

TERRITORY QUALITY AND MATING SUCCESS IN THE FIELD SPARROW (*SPIZELLA PUSILLA*)

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Territoriality in birds has stimulated considerable inquiry since the classical work of Howard (1920). Despite the profusion of literature on territorial behavior, our understanding of the factors involved in territory selection and of the relationship between territory quality and mating success is still in its infancy. Attempts to quantify territory features and evaluate their influence on differential mating and breeding success have generally concerned polygynous species. Pairing success has been correlated with two territory characteristics critical to reproductive success: the availability of suitable nesting substrates (Willson 1966, Zimmerman 1971, Martin 1971, Holm 1973) and the abundance of nestling food resources (Verner and Engelsen 1970, Willson 1966). These factors are equally important in monogamous species and should influence territory selection and pair formation.

The purpose of the present study was to investigate territoriality in a monogamous species, the Field Sparrow (*Spizella pusilla*), with the aim of elucidating factors influencing territory quality and mating success. The spatial heterogeneity of the study area vegetation resulted in a diversity of habitats for territory occupation. This provided an appropriate setting in which to evaluate the mechanisms of territory selection and maintenance, factors critical in pair formation and mate fidelity, and the potential of each territory for successful breeding.

STUDY AREA

The 23.6-ha study area is located in Allerton Park, near Monticello, Piatt County, Illinois. The topography is relatively flat with a maximum of 8 m difference in relief. An infrequently used dirt road passes through the area.

The periphery of the area studied was occupied by approximately 8.5 ha of shrub-woodland (fig. 1). Predominant overstory species (listed in order of decreasing abundance) included: shingle oak (*Quercus imbricaria*), wild black cherry (*Prunus serotina*), and slippery elm (*Ulmus rubra*). These trees attained heights up to 15 m. Poison-ivy (*Rhus radicans*), Virginia creeper (*Parthenocissus quinquefolia*), black raspberry (*Rubus occidentalis*), smooth sumac (*Rhus glabra*), Japanese

rose (*Rosa multiflora*), winter grape (*Vitis cinerea*), and hawthorn (*Crataegus mollis*) were the most prevalent woody, understory species. Common forbs included: tall goldenrod (*Solidago altissima*), parsnip (*Pastinaca sativa*), carrot (*Daucus carota*), early goldenrod (*S. juncea*), white avens (*Geum canadense*), giant ragweed (*Ambrosia trifida*), aster (*Aster pilosus*), and field goldenrod (*S. nemoralis*). Kentucky blue grass (*Poa pratensis*) was the only grass species of notable abundance.

The central portion of the study area was comprised of 9.0 ha of shrub-grassland and 6.1 ha of grassland (fig. 1). Formerly this region was forested, but in 1955 the area was cleared (by applying 2-4-5-T spray and burning) and seeded to tall-grass species. Since that time portions have been periodically burned, disked, and re-seeded, these activities being confined largely to the grassland region in the past 6 years.

Trees and shrubs, all under 8 m tall, were scattered throughout the shrub-grassland region. Predominant woody species included: smooth sumac, black raspberry, poison-ivy, and wild black cherry. Tall goldenrod, carrot, early goldenrod, field goldenrod, parsnip, yarrow (*Achillea millefolium*), aster, horsetail milkweed (*Asclepias verticillata*), wild lettuce (*Lactuca canadensis*), and ironweed (*Vernonia missurica*) were the most prevalent forbs. Predominant grasses were Kentucky blue grass, Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon furcatus*), panic grasses (*Panicum* spp.), and timothy (*Phleum pratense*).

With the exception of some black raspberry, the grassland region was nearly devoid of woody vegetation. Forbs commonly encountered included tall goldenrod, early goldenrod, field goldenrod, and yarrow. The majority of the area was covered by grasses, with Indian grass, big bluestem, Kentucky blue grass, and panic grasses predominating.

METHODS

During the spring and summer of 1971, the study area was visited on 72 days during the interval 26 April to 23 August, with more frequent visits following May. In 1972, 133 visits were made to the area from 9 April to 15 September.

The study area was gridded throughout at 25-m intervals. Vegetation was sampled 5 m from each grid marker in the four cardinal directions using a 1/16 m² circular plot. The canopy coverage of each plant species encountered within the plot was categorized as <5%, 25%, 50%, 75%, or >95%. Plant heights were classified 0–2 m, 2–4 m, or >4 m. Frequency of occurrence also was determined for each species. The vegetation composition of each territory was determined by considering all sample points falling within its boundaries. Territories contained an average of 51 (range 20–107) sample points each.

Each adult and nestling Field Sparrow was marked for individual identification by attaching a U.S. Fish and Wildlife Service band and two colored plastic bands to the legs. In addition, the tail of adults was marked with airplane paint in colors corresponding to the plastic leg bands. At the time of banding, adults were weighed and the tarsus measured. Adult females were captured by flushing them from the nest into a nearby mist net. Males were lured into a mist net placed within their territory using playback recordings of the male song. Additional adults were captured by judiciously placing mist nets at various locations within the territories. The banding of adults continued throughout most of the summer in 1971, but in 1972 birds were banded soon after their first appearance. Nestlings were banded when 5 days old.

All territories were checked during the early morning of each visit to the study area. The location, movements and noteworthy behavior of all observed adults and juveniles were recorded on a grid map, and the status of active nests noted. Nestling weight and tarsal length were recorded daily.

Territory boundaries were delineated by constructing a composite map of the observations of each male and his mate(s). Because aggressive encounters were limited (see also Crooks 1948), I considered the territory to be the total area used by the male, whether or not I actually saw it being defended. Where areas of utilization overlapped between adjacent territories, the following observations were given precedence in the order mentioned to establish territory boundaries: aggressive territorial encounters, the male alone, the pair together, the female alone, and the parents with fledglings. Regions of overlap were never extensive. Territory boundaries were less accurately defined in 1971 due to delay in banding some birds. A compensating polar planimeter was used to determine territory size.

Plant nomenclature follows Jones (1963). Statistical significance was set at $P \leq 0.05$ unless specified otherwise.

RESULTS AND DISCUSSION

GENERAL INFORMATION

The Field Sparrow breeds throughout the summer. Territory establishment begins soon after arrival from the wintering grounds (Crooks 1948, Walkinshaw 1968). The first males to arrive on my study area were unobserved although singing was recorded as early as 2 April in 1972. The last territory was occupied on 13 May (excluding replacements on previously established territories). Females first appeared on 12 April in 1972. Walkinshaw (1968) reported that females generally arrived in Michigan 3 weeks after the first appearance of males. The latest date a male remained on his territory on my study area was 15

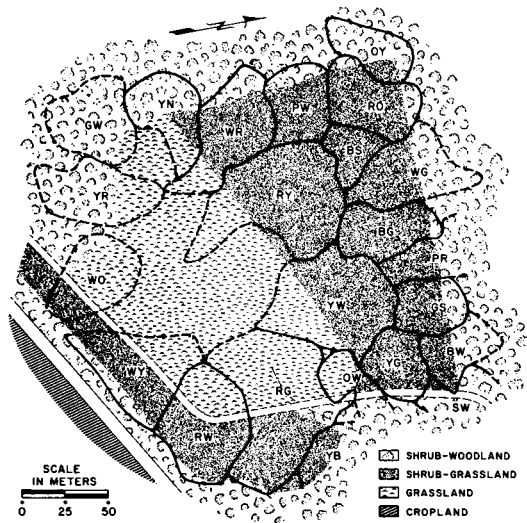


FIGURE 1. Territories present on the study area in 1972. Dashed lines indicate regions where territory boundaries were less certain.

September although I did not hear singing after 1 September. Females were last seen 9 September.

The length of time males occupied their territories ranged from 7 days for a male unsuccessful in mating before being replaced, to at least 153 days for a male forming a pair bond lasting 126 days. The mean territory occupancy for males holding permanent territories (i.e., territory occupancy greater than 1 week) was 111 days in 1972. All these males succeeded in mating although the duration of the pair bond and the number of mates per male were quite variable. Pair bonds in which at least egg-laying was attempted by the female lasted from 5 days to at least 129 days, with an average duration of 60 days. Field Sparrows mate monogamously although males will often form subsequent pair bonds within the same breeding season if deserted by their mates. No male abandoned his territory while the female persisted on the area.

LOCATION AND SIZE OF TERRITORIES

Twenty-five territories were established on the study area initially in 1971 and 23 in 1972. Figure 1 presents the locations of the 1972 territories. The shrub-grassland was the preferred habitat. Territories on this area were contiguous both years, and all available space was occupied. Stewart and Robbins (1958), Burleigh (1958), Sutton (1960), and Walkinshaw (1968) have observed also that old fields with scattered woody vegetation provide the most suitable habitat for the species. Territories on my study area extended into the grassland but were never confined to this vegetation. Twice, I saw transient males singing within the grassland, but they never established permanent territories. The extension of territories into the shrub-woodland also was limited, generally occurring where the forest canopy was more open.

Territory sizes in 1972 ranged from 0.31 to approximately 1.62 ha and averaged 0.76 ha. This was before any territorial shifting had occurred. Others have reported territories as small as 0.30 ha (= 0.75 acre, Crooks and Hendrickson 1953) and up to about 2.4 ha (= 6 acres, Walkinshaw 1968). The largest occupied territory measured approximately 3.41 ha and resulted when RW incorporated the abandoned territories of WY and WO into his original territory (fig. 1).

Territories extending into the grassland were significantly larger than those not associated with grassland, averaging 1.02 and 0.53 ha, respectively ($t = 3.78$, $df = 17$). Generally grassland territories were noncontiguous on the grassland boundary, making uncontested territory expansion possible. Wiens (1973) reported that "centrally located" Savannah Sparrow (*Passerculus sandwichensis*) territories were significantly smaller than "peripheral" territories. An inverse relationship between territory size and food abundance has been reported in the Winter Wren (*Troglodytes troglodytes*; Cody and Cody 1972) and the Ovenbird (*Seiurus aurocapillus*; Stenger 1958). This may further explain the larger territory size associated with grassland, as foraging was never observed in stands of tall grass, and its potential as a food resource is probably insignificant.

CHANGES IN TERRITORIAL CONFIGURATION

Changes in territorial configuration are common during initial territory establishment, but only those instances following the maintenance of permanent territories will be discussed below.

The eventual territory of RO in 1972 was originally occupied by GO, who had been present on the territory the year before (fig. 2). GO formed a pair bond in 1972 with the same female with whom he had mated in 1971. RO arrived late in 1972 (27 April) and spent his first 5 days moving around and even singing within GO's territory without any apparent aggressive interaction. WG and BS already had extended their territories to include almost all of the area formerly occupied by RO in 1971. Following the 5-day period, I never saw GO again. RO persisted on the territory of GO and formed a pair bond for the remainder of the season with the female formerly mated to GO. Walkinshaw (1945) reported a male returning to his territory for the sixth consecutive year, only to disappear after being "overcome" by aggressive neighboring males. Two other incidents of

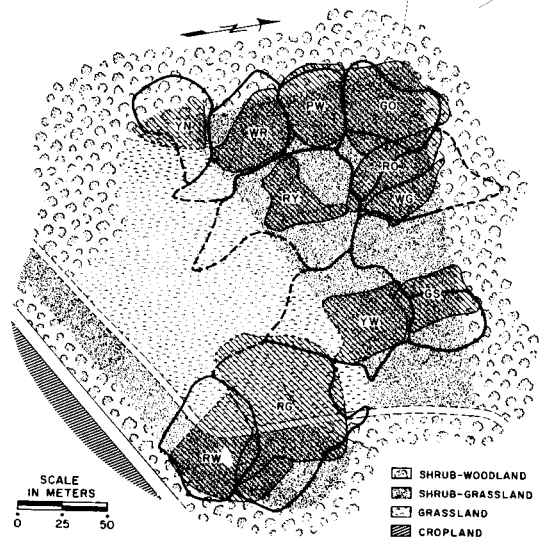


FIGURE 2. The location of "returning male" territories in 1971 and 1972. Cross-hatched areas outlined by light lines delimit the 1971 territories, and heavy lines delimit the 1972 territories.

territory replacement/displacement occurred, each within a single day. I witnessed aggressive interactions in only one case although they may have occurred in both. A male occupied the eventual territory of WO for 7 days before being replaced by the latter on 17 May. YR was replaced by another male on 21 June. In all three incidents, the territories of the replacing males encompassed approximately the same areas as those of the former occupants.

Territorial shifting occurred several times, all initiated by territory abandonment. SW abandoned his territory on 2 June, and the southern portion of it was immediately occupied by YG (fig. 1). By 8 June, however, the area had been included completely within the territory of BW, apparently a result of displacement of YG. YG also originally had occupied the eventual territory of BW during early April but was unsuccessful in retaining it after BW arrived. YG deserted his own territory on 19 June, and OW soon moved into the area, abandoning the grassland portion of his original territory. WY left his territory on 20 June and WO on 24 June. Within a short time RW had incorporated both of these territories into his own. In 1971 RW also enlarged his territory to include vacated adjacent territories. PW abandoned his territory 17 August, and it was immediately occupied by RY who deserted his own territory. RY remained on the newly acquired territory until 28 August.

INDIVIDUALS RETURNING A SECOND YEAR TO BREED—SITE TENACITY

Eleven of the 25 males present on the study area in 1971 returned to breed the following year (44%). Walkinshaw (1968) recorded a return rate averaging around 50%. All returning males established territories on the same areas they had used the year before (fig. 2; see also Walkinshaw 1968). Most territory boundaries shared by returning males on my study area remained relatively stable from one year to the next. Nero (1956) made a similar observation of the Redwinged Blackbird (*Agelaius phoeniceus*). RO was the only notable exception owing, undoubtedly, to his late arrival (see above).

The territories of all males returning in 1972 were either equal to or, more often, larger than they had been the preceding year. The mean territory size of returning males was 0.60 ha in 1971 and 0.95 in 1972. According to Southern and Morley, "well established" male Marsh Tits (*Parus palustris*) tended to enlarge their territories, and Nero (1956) found that male Redwinged Blackbirds who had previously held small territories usually attempted to increase their holdings, often with success. Walkinshaw (1945) reported that the territory of one returning male Field Sparrow increased in size the first two years and then remained stable for the next three. As the returning males had probably spent differing numbers of seasons on my study area, this may explain partially why some territories remained about the same size and others were enlarged considerably. After initial enlargements during the first years of territory occupancy, males may develop fixed limits to the size of territory they will actively defend. Territory expansion, however, also is dependent upon the presence or absence of adjacent territory owners. Territory expansion from one year to the next on my study area occurred primarily into areas occupied by males the previous year who failed to return in 1972. In 1971 males held territories between YN and WR, WR and RY, RY and PW, RY and YW (two territories), and to the north of WC, but did not return in 1972 resulting in expansion of the territories of WR, RY, YW, and WC, respectively.

Other minor yearly shifts in territory boundaries may have resulted from returning males selecting more desirable habitat adjacent to their former territory, competitive interaction during territory establishment, or the chronology of territory occupancy where earlier arriving males are more successful in defending specific areas. Returning males did not

arrive on my study area significantly earlier than those appearing for the first time (see below: Differences Between Returning Males and First-year Males), although Walkinshaw (1968) found that the "older males" were usually the first to arrive in the spring. Nice (1937) concluded that chronology of territory occupancy was insignificant in the Song Sparrow (*Melospiza melodia*) because returning males arriving late were usually successful in reclaiming their former territories from first-year males that had settled on them. Because all returning males on my study area (with the exception of RO) maintained the majority of their previously owned territory, prior occupancy must take precedence over other factors influencing the distribution of territories. RO may have succeeded in displacing WG and BS from at least part of his former territory had he not acquired the territory of GO.

The return rate of females is much lower than that of males (Walkinshaw 1968). Only three females nesting on the area in 1971 returned the following year to breed. These were the 1972 mates of RO, BG and YW (second mate). All three returned to the territory occupying the same area they had selected the previous year. The mate of RO originally formed a pair bond with GO, but when GO was replaced by RO, she persisted on the territory with RO. The mate of BG returned to the same territory in 1972 although she had been mated to a different male in 1971. The returning mate of YW was not his first mate of the season either year. I first saw this female in 1972 on 17 May with the male displaced that same day from the eventual territory of WO. I did not see her again until 12 June, when she formed a pair bond with YW. I did not know the whereabouts and activities of this female during the interim but she had several opportunities to mate with other unmated males on the study area before 12 June. The territory where I first sighted her was occupied by an unmated male at the time. This suggests a strong tendency for females to return to the same area selected the previous year regardless of the male occupying the territory and even at the cost of passing up opportunities to mate with males on other territories. Kendeigh (1941) reported cases of female House Wrens (*Troglodytes aedon*) returning to their former nesting area in preference to their former mate on an adjacent territory.

Some returning females probably failed to breed on the study area because the present owners of the territories they had occupied the

TABLE 1. Events immediately preceding mate desertion by females during the 1972 breeding season.

Event	Number of desertions
Snake predation	15
During egg-laying	3
During incubation	9
On nestlings	3
Mammalian predation during incubation	1
Cowbird parasitism	3
During egg-laying	2
During incubation	1
In the process of nest construction	1
Nest completed but no eggs laid	2
Egg-laying	1

previous year were already mated. Walkinshaw (1968) found that a male Field Sparrow would generally accept the first female arriving on his territory and considered this a causal factor in the smaller return percentage for females. Unlike my study, however, he reported that late-arriving females would often settle on a nearby territory if their former mate was already paired (see also Nice 1937).

The three returning females were among six who persisted until the end of the 1971 breeding season (after 15 August) and were among eight present after that date in 1972. All remained mated on the study area in 1972 until the last nest of the season had been constructed (21 August). This indicates that fidelity to the same territory from one year to the next is related to pair bond duration and nesting persistence. Apparently, factors inducing females to desert before the end of the breeding season also interfere with their returning to the same area the subsequent season. Martin (1974) reported that female Bobolinks (*Dolichonyx oryzivorus*) who were unsuccessful in nesting one year strongly tended not to return the following spring.

Initial territory selection by males and females depends largely upon availability. Younger males breeding for the first time occupy "leftover" spots or squeeze between already established territories (Walkinshaw 1968). Once the selection has been made, both sexes are predisposed to occupy the same area when returning for subsequent breeding seasons. Territory boundaries may change from one year to the next, but the site attachment persists. This suggests that the initial territory occupancy, which may be limited to suboptimal habitat, takes precedence over the selection of other more optimal areas vacated during subsequent seasons. This was exemplified by males who returned to territories associated with grassland, vegetation

that became unsuitable for breeding later in the season (see below: Temporal Changes in Territory Quality). Krebs (1971) found that when territories were vacated (through a removal experiment) in an optimal habitat, yearling male Great Tits (*Parus major*) were more likely to move from suboptimal to optimal habitat than were adult males that had once bred in the suboptimal area. The territory expansion characteristic of returning males may partially compensate for lower quality in the territory initially selected (see also Martin 1971). Returning yearly to the same area may also afford the advantage of greater familiarity with a specific site, enabling better exploitation of nesting and food resources. A strong tendency for males, and to a lesser degree females, to return to the same site used for breeding the previous year is common in other passerines (Nice 1937, 1941, Kendeigh 1941, Beer and Tibbitts 1950, Morton et al. 1972, Martin 1974).

Site tenacity depends upon an interplay between the differential attractiveness of territories and the relative advantage of relocating in a familiar area. The Field Sparrow may represent one extreme in a continuum of site attachment, where such species as the Bobolink and Henslow's Sparrow (*Ammodramus henslowii*) illustrate a tendency in the opposite direction. Field Sparrow territories on my study area apparently did not differ sufficiently in quality to offset the advantages gained by familiarity. The mating status of male Bobolinks may be improved by movement to different regions, or by enlargement or shifting of the territory to incorporate additional more suitable habitat not occupied the year before (Martin 1971). The Henslow's Sparrow apparently has limited tenacity for a specific site as territory shifting by males is common even within a single breeding season (Robins 1971).

DESERTION AND REMATING

Both years several females deserted their mates prior to the end of the breeding season. A variety of events immediately preceded mate abandonment (table 1). Predation by snakes during the nesting cycle was the paramount factor inducing desertion although other nesting disturbances also contributed. In the desertions during nest construction and egg-laying where no cause was apparent, females expended time and energy only to abandon their efforts later. Females who deserted their mates before the end of the breeding season were never seen again on the study area.

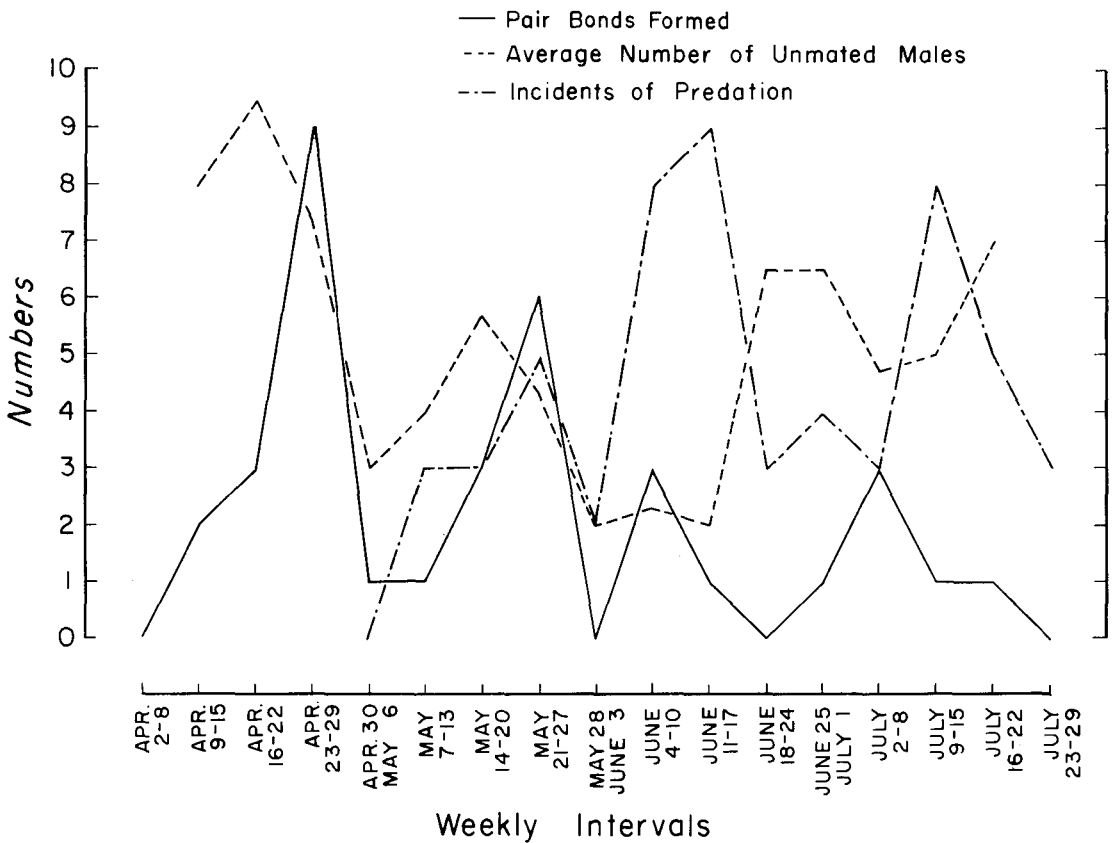


FIGURE 3. The relationship between frequency of pair formation, number of unmated males, and incidents of predation.

Either they did not attempt to remate for the remainder of the season or, more likely, they moved a considerable distance (off the study area) before forming another pair bond (see also Nice 1937).

Many males were successful in remating following desertion (one male mated five different times during the 1972 season). I do not know the source of replacement females because I never saw surplus, unmated individuals on the study area. Either they came from the surrounding shrub-woodland or were transients moving through the area. Walkinshaw (1945) also was uncertain of the origin of replacement females although he did report one female leaving her mate to form a pair bond with the owner of an adjacent territory.

Pair bonding apparently was related to the abundance of unmated males. The number of pair bonds formed oscillated throughout the entire season even after the initial mating in April (fig. 3). Unmated males were present on the study area during the entire season, so unavailability of mateless males was not responsible for the absence of pair bonding. The number of unmated males, however, also

oscillated throughout the season tending to peak about one week before the peaks in pair formation. Field Sparrows are notably more vocal when unmated, and increases in the number of singing males may have made the area more attractive to unmated females. May (1949) suggested that a group of adjacent territories of the Willow Warbler (*Phylloscopus trochilus*) has more chance of attracting females than an isolated territory because of the greater volume of song.

Frequency of predation, however, also oscillated throughout the season and may have influenced pair bonding. Nest predation preceded most mate desertions by females. If these females were a major source of mates for other unmated males, one might expect the availability of unmated females to correlate with incidence of predation. Peaks in predation did, in fact, correspond with peaks in pairing on the study area. If the pattern of predation were similar off the plot at the source of replacement females, then unmated females could be expected to become available roughly in proportion to the predation rate. Perhaps the frequency of pair forma-

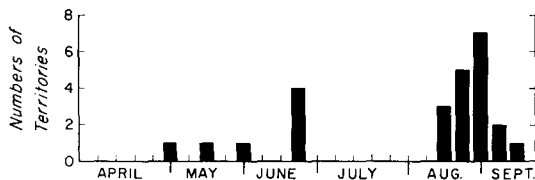


FIGURE 4. Dates of territory desertion during the 1972 breeding season, taken at weekly intervals. Period covered from 2 April to 16 September.

tion involves an interaction of both male vocalization and predation.

The availability of mateless females apparently varies considerably from one year to the next. Six males acquired new mates after 29 June in 1972 although this was the last date a pair bond was formed the preceding year. Mating in 1972 extended until 26 July. Unmated males were present on the study area both years after 26 July.

TERRITORY ABANDONMENT

Males deserted their territories only occasionally early in the breeding season in 1972, but during the third week in June, four of the 21 active territories were abandoned (fig. 4). The reason for this sudden increase in territory abandonment was undetermined. All four territories were along a dirt road (fig. 1) infrequently used by automobiles but commonly used by people afoot. This may have induced the males to depart early from their territories. Following this week of heavy desertion, no male left his territory until mid-August. The absence of territory desertion throughout July and early August suggests that if males persist on their territories until the end of June, they will generally remain until the end of the breeding season.

FACTORS RELATED TO TERRITORY QUALITY AND MATING SUCCESS

To determine those factors potentially influencing territory quality and mating success, I conducted a correlational analysis between the following variables measured during the 1972 breeding season: male weight, male tarsal length, territory size (prior to any territory abandonment and subsequent shifting), chronology of territory occupancy, duration of territory occupancy, number of matings per male (excluding temporary pair bonds where nesting was not attempted), number of days from 1 May to 26 July when the male was unmated, proportion of the territory occupancy during this interval when

the male was unmated, number of days required to form a pair bond (after 12 April), pair bond duration (where nesting was attempted), number of nesting attempts per mate (at least to the egg-laying stage), nestling growth rate (weight gain), area covered by all plant species on each territory, frequency of occurrence of all plant species on each territory, and frequency of occurrence of plants 2 to 4 m tall, above 2 m and above 4 m on each territory. Nesting success was not used as a measure of territory quality because nest mortality was extremely high and rather uniform over the entire study area (Best 1978).

Several of the above variables require clarification. Because the exact date of territory occupancy was undetermined for several males (44%), I used the first date I observed them when considering the chronology of territory occupancy. The extent of matelessness was measured over the interval 1 May to 26 July because by 1 May almost all territories were occupied, and the surge of newly arriving females had subsided, and on 26 July the last pair bond was formed. I considered only males occupying territories during this entire interval. The proportion of the territory occupancy during this interval spent unmated was used to compensate for territories established after 1 May or abandoned before 26 July. This category included all territories. The time required to form a pair bond was determined after 12 April because on this date females first arrived on the study area. Average values were used for males forming multiple pair bonds during the season. Temporary pair bonds (no nesting attempt) were included in the unmated time because these represented unsuccessful attempts at mating. The average pair bond duration and the average number of nesting attempts per mate also were used for males forming multiple pair bonds. The overall growth rate (K) of each nestling was determined following a method presented by Ricklefs (1967, Best 1977). The mean growth rate for each brood was used in the analysis. Because growth rates differed significantly between early and late summer and between broods of three and four young (Best 1977), I classified growth data according to summer period and brood size. Late summer broods of four were excluded because of small sample size. The area covered by each plant species was determined by multiplying the canopy cover percentage of that species over the territory times the territory area. The frequency of occurrence estimated the dispersion of each plant species,

while the area covered was a measure of abundance. The frequency of occurrence of plant species over 2 or 4 m tall was used as an index of the vertical stratification of vegetation and, roughly, of the extent of woody vegetation.

Only relationships where the correlation coefficients were highly significant ($P \leq 0.01$) are discussed in the text, unless noted otherwise. Variability in those factors considered in the correlational analysis is presented in table 2. Male weight and tarsal length, chronology of territory occupancy, and nestling growth rate all showed minimal variation (coefficients of variation, CV, < 10). This probably largely accounts for the relative unimportance of these variables in the correlational analysis. The total number of days unmated, the area covered by several plant species, and the frequency of occurrence of plant species over 4 m tall were most variable among territories (CVs > 100).

Male size. Only one significant relationship existed between male size (either weight or tarsal length) and the other variables. Weight increased significantly with the area covered by rough-fruited cinquefoil (*Potentilla recta*; $r = .689$, $n = 19$), possibly indicating the importance of this species as a food (directly or indirectly) early in the breeding season although its frequency of occurrence was low. Differential male size apparently plays no significant role in the social structure of the Field Sparrow. Martin (1971) also considered characteristics of individual male Bobolinks to be of minor importance in attracting females as compared with qualities of the territories.

Territory size. Males with larger territories formed significantly more pair bonds during the breeding season than those with smaller territories ($r = .589$, $n = 21$) although there was no significant relationship between territory size and either pair bond duration or time required to mate; both related to the frequency of mating. A positive relationship between territory size and mating success has been reported in other passerine species (Stewart 1953, Stenger and Falls 1959, Tompa 1962, Zimmerman 1966, Verner and Engelsen 1970, Martin 1971). Crooks (1948) found that male Field Sparrows remaining mated during a greater portion of the breeding season tended to have larger territories. I did not find such a relationship in my study.

Territory size also was correlated positively with the area covered by the following plant species: Indian grass, tall goldenrod, big

TABLE 2. Mean, standard deviation, and coefficient of variation of variables related to territory quality and mating success.

Variable	N	\bar{x}	SD	CV
Male weight (g)	22	12.96	.65	5
Male tarsal length (cm)	21	2.08	.05	2
Territory size (ha)	21	.76	.36	47
Chronology of territory				
occupancy (Julian date)	16	111	10	9
Territory occupancy (days)	23	111	37	33
Matings per male	24	1.7	1.0	59
Period unmated (days)	16	12	13	108
Proportion of territory				
occupancy unmated (%)	23	23	21	91
Time to mate (days)	22	9	8	89
Pair bond duration (days)	23	60	42	70
Nesting attempts	20	3.4	2.5	74
Nestling growth rate				
Early summer, B/3 ¹	3	.524	.024	5
Early summer, B/4	6	.593	.034	6
Late summer, B/3	4	.572	.040	7
Plant species (A.C.) ² (ha)	21			
<i>Achillea millefolium</i>		.016	.016	100
<i>Andropogon furcatus</i>		.075	.084	112
<i>Carex</i> spp.		.004	.007	175
<i>Lactuca canadensis</i>		.006	.006	100
<i>Poa pratensis</i>		.138	.092	67
<i>Potentilla recta</i>		.006	.005	83
<i>Prunus serotina</i>		.024	.020	83
<i>Prunus</i> spp.		.008	.011	138
<i>Rhus glabra</i>		.066	.049	74
<i>Solidago altissima</i>		.146	.087	60
<i>Solidago juncea</i>		.051	.032	63
<i>Sorghastrum nutans</i>		.091	.104	114
<i>Vernonia missurica</i>		.012	.018	150
Plant species (F.O.) ² (%)	21			
<i>Andropogon furcatus</i>		19.8	15.8	80
<i>Sorghastrum nutans</i>		24.4	18.1	74
Plant height (F.O.) (%)	21			
2-4 m		6.8	4.2	62
Over 2 m		15.1	11.3	75
Over 4 m		9.4	9.5	101

¹ B/3 and B/4 refer to brood size.

² Only plant species significantly correlated ($P \leq 0.01$) with another variable are included. A.C. = area covered, F.O. = frequency of occurrence.

bluestem, sedges (*Carex* spp.), Kentucky blue grass, *Prunus* spp. (other than wild black cherry), ironweed, early goldenrod, yarrow, wild lettuce, wild black cherry, and smooth sumac ($r = .895-.562$, $n = 21$). Coverage by all other species was apparently independent of territory size. The frequency of occurrence of Indian grass and big bluestem also increased significantly with territory size ($r = .620$, $.590$; $n = 21$). The area covered by all other plant species mentioned was positively correlated ($P \leq 0.05$) with the area covered by Indian grass and, in several cases, with big bluestem, indicating that the significance of these species may result from their association with Indian grass and big bluestem. Indian grass and big bluestem were the only two species decidedly more abundant in the grass-

land than in the remainder of the study area, suggesting that territories associated with the grassland were larger (see above: Location and Size of Territories). The coverage of some plant species, however, may have increased proportional to the area included, independent of factors influencing territory size.

Chronology and duration of territory occupancy. The sequence of territory occupancy apparently was independent of all variables considered. Much of this independence resulted from males occupying approximately the same territory used the preceding year, regardless of their arrival date. Also, the exact arrival dates were unknown for many of the males.

The duration of territory occupancy was positively correlated with pair bond duration ($r = .647$, $n = 23$) and the number of nesting attempts per female ($r = .637$, $n = 20$), indicating that males whose mates are less prone to desert remain on their territories longer. All males who abandoned territories before the end of the breeding season were unmated at the time.

Frequency of mating. The frequency of pair formation was negatively correlated with pair bond duration ($r = -.538$, $n = 23$), verifying that males with more lasting pair bonds mate less frequently. A positive relationship also existed between mating frequency and the area covered by: smooth sumac, tall goldenrod, ironweed, Indian grass, and *Prunus* spp. ($r = .791-.571$, $n = 21$). Except for ironweed, all of these species were used for nest sites although they probably served other functions as well. Coverage by these species and the frequency of mating also were correlated significantly with territory size. The influence of territory size on successful remating may result directly from the physical limits of the territory, the coverage of these "key" plant species, or the interplay of both.

Period unmated. Because pairs with more lasting bonds made a greater number of re-nesting attempts and the males, as a result, spent less time unmated, the proportion of the period of territory occupancy spent mateless was negatively correlated with pair bond duration ($r = -.750$, $n = 23$) and the number of nesting attempts per mate ($r = -.636$, $n = 20$). The number of days spent unmated also was correlated negatively with pair bond duration ($r = -.706$, $n = 16$). The absence of a significant, inverse relationship between frequency of pair formation and either the period unmated or the time required to mate (see following section) suggests that mate

loss and mate acquisition operate independently. The extent of matelessness depends upon the females' tendency to desert and the males' ability to acquire new mates. The former could operate independently of territory quality as inherent differences may exist in the females' propensity to re-nest following nesting disturbances (re-nesting attempts per female ranged from 0 to 9). The latter also may be largely independent of males or their territories, as extrinsic factors may affect female availability (see above: Desertion and Remating). Independence between mate loss and mate acquisition might also result from temporal shifts in territory quality between pair formation and mate desertion (see below: Temporal Changes in Territory Quality).

Time required to mate. The time required to form a pair bond was not significantly related to any other variable. This may have resulted from fluctuation in the availability of unmated females, operating independently of territorial features (see above: Desertion and Remating).

Pair bond duration. In addition to the significant relationships previously mentioned, pair bond duration also was correlated positively with the number of nesting attempts per female ($r = .929$, $n = 20$). This indicates either that more lasting pair bonds increase the time available for re-nesting or that females more persistent in re-nesting remain mated longer as a result.

Nesting persistence. Aside from the significant relationships already discussed, the number of nesting attempts per mate correlated positively with the early summer growth rate in broods of three ($r = 1.000$, $n = 3$), but correlated negatively with the late summer growth rate ($r = -.970$, $n = 3$, $P > 0.05$). The number of nesting attempts depends upon the female's persistence and the duration of each nesting effort. Females more prone to re-nest may provide better parental care early in the breeding season, but with each additional re-nesting attempt, the effort expended in rearing the young may decrease. For young of three of the four pairs where growth data were collected from more than one nesting attempt, the growth rate decreased in subsequent broods. The number of nesting attempts also was correlated negatively with the frequency of occurrence of Indian grass ($r = -.592$, $n = 18$), suggesting that territories with this species may become less attractive for nesting as the season progresses. Two of the four territories abandoned in June extended into the grassland (territories of WY and

TABLE 3. Mean and standard deviation of variables differing significantly ($P \leq 0.05$) between returning males and first-year males.

Variable	Returning			First-year		
	N	\bar{x}	SD	N	\bar{x}	SD
Male weight (g)	8	13.41	.6	12 ¹	12.70	.6
Territory size (ha)	10	.95	.41	9	.60	.21
Territory occupancy (days)	10	131	11	12 ¹	92	41
Nestling growth rate						
Early summer, B/4	2	.557	.001	4	.612	.025
Plant species (A.C.) ² (ha)	10			9		
<i>Andropogon furcatus</i>		.110	.100		.048	.056
<i>Andropogon scoparius</i>		.013	.013		.001	.003
<i>Panicum</i> spp.		.012	.009		.004	.003
<i>Potentilla recta</i>		.008	.006		.003	.005
<i>Prunus</i> spp.		.015	.013		.002	.004
Plant species (F.O.) ² (%)	10			9		
<i>Pastinaca sativa</i>		23.2	10		37.2	16
<i>Andropogon scoparius</i>		3.0	3		.6	2

¹ Includes replacement males.² A.C. = area covered, F.O. = frequency of occurrence.

WO), and a territorial shift (territory of OW) excluded the grassland portion of the original territory (fig. 1). Although grass litter was the predominant nesting substrate early in the season, its use declined sharply in June (Best 1978).

Nestling growth rate. The relationship between growth rates (3-nestling broods) and the vegetation composition on territories (both frequency of occurrence and area coverage) imply a seasonal shift in the plant species important for nestling growth. Only those cases where the correlation coefficient had the same sign for both frequency and coverage and where the probability of at least one of these was less than 5% were considered. Shingle oak was positively correlated with nestling growth rate early in the summer but negatively correlated during late summer. Indian grass, rough-fruited cinquefoil, yarrow, and field goldenrod showed an opposite trend. The above relationships reflect the observed seasonal transition in foraging sites for nestling food (Best 1977) and suggest a temporal shift in territory quality; wooded areas provided a greater abundance of nestling food early in the breeding season, and more open sites, with low, herbaceous vegetation, received the greatest use later. Shingle oak was more abundant in the shrub-woodland habitat than in the other two vegetation types, while the other species mentioned were more prevalent in the shrub-grassland and grassland areas. A nonsignificant, positive correlation also existed between early summer growth rate and the frequency of occurrence of plant species taller than 4 m. The relationship was negative during late summer.

DIFFERENCES BETWEEN RETURNING MALES AND FIRST-YEAR MALES

Males returning to the study area a second year were compared with those appearing for the first time in 1972, using a *t*-test of means for all variables considered in the correlational analysis. Variables showing significant differences are presented in table 3.

Body weight, territory size, and duration of territory occupancy were all significantly greater for returning males than first-year males. All returning males were at least 2 years old while most first-year males were probably yearlings. This might explain the difference in weight. Larger territory size and greater territory tenacity may result from increased experience gained with age, or more specifically, from more extended exposure to the study area. The territories of almost all returning males were larger in 1972 than in 1971, and with the exception of GO, only first-year males deserted their territories before mid-August. Younger males reportedly have smaller territories in the Great Tit, (Dhondt and Hublé 1968) and the White-crowned Sparrow (*Zonotrichia leucophrys*) (Ralph and Pearson 1971) although Weeden (1965) concluded that the size of the "total activity space" of male Tree Sparrows (*Spizella arborea*) was not influenced by age or experience. The growth rate of early summer, 4-nestling broods with first-year male parents was higher than for those with returning male parents. This differential growth is unexplained. Inadequate sample size prevented comparison between 3-nestling broods.

Parship occurred significantly more frequently in territories of first-year males than

in those of returning males (table 3). The opposite was true with the frequency of occurrence of little bluestem (*Andropogon scoparius*) and the area covered by big bluestem, *Prunus* spp., little bluestem, panic grasses, and rough-fruited cinquefoil. This relates to the relative extension of territories into the shrub-woodland. Parsnip was much more abundant in the shrub-woodland than other regions of the study area while the other species showed an opposite trend. All but one territory of a first-year male extended into the shrub-woodland (fig. 1). The proportion of the total territory area within the shrub-woodland averaged 36% for first-year males but only 20% for returning males.

TEMPORAL CHANGES IN TERRITORY QUALITY

A Field Sparrow territory is used for mating, nesting, and feeding. The present study focused on territory characteristics potentially affecting pair bonding, nesting activities, and nestling growth, and not on the territory as a food source for adults.

Territory establishment and mate selection occur early in the growing season. Subsequent foliage development and plant growth modify the physiognomy of vegetation as the breeding season advances, ultimately causing seasonal shifts in nest placement and foraging patterns for nestling food. The preferred nesting substrate changes from grass litter to trees and shrubs (Best 1978), and the foraging sites for nestling food shift from wooded areas to low, herbaceous vegetation (Best 1977). As a result, the suitability of each territory for nesting and rearing young may change markedly over the 4-month-long breeding season. Concurrent with (but not necessarily caused by) the seasonal changes in habitat quality is a reduction in clutch size, common in many birds. Territories providing the most desirable nesting and foraging sites early in the season have a greater reproductive potential than those becoming desirable later in the season when clutch size is reduced.

The overall suitability of each habitat type involves an interaction of factors often changing with time. Territories associated with shrub-woodland are more vulnerable to brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) early in the breeding season (Best 1978), a time when wooded areas also are predominant foraging sites for nestling food. Mammalian predation is infrequent in grassland areas, but the desirability of grass litter for nesting decreases as the season pro-

gresses (Best 1978), and the food resource potential of this habitat may be limited. The propensity to establish territories in shrub-grassland may result from its intermediate nature between grassland and shrub-woodland. Although the latter two habitats change markedly in their suitability for breeding as the season advances, the shrub-grassland may have a sufficiently varied assemblage of grasses, forbs, trees and shrubs to provide the advantages of each vegetation type and yet accommodate temporal shifts in their desirability for nesting and foraging.

Territory and mate selection and the subsequent fidelity to the territory and mate apparently are not responses to mere presence or absence of critical resources but rather to relative abundance above certain threshold levels. Potential nest sites were available on all territories during the entire breeding season although their relative abundance varied markedly among territories and within the same territory over the course of the season. Similar conditions could exist for nestling food, but the absence of nestling starvation and the low variation in nestling growth rate among territories suggest that nestling food remained adequate on all territories throughout the season. The apparent opportunistic foraging behavior of the Field Sparrow (at least for nestling food, Best 1977) indicates that potential nesting sites may be more significant than the potential food supply in selection of breeding habitat. Hildén (1965) concluded that, "In most species food does not seem to have any proximate effect on habitat selection," but rather the species utilizes "food that is easily available in an environment selected on other grounds."

SUMMARY

Territory quality and mating success of the Field Sparrow were studied during two breeding seasons in central Illinois on a 23.6-ha tract composed of grassland, shrub-grassland, and shrub-woodland.

Males arrived on the study area by 2 April; females first appeared 12 April. Males occupied their territories from 7 to 153 days with a mean of 111 days for those who mated successfully. All males with permanent territories mated successfully. Pair bonds lasted from 5 to 129 days and averaged 60 days. Shrub-grassland was the preferred habitat with contiguous territories occupying all available space. Extension of territories into the grassland and shrub-woodland was limited. Terri-

tory size averaged 0.76 ha but ranged from 0.31 to about 1.62 ha. Territories extending into grassland were significantly larger than those not associated with grassland. Territorial configuration changed under some circumstances. Eleven of the 25 males present in 1971 returned in 1972, all establishing territories on the same sites occupied the year before. Territories of returning males were equal to or larger than they were the preceding year. The return rate of females was low, but all settled in territories occupying the area selected the previous year. Site tenacity is discussed. Several females deserted their mates during the breeding season, usually after snake predation on the nest. Many males remated successfully. Frequency of pair formation oscillated throughout the season, possibly influenced by the number of unmated males and/or the frequency of nest predation.

A correlational analysis was made between several variables potentially related to territory quality and mating success. Differential male size is apparently unimportant in the social structure of Field Sparrows. Males with larger territories mated more frequently. Territory size also was correlated positively with the coverage of Indian grass, big bluestem and other associated plant species. The sequence of territory occupancy was independent of all variables considered. Males with more lasting pair bonds remained on their territories longer. The frequency of pair formation was positively correlated with the coverage of several plant species. Loss and acquisition of mates are apparently independent. The time required to form a pair bond was independent of all variables considered. Nesting persistence correlated positively with nestling growth rate in early summer but negatively in late summer, suggesting a decline in parental care with subsequent nestings. The relationships between nestling growth rate and the abundance of several plant species suggested a seasonal transition in the optimal foraging sites for nestling food from wooded areas to more open sites with low, herbaceous vegetation.

Body weight, territory size and duration of territory occupancy were greater for returning males than first-year males. Several plant species differed in their abundance in territories of returning males and those of first-year males, indicating greater extension of the latter into the shrub-woodland.

Temporal shifts in the suitability of territories for nesting and rearing young, and the propensity to establish territories in shrub-grassland are discussed.

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LITERATURE CITED

- BEER, J. R., AND D. TIBBITTS. 1950. Nesting behavior of the Red-winged Blackbird. *Flicker* 22: 61-77.
- BEST, L. B. 1977. Nestling biology of the Field Sparrow. *Auk* 94:308-319.
- BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. *Auk*, in press.
- BURLEIGH, T. D. 1958. Georgia birds. Univ. Oklahoma Press, Norman.
- CODY, M. L., AND C. B. J. CODY. 1972. Territory size, clutch size, and food in populations of wrens. *Condor* 74:473-477.
- CROOKS, M. P. 1948. Life history of the Field Sparrow, *Spizella pusilla pusilla* (Wilson). M.S. thesis, Iowa State College, Ames.
- CROOKS, M. P., AND G. O. HENDRICKSON. 1953. Field Sparrow life history in central Iowa. *Iowa Bird Life* 23:10-13.
- DHONDT, A. A., AND J. HUBLÉ. 1968. Age and territory in the Great Tit (*Parus m. major* L.). *Angew. Ornithol.* 3:20-24.
- HILDÉN, O. 1965. Habitat selection in birds. A review. *Ann. Zool. Fenn.* 2:53-75.
- HOLM, C. H. 1973. Breeding sex ratios, territoriality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Ecology* 54: 356-365.
- HOWARD, H. E. 1920. Territory in bird life. John Murray, London.
- JONES, G. N. 1963. Flora of Illinois, 3rd ed. Am. Midl. Nat. Monogr. No. 7.
- KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. *Illinois Biol. Monogr.* 18(3).
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology* 52:2-22.
- MARTIN, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Ph.D. thesis, Oregon State Univ., Corvallis.
- MARTIN, S. G. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. *Am. Zool.* 14:109-119.
- MAY, D. J. 1949. Studies on a community of Willow Warblers. *Ibis* 91:24-54.
- MORTON, M. L., J. L. HORSTMANN, AND J. M. OSBORN. 1972. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. *Condor* 74:152-163.
- NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. II. Territoriality. *Wilson Bull.* 68:129-150.
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc. N.Y.* 4:1-247.

- NICE, M. M. 1941. The role of territory in bird life. *Am. Midl. Nat.* 26:441-487.
- RALPH, C. J., AND C. A. PEARSON. 1971. Correlation of age, size of territory, plumage, and breeding success in White-crowned Sparrows. *Condor* 73:77-80.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978-983.
- ROBINS, J. D. 1971. Differential niche utilization in a grassland sparrow. *Ecology* 52:1065-1070.
- SOUTHERN, H. N., AND A. MORLEY. 1950. Marsh-Tit territories over six years. *Br. Birds* 43:33-47.
- STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. *Auk* 75:335-346.
- STENGER, J., AND J. B. FALLS. 1959. The utilized territory of the Ovenbird. *Wilson Bull.* 71:125-140.
- STEWART, R. E. 1953. A life history study of the Yellow-throat. *Wilson Bull.* 65:99-115.
- STEWART, R. E., AND C. S. ROBBINS. 1958. Birds of Maryland and the District of Columbia. N. A. Fauna, No. 62, U.S. Dept. Interior, Fish Wildl. Ser., Washington, D.C.
- SUTTON, G. M. 1960. The nesting fringillids of the Edwin S. George Reserve, southwestern Michigan (part VI). *Jack-Pine Warbler* 38:46-65.
- TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. *Auk* 79:687-697.
- VERNER, J., AND G. H. ENGELSEN. 1970. Territories, multiple nest building, and polygyny in the Long-billed Marsh Wren. *Auk* 87:557-567.
- WALKINSHAW, L. H. 1945. Field Sparrow, 39-54015. *Bird-Banding* 16:1-14.
- WALKINSHAW, L. H. 1968. *Spizella pusilla pusilla*: Eastern Field Sparrow, p. 1217-1235. In O. L. Austin, Jr. [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237, part 2.
- WEEDEN, J. S. 1965. Territorial behavior of the Tree Sparrow. *Condor* 67:193-209.
- WIENS, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah Sparrows. *Ecology* 54:877-884.
- WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. *Ecol. Monogr.* 36:51-77.
- ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. *Auk* 83:534-546.
- ZIMMERMAN, J. L. 1971. The territory and its density dependent effect in *Spiza americana*. *Auk* 88:591-612.

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