Hondo. Area 2 was 6 hectares in size. The vegetation consisted of willow (*Salix* sp.), coastal scrub species including coyote bush (*Baccharis pilularis*), California sage (*Artemesia californica*), coffeeberry (*Rhamnus californica*), and thimbleberry (*Rubus parviflorus*). The height of the willow cover was approximately 5.5 m. The understory in the willow habitat was similar to the understory in Area 1, despite the different cover vegetation. (Names of plants taken from Munz, 1970.)

ARRIVAL DATES

During the spring of 1970 I determined first arrivals (Table 1). In some species (Dorst, 1962) older males return to the breeding ground before second-year males. My data suggest this for Wilson's Warbler as the males

[1] Contribution No. 28 of the Point Reyes Bird Observatory.

TABLE 1

ARRIVAL DATES OF WILSON'S WARBLER IN 1970

Territory	Male	Female
	AREA 1	
1	6 April	?
2	27 March	4 April
3	27 March	15 April
4	29 March	9 April
5	27 March	10 April
6	?	?
7	26 March	?
	AREA 2	
1	20 March	?
2	19 March	5 April
3	5 April	?
4	?	?
5	19 March	?
6	5 April	7 April
7	20 March	12 April
8	20 March	16 April
9	16 March	12 April

arrived in two distinct groups in each study area. In Area 1, five males arrived between 26 and 29 March, and one on 6 April. In Area 2, six males arrived between 16 and 20 March, and three others not earlier than 5 April. The earlier arriving males were returns from previous years in Area 1, as they had all been color-banded during the previous year. Female arrival was marked by the cessation of male advertising song and by observation that the male was being followed by a female. The elapsed time between first arrivals of males and the beginning of pair formation averaged 15 days.

TERRITORY AND TERRITORY DEFENSE

Only slight modifications of territorial boundaries occurred between 1969 and 1970 (Fig. 1). M6 enlarged his 1969 boundary to include the territory of a male that did not return. The other territorial changes were affected by M1 (two years old) who moved 150 m south upon his return on 27 March 1970. Two days later when M3 (at least four years old) returned, he found the younger male in his old territory. A long, intensive boundary dispute (over an hour) ensued, resulting in a division of the older male's 1969 territory.

The mean territory size defended by males in Area 1 was 0.57 hectares

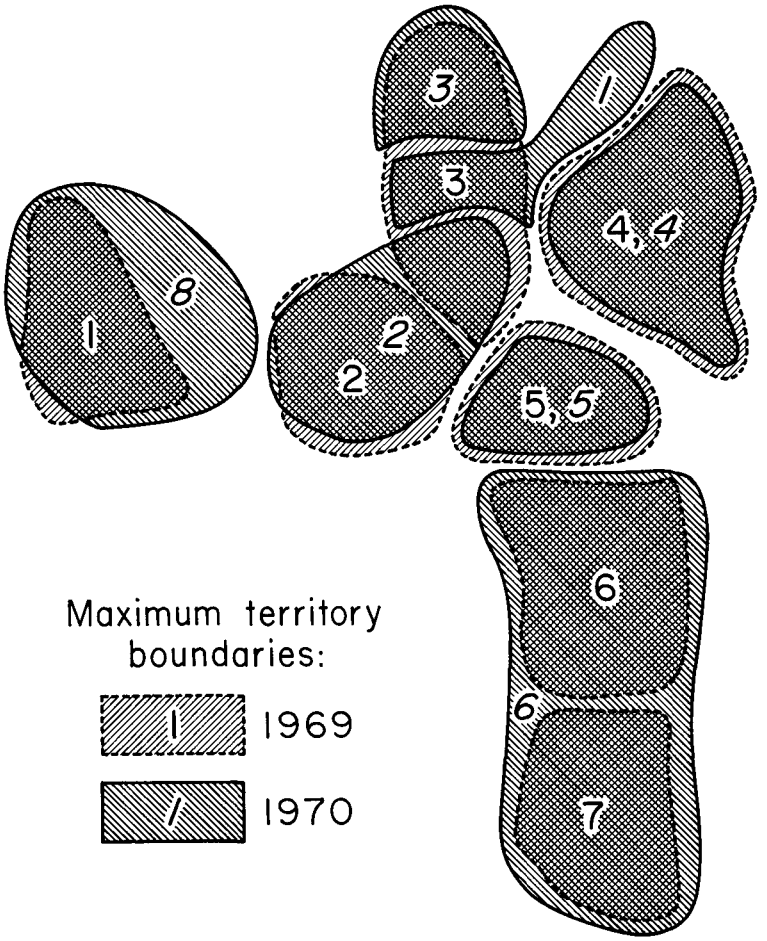

FIG. 1. Territory boundaries in area 1. Straight numerals with dotted boundaries represent territories in 1969. Slanted numerals with solid boundaries represent territories in 1970.

(S.D. = 0.3), ranging from 0.2 to 1.3 hectares. The mean defended territory size in Area 2 was 0.48 hectares (S.D. = 0.2), ranging from 0.3 to 1.0 hectares.

Occasionally, breeding birds were captured or seen away from their normally defended territories, indicating larger home ranges. On five occasions males were seen or captured from 125 to 300 m from their normally defended territory boundaries. In one instance, a *pair* was observed 135 m from their boundary in the extreme edge of the adjacent territory.

Four boundary disputes were observed, which were probably the first such

TABLE 2

MEASUREMENTS OF WILSON'S WARBLER NESTS AT POINT REYES BIRD OBSERVATORY

	Number of nests	Mean ± S.D.	Range
Nest height from ground to top of nest	11	68.0 cm ± 18.0	32.5–82.5
Outside diameter	9	14.5 cm ± 2.4	10.0–17.5
Inside cup diameter	7	5.2 cm ± 0.9	5.0–7.5
Depth of cup	7	3.3 cm ± 0.2	2.5–5.0
Weight of nest	9	27.7 g ± 8.1	10.0–38.0

disputes for the season between neighbors. These lasted from 30 to 60 minutes, occurred 0.5 to 1.5 m off the ground in dense tangles, and occupied a total area of no more than 10–15 m^2. Long chases in a restricted area were interspersed with short encounters where the first bird to arrive flew at or near the second, causing the latter bird to move to another perch. This sometimes continued at a rapid pace. Singing bouts of eight or nine complete songs per minute accompanied two of the disputes, but in the others chipping predominated. No physical contact was ever observed during these disputes.

FORAGING OF ADULTS

Males, being more conspicuous than females, were more easily observed throughout the territory. They fed in both understory and trees, but generally not higher than 1.5 m below the roof of the canopy. In Area 2, where the willow was the dominant cover, males fed no higher than 4 m from the ground. In Area 1, however, males were frequently observed foraging 10–17 m from the ground, suggesting that this species is not necessarily restricted to low vegetation for its foraging habitat.

NESTS

Fourteen nests were found during the study. The dimensions of nests are shown in Table 2. Because the understory of both areas was similar, the composition of the nests was the same. The outside of the nest was composed of leaves, twigs and small branches of blackberry (*Rubus* sp.), nettle (*Urtica* sp.), and oak (*Quercus* spp.). The inside was made of animal hair interwoven with fine stems, moss and deteriorated leaves. By far the major support plant for the nests was blackberry which offered three advantages: horizontal runners for support of nests, overhanging leaves for concealment of the top of the nest, and a dense tangle sometimes so thick that ground predators would find it hard to penetrate. In the two cases studied in detail,

nest building was completed in five days. Two to three days later, the first egg was laid and the other eggs were layed one each day thereafter.

CLUTCH SIZE AND INCUBATION

Five nests were found with eggs. Of these, four contained four eggs and one contained three. In one clutch of three eggs, two eggs hatched 11 days and one hatched 12 days after the last egg was laid; and in one clutch of four, all hatched 13 days after the last egg was laid. In both instances incubation did not begin until after the last egg was laid.

DEVELOPMENT OF NESTLINGS

As young Wilson's Warblers develop in the nest, changes take place which are characteristic of their age. Most young appeared to develop at the following rate:

1st day—Young all pink, from 10–15 long downy feathers present;

2nd day—Primaries and secondaries begin to grow and show up as dark areas on the wings. Young gape readily;

3rd day—Prominent dorsal feather tract shows up as a dorsal black stripe;

4th day—Pin feathers on wings are ½ cm long. So much down has grown that young appear all brown with no pink showing;

5th day—Pin feathers on wings one cm long. Eyes begin to open;

6th day—Eyes are open wide, "cheeping" heard for the first time. Pins on wings and head are not erupted, but some dorsal tract feathers are erupted;

7th day—Upper wing coverts are erupted, primaries and secondaries not erupted;

8th day—All feathers are erupted.

ADULT FEEDING OF YOUNG

On the day that young hatched, males appeared in the vicinity of the nest with food in their beaks, but they did not actually feed young until several days later, if at all. Indeed, for one clutch of three, the male was never observed feeding young at the nest. In one clutch of four, I watched the nest at the same time each day (Table 3). Before the fourth day, the male came to the vicinity of the nest with food in its beak, hovered near the entrance, and then flew back to a perch several feet away. After this had occurred several times a minute, he left only to come back several minutes later with the same mass of insects in his beak to repeat the performance. (I was close enough to see the arrangement of green larvae, etc., in his beak.) After the fourth day he regularly fed the young. This behavior cannot be construed as shyness resulting from my presence. Where I discovered nests for the first time and the young were over five days old, this behavior was not

TABLE 3

FEEDING TRIPS TO NEST BY ADULTS WITH FOUR YOUNG
(Between 07:00 and 08:00)

Day after hatching	Female	Male
2nd	5	0
3rd	7	1?
4th	9	4
6th	36	12

shown; that is, the male would routinely make feeding trips to the young despite my first sustained observation of the nest.

One nest with four young was watched for 13 hours on the ninth day after hatching (Fig. 2). The number of feeding visits to the nest by the male averaged 17.2 per hour while the female averaged 40.8 visits per hour, giving an average of 58 visits by parents per hour. If I extrapolate the observations made during 13 hours to include a normal 14-hour day, the male made 241 trips and the female 571, for a total of 812 feeding trips per day. On four previous days, the data from one-hour observations in the morning and afternoon indicated the same level of feeding effort. The rate of feeding was highest between 08:00 and 09:00, but never dropped below 50 trips per hour in the afternoon. This constancy was maintained by the adults relieving each other at the nest. For instance, from 13:00–14:00, when the male reached one of his lowest feeding rates, the female made more trips than she had previously. Later, from 16:00–17:00, when the female made only 29 trips, the male showed his highest feeding rate. The number of fecal sacs removed increased gradually until between 17:00 and 19:00, six sacs were removed per hour. Seventy percent of the sacs were removed by the male.

DEVELOPMENT OF FLEDGLINGS

The young left the nest 8 days after hatching in a brood of three, and 10 days after hatching in a brood of four. Observations of four fledglings from the same nest revealed several plumage changes. Upon leaving the nest, the young were brown except for dull yellow underparts. By 21 days old, the lores and eye ring became bright yellow, while the rest of the plumage remained brown. At 32 days of age bright yellow feathers had grown in on the chin, upper breast and flanks, but the lower breast and belly remained in dull yellow juvenal plumage. The crown was brown with a few black cap feathers beginning to grow in. At this age the young fed on their own for the most part, and in a few days began to leave their parents' territory. As

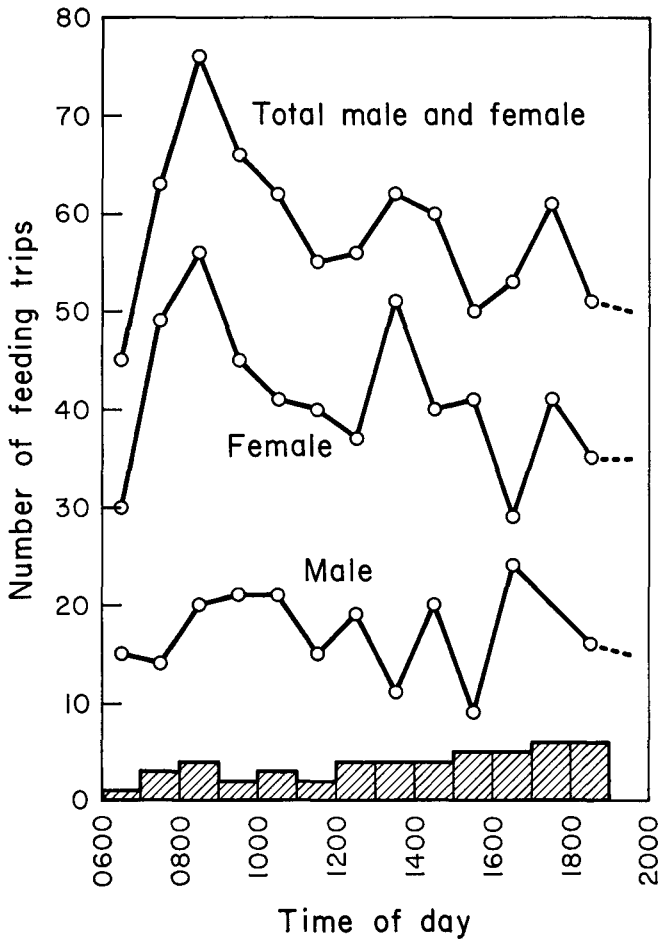

FIG. 2. Number of feeding trips by adults to nest with four, 8-day old young during 13 hours of a 14-hour day. Lined bars at bottom of graph represent the number of fecal sacs removed.

the black cap feathers continued to grow, the sides of the crown remained brown. At 39–40 days of age, these brown juvenal feathers were replaced with yellow.

In the eastern race (*W. p. pusilla*) according to Dwight (1902) young females lack a black cap until the first pre-nuptial molt. Since all 192 young captured in 1969 had black caps, I suggest that this does not apply to individuals breeding in central coastal California. Young Wilson's Warblers remained in quite heavy body molt until early August (Fig. 3).

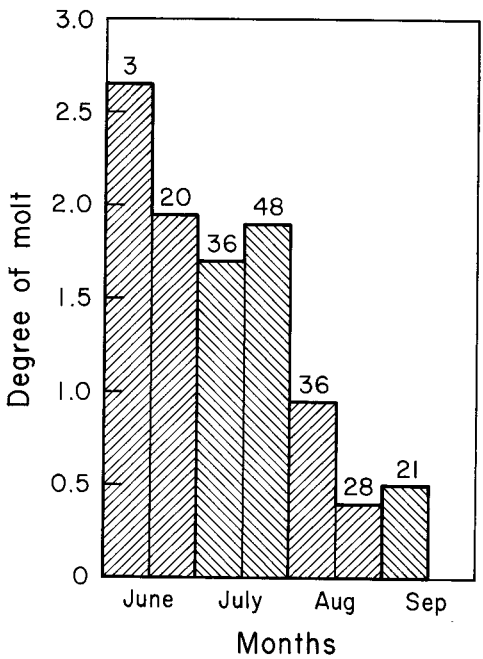

FIG. 3. Body molt of young birds captured in mist nets in 1969. Numbers above bars represent the actual number of individuals.

BREEDING SUCCESS

During 1969 six pairs of adults produced 26 fledglings. In 1970 16 pairs produced 20 fledglings. Only four of 22 pairs were known to attempt a second clutch after successfully raising a first brood, and in only two did young leave the nest during the second attempt. Possible predators observed near the nests were the Scrub Jay (*Aphelocoma coerulescens*), the Steller's Jay (*Cyanocitta stelleri*), and garter snake (*Thamnophis* sp.).

WANDERING OF POST-BREEDING ADULTS

There is good evidence that the peak of adult post-breeding "wandering" occurred in late June. Few second clutches were laid after successful fledging of first broods, and first broods were finished by late June. These facts support data from continuous netting in Area 1 which showed that in both 1969 and 1970 there was a peak increase of unbanded adults between 16 and 30 June (Fig. 4). The unbanded adults in June were probably not part of a surplus breeding population, since it is probable they would have been captured earlier. The sex ratio of these unbanded adults was 1:1. They were

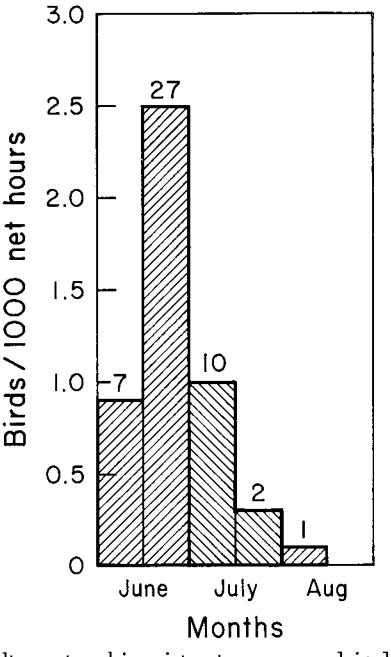

FIG. 4. Unbanded adults captured in mist nets near area 1 in 1969 and 1970. Numbers above bars represent actual number of individuals captured.

all in late stages of breeding condition with a brood patch or cloacal protuberance and had low subcutaneous fat levels. Adult wandering probably occurs after breeding or attempted breeding at a time when territoriality is waning. For whatever functions the territory serves, continued energy expended in defense of a territory after breeding for a migratory passerine species would not benefit the adult. The *unrestricted* search for food in preparation for molt and migration would be appropriate to the bird's survival during the post-breeding period.

SUMMARY

A two-year study of the Wilson's Warbler was made in two different habitats. Older males appeared to return earlier than second-year males and females. With one exception, males returned to essentially the same territories in 1970 they occupied in 1969. The average area of the defended territory was 0.54 hectares. Most of the nests found were supported by blackberry and averaged 68 cm from the ground. Aspects of adult behavior were discussed including territory defense and feeding rates of young by adults. In one 14-hour day, the parents made an estimated 812 feeding trips to the nest, an average of 58 trips per hour. Plumage changes in young from hatching to 40 days of age were described. Field observation and mist net data suggest peak adult post-breeding wandering occurred in late June.

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