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NESTING RESPONSES OF FIELD SPARROWS (*SPIZELLA PUSILLA*) TO PLANT SUCCESSION ON A MICHIGAN OLD FIELD

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Adams (1908) was the first to note that an avian succession or species turnover accompanies plant succession. Subsequent investigators have pursued the subject typically by estimating densities of breeding birds in a successional series of habitats (e.g., Saunders 1936, Kendeigh 1946, Odum 1950, Johnston and Odum 1956, Karr 1968, Shugart and James 1973). These studies document effects of dramatic changes in habitat on the dynamics of bird communities but do not reveal which aspects of plant succession evoke changes in population density of individual bird species. Lack (1933), in contrast, focused on single bird species, identifying features of habitat that determined the birds' presence or absence. Akin to Lack's approach, my study examines a particular bird population's responses to the gradual, year-to-year changes in vegetation that characterize succession.

This population was first studied in 1949 to 1957, when F. C. Evans and his assistants followed the histories of nesting birds on an old field in southeastern Michigan. The research was part of a broader survey of the old field community, begun in 1948 and continuing to the present, which has also considered plant succession (Evans 1975). In the summers of 1974 and 1975, I renewed study of the bird populations (Evans 1976). Here I report the responses of Field Sparrows (*Spizella pusilla*) to the increase in numbers and size of juniper bushes (*Juniperus communis*) (common nesting sites for the sparrows) between 1949 and 1975.

THE OLD FIELD

The study field is on the Edwin S. George Reserve, Livingston Co., Michigan. The field was cleared of oak-hickory woods about 1850. Farming was abandoned in 1925 or 1926, and the field has since been undisturbed, subjected neither to fire nor to extensive grazing by livestock. The field's forbs and shrubs have been heavily browsed, however, by a herd of 50–200 White-Tailed Deer (*Odocoileus virginianus*) confined to the reserve.

Oak-hickory woods surround and are slowly encroaching upon the open area of the field. The old fence lines suggest that when abandoned, the field covered 7.7 ha. F. C. Evans estimated the field's open area as 5.7 ha in 1957; the field then still extended beyond the boundaries of a 4.3-ha gridded area established in 1949. By 1974, the adjacent woodlots had invaded the grid boundaries in many places. Open field was further diminished by stands of young hickories (*Carya ovalis*), black oaks (*Quercus velutina*), and aspens (*Populus tremuloides*) that grew up around three large hickory trees left standing when the field was cleared. F. C. Evans and A. Bady estimated the 1974 open area as 4.3 ha, a reduction of 24% since 1957 and 56% since 1926.

In 1949–57, the field was essentially grassland, containing over 100 species of grasses and forbs up to 1 m high; two grasses, *Poa compressa* and *Aristida purpurascens*, were dominant. Species inventories (for 1953, 1964, and 1974) of the field's more abundant grasses and forbs, show that species composition remained stable; few species present in 1953 were absent in 1974, and few new species colonized the field in the interim (Evans 1975). Relative abundances of many individual species, however, changed markedly over the years. In general, the relative standing crop biomass of forbs increased at the expense of grasses. From 15% of the peak standing crop biomass in 1949, forbs increased to 53% in 1960 (Wiegert and Evans 1964) and probably to at least 77% in 1975 (Evans 1976).

Woody plants, including junipers, were relatively small and few in number in 1949–57. By 1974–75, the increase in numbers and size of woody plants made the field less open. Junipers, red cedars (*Juniperus virginiana*), and hawthorns (*Crataegus crus-galli*), which grew to heights of several meters, dotted the field in 1975. Cherry saplings (*Prunus serotina*), 60 cm or less in height, were scattered about, and blackberry (*Rubus flagellaris*) grew in dense patches up to 150 cm high.

Plant succession proceeded slowly on the field in the 50 years following abandonment. Despite growth of woody plants, the grassland character of the early 1950's still remained in 1975. The slow pace of succession probably resulted mainly from low soil fertility

and from browsing by deer. Evans and Dahl (1955), Wiegert and Evans (1964), and Evans (1975) described the vegetation and history of the field more fully.

METHODS

I observed Field Sparrows on the study area from late May until early August 1974, and from mid-April until early August 1975. Observations from 1949 to 1957 were generally made from April through early August. Many of the sparrows were color-banded in 1951–57 and in 1975.

The number of Field Sparrow pairs nesting on the field each year during May, June, and/or July was determined by observing color-banded adults and by knowing the timing and location of nests. Observation of marked Field Sparrows confirmed that (1) matings were monogamous and season-long, (2) individual pairs built and attended only one nest at a time, and (3) pairs always nested within territories with season-long stable boundaries. Similar methods (see Evans 1976) were used for other bird species nesting on the field (Table 1). Censuses were not made in 1957.

I found nests in 1974–75 by watching adults going to nests and by searching areas where I suspected active nests were hidden. In addition, I systematically searched the field three to four times each season. Similar methods were used in 1949–57. Because most, if not all, nests were discovered each year, I was able to accurately calculate the frequencies with which Field Sparrows selected nest sites of various kinds (see Results and Discussion).

Throughout the study, nests were checked daily (generally in the afternoon in 1974–75). To prevent leading predators to nests, I approached nests from different directions on successive days. Visits were as brief as possible. The influence of such visits on nest fate is difficult to assess, but the method of checking nests was the same in all cases, thereby justifying direct comparison of success of nests in different sites. Data for such comparison (Fig. 2) include fates of the field's nests, 1949–75, and fates of some nests built in 1975 in nearby fields of similar vegetation.

Nests usually either fledged young or were totally destroyed by predators. In most cases nest fate was clear. Most nests destroyed by predators were torn out of position and/or were empty when either the eggs were too young to hatch or the nestlings too young to leave. I often confirmed that nests were successful by seeing the parents feeding fledglings nearby. I determined the grid position of each nest when the nest became inactive.

In 1950, F. C. Evans censused the juniper bushes of the field by recording the height (to the nearest cm) and position of each bush within the grid. He and I made a similar census 8–12 July 1975, also measuring width at the bush's broadest point. Neither census included junipers less than 15 cm tall.

In 1974–75, I measured bush heights of junipers containing Field and Chipping sparrow (*Spizella passerina*) nests. I obtained heights of nest bushes for 1949–52 (Fig. 3) by matching their grid position with their 1950 heights. I allowed for growth in determining approximate bush height in years other than 1950.

I tested data statistically with the analysis of 2×2 contingency tables corrected for continuity (Snedecor and Cochran 1967:215–219).

TABLE 1. The estimated numbers of pairs of bird species found nesting on the field in May, June, and/or July from 1949 to 1956 and in 1974 and 1975.

Species[1]	FS	CS	VS	GS	RST	IB	SS
1949	7	8	8–9*	1	–	–	–
1950	7	9	7–8*	1	–	–	–
1951	4–5*	9–10*	7–8*	–	–	–	–
1952	7	9–10*	7–8*	1	–	–	–
1953	7	9	10	1	–	–	–
1954	8	6–7*	10	–	–	–	–
1955	7	4**	10–11*	–	–	–	–
1956	9	4**	10	–	–	–	–
1974	10	8	1–2*	–	2–3*	2–3*	–
1975	12	8	1–2*	–	2–3*	2–3*	1

[1] FS: Field Sparrow; CS: Chipping Sparrow; VS: Vesper Sparrow; GS: Grasshopper Sparrow; RST: Rufous-sided Towhee; IB: Indigo Bunting; SS: Song Sparrow.
* The data are insufficient to choose one estimate over the other.
** There were probably four pairs present, but the observers were uncertain.

RESULTS AND DISCUSSION

THE JUNIPER POPULATION

The number of junipers growing within the grid increased from 82 to 273, 333%, from 1950 to 1975. I grouped junipers into size classes on the basis of height, because bush diameter generally increased with bush height (see Fig. 3, left). Average size and range of sizes of junipers also increased over the years (Fig. 3).

THE BIRDS' ANNUAL BREEDING PATTERN

Male Field Sparrows returned to the field each spring in April, followed by females one or more weeks later. Nesting began in early May. Individual pairs nested, often several times, both after successful (i.e., young left the nest) and unsuccessful nestings. Nesting activity was most intense in May and June, diminishing in July, and ceasing altogether by mid-August.

NESTING SITE PREFERENCES

Female Field Sparrows built their nests in a variety of sites which I have grouped into four categories, including nests built (1) on the ground (i.e., with the bottom of the nest resting on the ground); (2) near the ground, supported 5–25 cm above the ground by herbaceous vegetation such as *Lespedeza hirta*, *Solidago rigida*, and blackberry; (3) 5–90 cm above the ground in crotches of small woody saplings such as cherries, oaks, hickories, and in two cases red cedars; and (4) 7–90 cm above the ground in the branches of junipers. All nests were built within 90 cm of the ground.

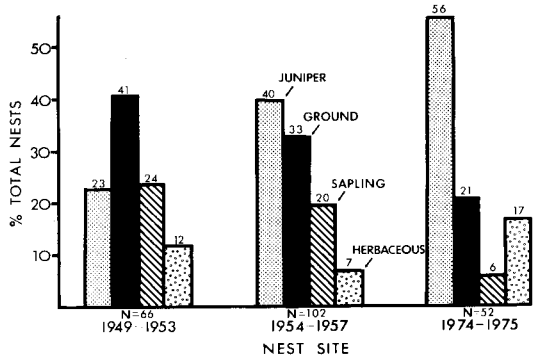

FIGURE 1. The relative frequencies with which Field Sparrows built nests in four types of nest sites (juniper = nests in junipers; ground = nests on the ground; sapling = nests in non-juniper woody saplings; herbaceous = nests near the ground in herbaceous vegetation) during the periods 1949–53, 1954–57, and 1974–75. For each time period, N = total number of nests built in all sites. Numbers above columns indicate percentage of N occurring in the given category.

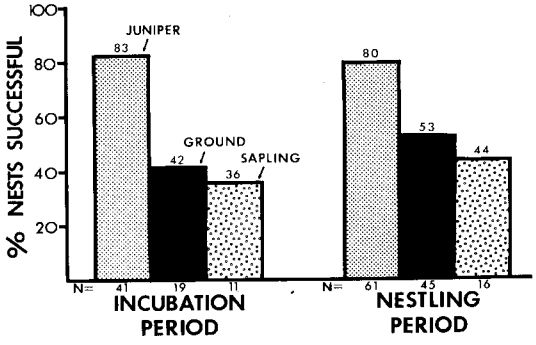

FIGURE 2. The success during the incubation and nestling periods, of nests built in different types of nest sites (terms as in Figure 1, except that ground nests and nests near ground in herbaceous vegetation are here combined and labeled "ground"; they had very similar success in both the incubation and nestling periods). Success is defined (1) for the incubation period as the percentage of nests found before incubation began (i.e., before the clutch was complete), in which at least one egg hatched; and (2) for the nestling period as the percentage of nests found before the nestling period (i.e., before any eggs hatched), from which at least one young left the nest.

Figure 1 shows the relative frequencies with which Field Sparrows used these four kinds of nest sites in three periods: 1949–53, 1954–57, and 1974–75. Occasionally in 1949–57, nests on the ground were not distinguished from those near the ground in herbaceous vegetation. I assumed that such nests were built in the same ratio as nests of known exact location in estimating the 1949–53 and 1954–57 frequencies of nests in these two kinds of sites. As the years passed, Field Sparrows built relatively fewer nests directly on the ground or in woody saplings (sapling vs. other nests: 49–57 vs. 74–75, $\chi^2 = 3.83$, $P = 0.05$), and relatively more nests in junipers (juniper vs. other nests: 49–53 vs. 54–57, $\chi^2 = 4.74$, $P < 0.05$; 54–57 vs. 74–75, $\chi^2 = 2.77$, $0.05 < P < 0.10$). When data for each month (May, June, July) are considered separately the same trends are apparent (Evans 1976). Thus, even in May, when Field Sparrows generally nest on the ground (Best 1974, Walkinshaw 1968), nests in junipers increased from 24% to 50% of all nests from 1949–53 to 1974–75, while nests on the ground declined from 76% to 50% (Evans 1976).

The proportion of nests placed in junipers increased 2.4 times from 1949–53 to 1974–75. While the tremendous increase in numbers of junipers over the years made these bushes more available as nest sites, even in 1974–75 junipers constituted a minor portion of available nest sites as much of the field was still covered by herbaceous vegetation and dotted with saplings. Thus, Field Sparrows preferred nesting in junipers (Fig. 1); the birds took advantage of the successional increase of junipers by switching from other nest sites to junipers as the latter became more available.

Additional 1974–75 data support these conclusions. In 1974–75, junipers were approximately four times more abundant in the northeastern half of the field than in the southwestern half. Field Sparrows nesting in the northeastern half in 1974–75 built 76% of 25 nests in junipers, whereas Field Sparrows nesting in the southwestern half built only 37% of 27 nests in junipers.

NESTING SUCCESS

The Field Sparrows' preference for junipers as nest sites is easily understood when one considers the relative success, during the incubation and nestling periods, of nests built in the various types of sites (Fig. 2). The percentages of eggs that hatched and of young that left the nest are nearly equal to the percentages of these nests that were successful in the incubation and nestling periods (Evans 1976). Nests built in junipers were considerably more successful in both the incubation and the nestling periods than nests built in other sites (successful vs. unsuccessful nests, juniper vs. other nest sites: incubation period, $\chi^2 = 12.19$, $P < 0.005$; nestling period, $\chi^2 = 10.49$, $P < 0.005$). Predation, the major cause of nest failure throughout the study, accounted for 90% of those nests which failed. Nests built in junipers were destroyed by

predators much less often than nests built elsewhere; predators destroyed only 12% and 15% of juniper nests vs. 57% and 49% of other nests during the incubation and the nestling periods, respectively (incubation period: $\chi^2 = 13.98$, $P < 0.005$; nestling period: $\chi^2 = 15.08$, $P < 0.005$). Thus, the increase in numbers of junipers over the years created more superior nest sites on the field for Field Sparrows.

Differences in nesting success between species nesting in different kinds of sites (e.g., hole- vs. open-nesters) due to differences in predation rates are well known (Ricklefs 1969). Robertson (1972) and Catchpole (1974) found differences within a species between nests in different habitats. The superiority of nest sites in junipers in the present study demonstrates substantial variability in suitability of actual (vs. potential) nest sites of a species in the same habitat. Best (1974) did not find differences in frequencies of desertion, cowbird parasitism, snake predation, and successful fledging for Field Sparrows nesting in grasses, forbs, and trees or shrubs (which did not include junipers). Mammalian predators destroyed nests built in forbs and trees or shrubs significantly more frequently than nests built in grasses, but these nests accounted for only 16% of all nests destroyed by predators. Longcore and Jones (1969) and Harmeson (1974) also considered variation in nesting success within a habitat with regard to nesting substrate, but their data are too few to be conclusive. Others have found that nesting success varies with nest height within a habitat (e.g., Holcomb and Twiest 1968, Holcomb 1969, Longcore and Jones 1969, Holcomb 1972). Austin (1974) found the success of Cactus Wren (*Campylorhynchus brunneicapillus*) nests in cacti dependent upon orientation of nest holes with respect to prevailing winds.

Why were juniper nests comparatively safe from predators? I did not see any predators visit nests, but they probably include Red Foxes (*Vulpes fulva*), raccoons (*Procyon lotor*), weasels (*Mustela* spp.), skunks (*Mephitis mephitis*), ground squirrels (*Spermophilus tridecemlineatus*), chipmunks (*Tamias striatus*), Blue Jays (*Cyanocitta cristata*), and blue racers (*Coluber constrictor*). While some of these predators (e.g., Blue Jays and Blue Racers) may seek out nests, others (e.g., foxes and ground squirrels) are often opportunistic, preying on nests that they happen to find. These opportunists may have found nests in junipers less often than nests built more in the open. Nest height may also be important, as nests in junipers were comparatively high above ground. Nests in saplings, however, were often as high or higher than those in junipers (Evans 1976). The latter were well concealed, and large juniper bushes in particular allowed parents to approach nests secretively. Finally, some predators (e.g., foxes) may have been deterred from seeking nests in junipers by the bushes' sharp needles.

Nests in junipers apparently were not better protected from Brown-headed Cowbird (*Molothrus ater*) parasitism than nests in other sites. All but two cases of cowbird parasitism occurred in 1954–56. Of the 26 nests in junipers in those years, 39% were parasitized vs. 28% of 46 nests in other sites. Parasitized nests were usually deserted before incubation began.

Each year the number of junipers available for nesting greatly exceeded the total number of nests built, yet many nests were not built in junipers. In 1974–75, for example, only 29 of 52 nests (56%) were built in junipers, although more than 200 bushes of preferred height (see below and Fig. 3) were available. Why did the Field Sparrows not make greater use of juniper bushes? If protection from predators is a major factor in nest site selection, then heavy predation pressure should be a strong influence in limiting nest placement to the most favorable sites. Junipers varied considerably in form and foliage density; certainly they were not all equally suitable as nest sites or superior to the best sites of other categories. Many of those junipers not selected by Field Sparrows may have had subtle features that lowered the probability of success they offered as nest sites. The spatial relation of a juniper to nearby vegetation could affect its suitability as a nest site; a nest in a juniper surrounded by other junipers may be better concealed from visually orienting predators than a nest in a juniper amidst open herbaceous cover. Territorial boundaries, superimposed on the uneven dispersion of junipers, restricted availability of junipers to some Field Sparrow pairs. In 1975, for example, two Field Sparrow territories contained, respectively, only 5 and 6 suitable junipers (i.e., > 50 cm high; Fig. 3). Finally, the sparrows' tendency to build some nests in sites other than junipers may be adaptive. Building nests in various places may foil predators systematically searching in likely spots, e.g., places similar to previously discovered nest sites. The probability of a predator's finding a nest would be spread more evenly over the territory.

The explanation may involve more than the birds' adjustments to the local environment. That Field Sparrows built so many nests in junipers in 1974–75 illustrates their responsiveness to gradual change in their surroundings. That they did not place more nests in junipers in 1974–75, however, may reflect the limits of such responsiveness. The Field Sparrows' nesting behavior should be adapted to the variety of conditions the birds encounter within the species' range. Such flexibility may limit the fine adjustment of any one population to its environment. Thus, predator pressure may vary with habitat, not always favoring junipers as nesting substrate. Furthermore, junipers are not available in many nesting areas within the Field Sparrows' breeding range; neither Best (1974) nor Walkinshaw (1968), for example, listed junipers in their descriptions of study areas and their extensive compilations of nesting substrates.

NUMBERS OF BREEDING PAIRS

Table 1 presents the estimated number of pairs of Field Sparrows and other birds nesting on the field in May, June, and/or July in each year of the study (except 1957). From 1949 to 1975, birds characteristic of grasslands—the Grasshopper Sparrow (*Ammodramus savannarum*) and the Vesper Sparrow (*Pooecetes gramineus*)—disappeared and were replaced by Rufous-sided Towhees (*Pipilo erythrophthalmus*), Indigo Buntings (*Passerina cyanea*), and Song Sparrows (*Melospiza melodia*), birds more characteristic of shrubland. This change in the avifauna attests to the considerable change in habitat. Presumably in response to this change, Field Sparrow numbers increased over the years; more pairs bred on the field in 1974 and 1975 than in any of the years 1949–56. At the same time, the open area of the field decreased. While territories may have extended into adjacent woods, the birds built all nests on non-overlapping sections of this open area. The 9 pairs in 1956 nested on at least 5.7 ha of open field; individual pairs had an average nesting area of 0.63 ha. In 1974, 10 pairs nested on 4.3 ha, each nesting area averaging 0.43 ha, whereas in 1975, 12 pairs nested on at most 4.3 ha, each nesting area averaging 0.36 ha. The nesting area per pair was thus 32% smaller in 1974 than in 1956 and 43% smaller in 1975, as the birds became more tightly packed together. These figures probably underestimate territory size, but fall near the lower end of the range in sizes, 0.3–2.4 ha, of reported Field Sparrow territories (Best 1974).

This closer packing suggests that the field gradually became more favorable for Field Sparrow nesting. Plant succession probably did not substantially change the field's favorability by affecting the birds' food supply. Evans (1964) concluded food was abundant and not limiting in 1949–57. Furthermore, Field Sparrows foraged much of the time in the stable oak-hickory woods surrounding the field (but see Best 1977, who documented a shift in foraging site from wooded to open areas as the summer progressed). As the number of junipers increased from year to year, more migrating males in the spring may have been attracted to the field. If more males remained to compete for territory, territory owners might be forced to yield more area each year as more competitors challenged them and successfully established territories (e.g., Kendeigh 1941, Nice 1941, Krebs 1971). Such a process may account, at least in part, for the increase in numbers and density of nesting pairs over the years.

The increase in numbers of junipers may have influenced Field Sparrow density not only by requiring, but also by allowing, territories to be smaller. Krebs (1971) suggested that a likely ultimate function of territoriality for Great Tits (*Parus major*) is to space out pairs as defense against nest predators. If a similar function holds for Field Sparrows, required territory space may diminish as the number of superior, potential nest sites increases within a territory. The probability that a predator may discover the nest therefore decreases.

COMPETITION WITH CHIPPING SPARROWS

Field Sparrows shared the field with their congeners, the Chipping Sparrows (Table 1). Chipping Sparrows nested commonly in red cedars (33%), but most frequently in junipers (56%; Evans 1976). In general, the two sparrow species coexisted peacefully, feeding on the same foods (Evans 1964, Allaire and Fisher 1975) and nesting on overlapping territories. In 1974–75, however, I observed pairs of both species nesting in junipers aggressively drive off members of either species that approached the pair's nest bush. As a result, only one pair of birds at a time nested in a juniper, except once in 1974 when a Field Sparrow nest was initiated in a large juniper (5 m in diameter) as young Chipping Sparrows were leaving their nest on the opposite side of the bush.

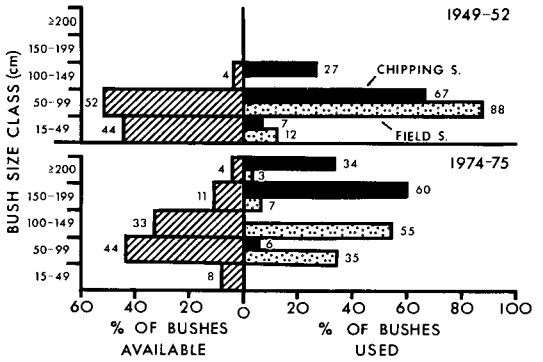

FIGURE 3. The approximate relative availabilities of variously sized junipers in 1949–52 and 1974–75 (i.e., the juniper census results for 1950 and 1975), compared to the relative use of these bushes by Field and Chipping sparrows. Number of bushes available = 82 (1949–52) and 273 (1974–75). Number of bushes used: Field Sparrow = 8 (1949–52), 29 (1974–75); Chipping Sparrow = 15 (1949–52), 17 (1974–75).

Figure 3 compares the relative availability of variously sized juniper bushes to their relative use as nest bushes by Field and Chipping sparrows in 1949–52 and 1974–75. In 1949–52 the tallest junipers did not exceed 150 cm. The two sparrows built most nests in bushes 50–99 cm high and overlapped considerably in bush height chosen. In 1974–75, however, such overlap was much less as the two species differed in response to the greater range of bush sizes now available. Chipping Sparrows built 90% of their nests in bushes 150 cm or more in height while Field Sparrows built 94% of their nests in bushes less than 150 cm tall. The divergence in nest site selection seems beneficial to both species by reducing direct competition between them. The increase in size and number of junipers apparently allowed a partitioning of these nesting resources in 1974–75 not possible 25 years earlier.

Partitioning of nest sites and the consequent reduction in competition possibly contributed to the increase in Field Sparrow density by magnifying the increase in superior nest sites available. Furthermore, the quality of junipers less than 150 cm high available to Field Sparrows may have improved as the Chipping Sparrows shifted to taller bushes. From an analysis of perching site preferences in laboratory and field, Hebrard (1974) suggested that Chipping Sparrows are ecologically dominant to Field Sparrows. If so, Chipping Sparrows may have preempted the most suitable junipers for nesting in 1949–52.

SUMMARY

This study considers responses of a Field Sparrow population over 26 years (1949–75) to the successional increase in numbers and size of juniper bushes on an old field in southeastern Michigan. The sparrows often used junipers as nest sites; nests in junipers were significantly more successful than other nests in both the incubation and nestling periods. Predators, responsible for 90% of all nest failures during these periods, destroyed only 12–15% of nests in junipers vs. 49–57% of other nests. A 333% increase in numbers of junipers from 1950 to 1975 created more of these superior nest sites. Field Sparrows responded by switching from other sites to junipers; the percentage of nests built in junipers increased from 23% in 1949–53 to 56% in 1974–75. While encroaching woodland shrunk the nesting area, the number of Field Sparrow pairs nesting on the field increased, apparently in response to the growing suitability of the field.

Juniper growth further affected Field Sparrows in their relations with Chipping Sparrows. The two species competed for nest sites in junipers in 1949–52. The subsequent increase in numbers and size of junipers, however, permitted divergence in the size of bushes chosen. In 1974–75, Chipping Sparrows nested mostly in bushes 150 cm or more in height, while Field Sparrows nested mostly in bushes less than 150 cm.

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