

HABITAT STRUCTURE IN RELATION TO POPULATION DENSITY AND TIMING OF BREEDING IN PRAIRIE WARBLERS

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Brown (1964) argued that territoriality results when it is economically feasible to defend a limiting resource. Perrins (1970) and Slagsvold (1976) reviewed evidence that timing of breeding is also related to resource availability. However, studies in which the limiting resource is identified are few (see Wilson 1975:263-264), largely because environmental complexities make interpretations difficult.

Any study of resource relationships is greatly facilitated by a simple environment, and the pine barrens of Plymouth County, Massachusetts, offer an ideal situation in this respect. This habitat has fewer than 6 principal plant species. Frequent fires have created a patchwork of uniform tracts in various stages of regeneration, each differing in structure, but not composition, of its vegetation. Prairie Warblers (*Dendroica discolor*) are one of the commonest breeding birds of these barrens, and in this study I examined the role that vegetation and related resources play in territory size, breeding density and timing of breeding of this species.

METHODS

Description and vegetation of study plots.—I selected two 7.5-ha plots less than 2 km apart, each marked with a 50-m grid and representing different stages of regeneration after fire. Fires are common in these barrens, and Prairie Warbler breeding densities apparently differ according to stage of regeneration (Lloyd-Evans 1973). Plots selected were those that appeared to promise the greatest contrast in Prairie Warbler densities. One (hereafter called REGN) was regenerating from a fire in 1963, and the other (hereafter called BURN) had burned in 1974. Care was taken to insure within-plot uniformity by selecting level ground and by avoiding edges between tracts in different stages of regeneration. However, REGN did contain a small area, less than 18% of the plot, that had been bulldozed in an effort to stop the fire. It differed from the rest of the plot in having no trees, but the presence of this small area had no discernible effect on the results reported herein. Data for the following descriptions of the vegetation were collected in 1973 for REGN and in 1975 for BURN, but because regeneration in the pine barrens is slow the data are believed to be adequate to depict conditions of the plots in 1976, the year that I studied the Prairie Warblers.

Much of the vegetation of Plymouth County is a coastal pine barrens growing on sandy soil comprised largely of glacial till. Older forest is characterized by 3, essentially monospecific, vegetative layers: (1) a tree layer, largely pitch pine (*Pinus rigida*) more than 3 m high; (2) a shrub layer, mostly scrub oak (*Quercus ilicifolia*) 1-3 m high; and (3) an herb layer, mostly black huckleberry (*Gaylussacia baccata*), low blueberry (*Vaccinium vacillans*) and dwarf blueberry (*V. angustifolium*), all less than 1 m tall (all botanical names from Gleason 1968). I have used these 3 natural layers to describe the vegetative structure of the plots,

even though the heights of the layers in the more recently burned plots are less than those in the older forest.

For purposes of describing the vegetation, a map of each study plot was divided into 125 numbered 25-m squares. Using a random number table, 5 squares were selected to be described. For each of these, species composition and vegetation density, height and percentage cover were measured in the following manner: tree layer species composition and density were measured for the entire 25-m square, but tree height and percentage cover were taken only in a 10-m square in the SW corner of the 25-m square. All shrub layer measurements were taken in the smaller square just described and all herb layer measurements were made in each of 5 randomly thrown 1-m squares within it. Percentages of cover are estimates of the amount of area covered as if looking down from above, so layers could overlap and total more than 100% cover. *Q. ilicifolia* densities are expressed in clumps per unit area, a clump being all stems growing from the original root stock.

Prairie Warblers.—Except during settlement, when both plots were visited daily, visits were on alternate days from 6 May to 3 July 1976, between 05:00 and 11:00. Behavior of randomly selected males was recorded for 30–90 min per bird. Individuals were recognized by song during the first three weeks. Thereafter songs became more variable (Nolan 1978, pers. obs.) and less recognizable, but by that time stages of reproduction of the various males were less in phase than at the beginning of the season and territories were well delineated. Therefore, individuals could be identified by location and continuity of behaviors other than song.

Male densities were determined on the basis of the number of territories or parts of territories in each plot after pair bond formation was completed (ca. 20 June). Territories were mapped by a method adapted from Odum and Kuenzler (1955). At the end of each observation period the male's activity space was plotted, and plotting was repeated until a further observation period added no appreciable new area to the total. The resulting area, excluding obvious encroachments into neighboring territories, represents at least 4 h of observation per male and constitutes the seasonal activity space. Areas were calculated by tracing territories on graph paper and counting the squares or parts of squares covered. (For a few males, enough defense was observed to permit mapping a defended area; these areas were identical to their respective activity spaces.) Stage specific variations in territory size during the breeding cycle, known for some species (Odum and Kuenzler 1955, Stenger and Falls 1959, Stefanski 1967), have not been found in *Prairie Warblers* (Nolan 1978). None were noted in the present study and, in any event, since territories were small, fluctuations in daily activity were probably not important (Weeden 1965).

A pair is defined as a male and female whose association led to nest-building, and the date of pair bond formation is defined as the date of the first persistent association between a male and a female. While individual females were not marked, a male found courting a female and in the company of a female on subsequent days was assumed to have paired on the day he first was observed courting.

RESULTS

Vegetation.—The tree layer of REGN consisted entirely of *P. rigida* (N = 404). The density of live trees was 1293/ha with a mean height of 3.0 m (range 2.0–6.0 m) and 25.8% cover. The density of standing dead trees was 141/ha. In BURN all sampled trees were standing dead (N = 249), so that species differences (71% *P. rigida*, 29% seven other species) were unimportant for this study. The density of these dead trees was 794/ha and the mean height was 6.4 m (range 3.0–11.0 m). The shrub layer of



FIG. 1. The REGN study plot at the time of the study (13 years after the fire). Note that both oak and pine layers have regenerated (compare Fig. 2).

REGN was also monospecific and contained only *Q. ilicifolia* ($N = 470$) with a mean height of 1.10 m, a density of 9400 clumps/ha and 53.0% cover. In addition, the BURN's shrub layer was slightly more diverse (85% *Q. ilicifolia*, 15% six other species; $N = 541$). This layer had a mean height of 0.72 m, a density of 10820 clumps/ha and 40.6% cover. Herb layers in both plots were essentially identical. Fewer than 6 species accounted for over 90% of the total herb cover (principally *G. baccata*, *V. vacillans*, *V. angustifolium* and spring wintergreen, *Galtheria procumbens*) and only 19 herb species were found in the sample squares.

The preceding data show that the 2 plots were very similar in that: (1) both had the same 6 principal plant species; (2) each was internally homogeneous because all vegetation had burned at the same time; (3) herb layers were nearly identical; and (4) *Q. ilicifolia* densities were similar (suggesting similar *Q. ilicifolia* layers previous to the fire, since these oaks regenerate from the old root stock). Differences between the plots were few: (1) *Q. ilicifolia* was slightly taller in REGN, and (2) the presence of live *P. rigida* in REGN gave it a more closed tree canopy (Fig. 1), whereas the more open tree canopy of BURN consisted entirely of dead *P. rigida* (Fig. 2).



FIG. 2. The BURN study plot at the time of the study (2 years after the fire). Note that only the oak layer has regenerated and that the tree layer consists entirely of dead trees (compare Fig. 1).

Additionally, the plots differed in that: (1) the unusually dry spring of 1976 delayed the emergence of *Q. ilicifolia* in BURN by nearly a month (some leaves emerged from buds as early as 10 June, but most emerged between 15 and 22 June), whereas oak in REGN emerged at the normal time (20–28 May), presumably because it was protected by the shade of the live pines; and (2) the proximity (50–150 m) of the BURN to the edge of the unburned forest (Fig. 3), which consisted of large live *P. rigida* and *Q. velutina*, may have been an important factor to Prairie Warblers breeding in BURN. Oak leaves in this forest emerged normally, *Q. velutina* in early May and *Q. ilicifolia* in late May, and Prairie Warblers often foraged there.

Settlement of study areas by Prairie Warblers.—As shown below, settlement dates of the study plots were strikingly different. REGN was settled early and quickly, while BURN was settled later and more slowly.

The first Prairie Warbler was seen on 3 May, and many appeared on 4–5 May (T. L. Lloyd-Evans, pers. comm.). I first visited both plots on 6 May. On 6 May I did not count males in REGN, but the frequent singing there by many individuals suggested that territory establishment had be-



FIG. 3. The edge between recently burned forest (shown in Fig. 2) and more mature forest (ca. 25 years after the most recent fire).

gun (Nolan 1978). On 11 May I estimated that 30–35 males were singing in REGN; many seemed to be individuals that had first been seen on 6 May and had occupied the same locations every day since. By 13 May I estimated 20–25 singing males, a figure which approximated the final breeding density (see below).

BURN, in contrast, on 6 May held no males, but 2 or 3 sang infrequently in the adjacent unburned forest. (This older forest has been shown by Lloyd-Evans [1973] to support a high density of Prairie Warblers.) On 7 May, 6–8 males sang infrequently and ranged widely over the plot itself, but on 9 May the plot was deserted. Not until 13 May, with the arrival of 2 birds, did any males settle. An additional 5 males established territories in the next few days, the last on 22 May.

Timing of pair bond formation.—Although the first female arrived on 8 May, no others were found until 16 May (compare Nolan 1978). Thereafter I saw them regularly.

Visibility of females was poor in the thick vegetation of REGN and I relied on various kinds of observations to establish timing of pair bond formation: direct observation of the first persistent association with a female by 5 males; discovery of first nesting for 3 males (in these laying

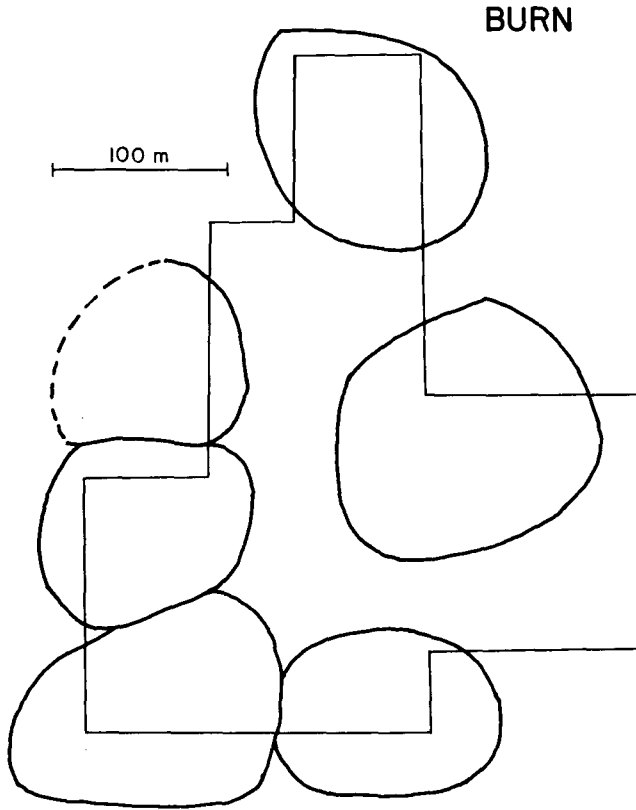


FIG. 4. Map of BURN indicating boundaries of territories of the male Prairie Warblers that bred there in 1976.

began on 2, 3 and 11 June), and extrapolation using the average lengths of breeding stages determined by Nolan (1978); and determination of the day of first occurrence of certain behaviors associated with pairing, e.g., changes in male vocal behavior (Nolan 1978). All these lines of evidence coincided well, indicating that pair bonds were formed in REGN from 18 May to 5 June.

Pair bond formation occurred much later in BURN, between 11 June and 21 June. Here visibility was not a problem and all first associations of male and female were observed on the day the association began. Prior to 11 June there were only 2 brief observations of females in BURN, whereas in REGN I had seen them regularly since 16 May in spite of the

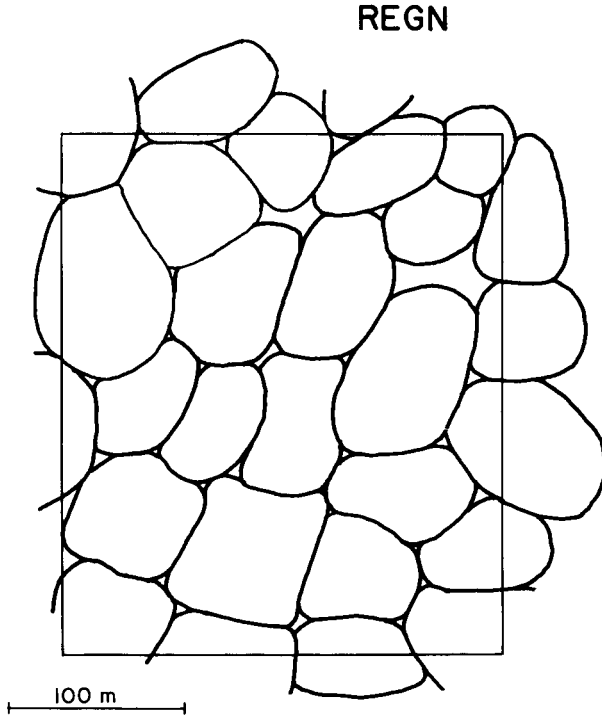


FIG. 5. Map of REGN indicating boundaries of territories of the male Prairie Warblers that bred there in 1976.

poorer visibility. BURN females apparently nested late, as well, and in the 2 nests discovered laying began on 26 and 28 June.

Breeding density and territory.—Breeding density was much lower in BURN than in REGN (Figs. 4 and 5). Only about 54% of the area in BURN was included in a Prairie Warbler territory, while in REGN about 98% was occupied. Most territory boundaries in REGN were contiguous, whereas in BURN large unoccupied areas often separated territories.

None of the 6 males in BURN confined his whole territory to the plot. Therefore, the 7.5 ha held only 3.8 territories, a density of 0.51 territories/ha. In REGN there were 20.1 territories, representing 26 males, a density of 2.68 territories/ha.

Mean territory size of males in BURN was 1.38 ± 0.30 ha ($N = 5$, range 1.06–1.78 ha), almost 4 times greater than the mean in REGN, which was 0.36 ± 0.12 ha ($N = 22$, range 0.18–0.64 ha). In a test of significance: $t = 7.29$, $df = 25$, $P = <0.005$.

All males in BURN foraged frequently in the portions of their territories in the unburned forest outside the plot, especially before *Q. ilicifolia* emerged. One male initially stayed entirely within BURN until his neighbor of the preceding 3 weeks disappeared. He then shifted his boundaries to take in most of the latter's territory, including the portions in unburned forest. Before this shift I had occasionally seen him fly 75–150 m to forage in unoccupied portions of the unburned forest.

Food for young.—Fifteen of 16 food items brought to young were the small caterpillars that are abundant on *Q. ilicifolia*. Similarly, 82% of food items brought to young Indiana Prairie Warblers were caterpillars (Nolan 1978).

DISCUSSION

Considering the proximity of the 2 plots and the considerable similarity of their plant species, the few distinct differences in their vegetation structure almost certainly account for the different breeding densities of their Prairie Warbler populations.

Q. ilicifolia leaves emerged 2 weeks after male arrival, and therefore the minor differences in this layer were probably of little importance to arriving males and are unlikely to account for density differences. The herb layers were nearly identical and, in any event, were rarely used by Prairie Warblers. Therefore, considering that: (1) *P. rigida* was the only arboreal foliage present when males arrived and (2) the plots differed substantially only in the *P. rigida* layer, it appears that the presence of live pines in REGN and their absence in BURN most likely accounts for density differences.

That Prairie Warbler breeding densities can respond to food abundance is suggested by the fact that they were twice as dense in unsprayed as in sprayed orchards (Springer and Stewart 1948, DeGarmo 1949). Other studies have cited food as an important variable in breeding density and territory size (Stenger 1958, Morse 1976, reviews by Lack 1966, Brown 1969). Male Prairie Warblers arrive as soon as there is enough food on the breeding grounds to support them (Nolan 1978) and, in Indiana, often concentrate on pines as a foraging substrate before deciduous leaves become available (Nolan 1978). Therefore, the absence of food available on live pines in BURN during this critical period may have been responsible for the low density of settling males, even though food supplies in the 2 plots are probably very similar after *Q. ilicifolia* leaves emerge (and therefore while nestlings are being fed). Though it is possible that the dead trees could have supplied sufficient food, a shortage of food in BURN is also suggested by the facts that: (1) males settling in BURN usually foraged in the adjacent unburned forest (where pines were abundant); (2) nearly all

males included portions of unburned forest in their territories and the sole exception soon shifted his territory to include a portion of unburned forest; and (3) males settled later in BURN than in REGN. However, it must be considered that in addition to providing an early food supply, *P. rigida* also protects *Q. ilicifolia* from drought by lowering evapo-transpiration rates, thus ensuring a more dependable food supply for the entire season. Prairie Warblers may favor evergreen-covered habitats for this reason, especially in regions susceptible to drought.

Another factor that may have contributed to the greater attractiveness of the plot bearing *P. rigida* is the concealment of nesting activities from Brown-headed Cowbirds (*Molothrus ater*), which were common on my plots (compare Nolan 1978), and from neighboring male Prairie Warblers, whose interference in efficient pair formation and nest-building is discussed by Nolan (1978).

In order to explain the difference in time of female settlement on the 2 plots, factors of importance to females must be considered. While females prospecting for breeding locations may have been influenced by the same factors as males (i.e., pines), it appears more likely that the delay in pairing in BURN was caused by the delay in leafing of *Q. ilicifolia*. The importance of this event to females is suggested by the fact that most females in 1976 (and probably other years as well) arrived from 16–20 May, just prior to the normal time of leafing of *Q. ilicifolia*. That the delay in leafing caused the BURN pairing delay is strongly suggested by the correlation between dates of pairing and leafing (even though delayed by nearly a month in BURN).

Harmeson (1974) and Wittenberger (1976) have argued that food available on the territory affects pairing success and it is known that a certain threshold of food abundance is necessary for the female to synthesize eggs (Lack 1963, Perrins 1970, Ankney and MacInnes 1978). Caterpillars are abundant on *Q. ilicifolia* leaves and the importance of *Q. ilicifolia* as a factor in influencing female settlement may be as a source of food required for egg-laying. These caterpillars are also an important source of food for young (see above). However, Zimmerman (1966, 1971) has shown that the amount of vegetative cover, independent of food, can influence pairing success, probably because greater cover provides better nest concealment. In my study area, all nests were placed in forks of *Q. ilicifolia* (Lloyd-Evans, pers. comm.; pers. obs.). These sites are very exposed before the leaves emerge, and therefore are probably unsuitable. The timing of nest-site availability may be important to the timing of pairing, and the lack of suitable nest-sites in BURN prior to leafing may have caused the pairing delay.

In either case, the delay in pairing indicates that females found the

territories unsuitable and would not settle until *Q. ilicifolia* leaves emerged. Lack (1966) and Slagsvold (1976) have reviewed evidence that timing of egg-laying (not pair formation) is related to vegetation phenology, but this paper is the first to present evidence that timing of female settlement is also dependent on vegetation phenology. While it is also possible that the males in BURN were in some way less suitable, the fact remains that they all acquired mates once oak leaves emerged. These facts are consistent with the predictions of Orians (1969) and Wittenberger (1976) that some sort of evaluation of the territory by the female is important during female settlement.

SUMMARY

The breeding Prairie Warbler populations of 2 uniform tracts of pitch pine forest in different stages of regeneration from fire were contrasted. One plot (BURN) had burned too recently for the tree layer to have regenerated, and it supported a much lower density of males compared to the second plot (REGN) which had burned less recently, and in which the tree layer had partially regenerated. Males in REGN also had much smaller territories. Reasons for these differences are suggested.

A drought during the study caused a delay in leafing of the oak shrub layer (whose leaves are the primary foraging substrate for Prairie Warblers during the breeding season) in BURN, but not in REGN where oaks were protected in the shade of live pines. While male settlement was unaffected (it was completed even before normal leafing time), pairing by males in BURN was delayed by almost a month (until after the oak leaves emerged) relative to males in REGN. The significance of this delay is discussed.

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