to breed. Two advantages that might accrue to the female by singing in this relationship to her mate are: (1) most of the information is likely to be received by the male at a time when he is silent; and (2) constant repetition of the message at a fixed time interval would more clearly inform the male that the female is responding directly to him.

The results of this preliminary study indicate that at times the female red-wing is timing her song to follow her mate's song. Although more work is needed to describe the content of the information being exchanged, the mode of information exchange described now in inter- and intra-sexual social contexts for Red-winged Blackbirds might present a common, but usually overlooked form of animal communication.

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Selection of song perches by sagebrush-grassland birds.—Although song perches have been recognized as important components of avian habitat (Hilden, Ann. Zool. Fenn. 2: 53–75, 1965; Wiens, Ornithol. Monogr. 8, 1969), few studies have examined selection and characterization of perches in detail. Harrison (Wilson Bull. 89:486–487, 1977) tried, but was unable to show selection of higher artificial perches by five of six grassland species studied. A minimum number of suitable perches is considered a necessary habitat feature for several species of grassland and shrubland birds (Lack, J. Anim. Ecol. 2:239–262, 1933; Lack and Vanables, J. Anim. Ecol. 8:39–71, 1939; Kendeigh, Condor 43:165–174, 1941; Kendeigh, Condor 62:418–436, 1945; Zimmerman, Auk 88:591–612, 1971). Harrison and Brewer (Jack-Pine Warbler 57:179–183, 1979) and Knodel-Montz (Wilson Bull. 93:547–548, 1981) concluded, however, that population densities of grassland birds were not increased by providing additional perches in their studies.

The purpose of this study was to examine in detail characteristics of song perches used by four species of passerines that breed in sagebrush-grassland habitats: Brewer's Sparrow (*Spizella breweri*), Vesper Sparrow (*Pooecetes gramineus*), Western Meadowlark (*Sturnella neglecta*), and Horned Lark (*Eremophila alpestris*). My objectives were: (1) to describe vegetational features of song perches used by each species; (2) to make interspecific comparisons; and (3) to determine if there were preferences in use of perches compared to what was available. Several questions were addressed. Do individuals tend to select relatively large and conspicuous perches from which to sing? Do individuals that occupy the same local area show species-specific patterns of use? How do perches differ among vegetationally different sites? Are available perches limiting to shrubland and grassland birds?

Study area and methods.—The study was conducted 20 April–18 June 1980 on three 16-ha sites on the Vernon Division of the Wasatch National Forest, 10 km S of Vernon, Tooele Co., Utah. This cold desert area is located at 1800 m elev. in the southern end of Rush Valley. Big sagebrush (*Artemisia tridentata*) dominated two sites: one that had been plowed and seeded to grasses in 1963 (NONMAN) and one that had been chained and seeded in 1976 (CHAIN). The remaining site (BURN) was dominated by grasses, but sagebrush islands missed by a controlled burn in 1976 comprised 8% of the site. The most common grasses were bluebunch wheatgrass (*Agropyron spicatum*), crested wheatgrass (*A. cristatum*), cheatgrass (*Bromus tectorum*), and Sandberg bluegrass (*Poa sandbergii*). More detailed site de-

TABLE 1
CHARACTERISTICS ($\bar{x}$ ± SE) OF RANDOMLY SAMPLED SHRUBS

Variable	Site		
	NONMAN N = 80	CHAIN N = 80	BURN N = 106[a]
Random shrub height (cm)	43.9 ± 2.1	38.7 ± 2.2	40.2 ± 2.3
Neighboring shrub height (cm)	42.6 ± 2.1	44.1 ± 2.3	38.1 ± 1.8
t	0.54 NS[b]	−2.4*	0.92 NS
Random shrub cover (dm^2)	18.9 ± 1.8	16.3 ± 1.9	16.8 ± 2.6
Neighboring shrub cover (dm^2)	18.9 ± 2.2	19.2 ± 2.2	12.7 ± 1.9
t	0.00 NS	−1.21 NS	1.51 NS
Random shrub volume (dm^3)	17.0 ± 2.2	14.4 ± 2.0	19.6 ± 4.1
Neighboring shrub volume (dm^3)	17.0 ± 2.5	19.7 ± 3.2	12.8 ± 2.6
t	0.01 NS	−1.70 NS	1.60 NS
Intershrub distance (cm)	66.6 ± 2.7	81.9 ± 5.2	315.5 ± 31.3
Shrub density (no./30 m^2)	22.2 ± 0.8	16.2 ± 1.0	3.4 ± 0.3

[a] Stratified sample: burned stratum (N = 83), unburned stratum (N = 23).
[b] Denotes statistical significance (NS $P > 0.05$; * $P < 0.05$) of paired *t*-tests between random and neighboring shrubs.

scriptions are given elsewhere (Castrale and Parker, Am. Birds 35:91, 1981; Castrale, J. Wildl. Manage. 46:945–952, 1982). Precipitation averages 32 cm in the area with 60% falling as snow (Frischknecht, Proc. Int. Rangeland Congr. 1:633–635, 1978). Cattle-grazing occurs in spring and autumn months. The management and land use history of this area were discussed by Frischknecht (1978).

Singing males were observed primarily in the mornings. When a bird was heard singing, it was located and the song perch measured immediately or marked with flagging and measured at the end of the sampling period. No more than 10 observations were taken on any individual during a sampling period. A minimum of 14 Brewer's Sparrows and 11 individuals of each of the other species were represented. For each perch, the following measurements were recorded: bird species, shrub species, shrub condition, and height and maximum diameters of shrub crown taken perpendicular to each other and parallel to the ground. The horizontal distance from the center of the song perch to the center of the nearest shrub was recorded and identical shrub measurements taken on the latter.

Shrub density was determined by counting all shrubs in a 30-m^2 circular plot around the song perch. Shrub cover was estimated by calculating the area of an ellipse using shrub diameter values. An estimate of shrub volume was obtained by using height and diameter measurements in the formula for the volume of an ellipsoid. To determine preferences for perch-sites, data were taken on 80 shrubs and their nearest neighbor on both the NONMAN and CHAIN sites along eight randomly located transects stratified to cover all four quadrants of each site. The BURN site was sampled with a stratified random design with 83 points located in the grassland portions and 23 in the sagebrush islands.

Relative availability of shrubs for perches was obtained by weighting the shrub composition of each study site by the number of observations for each bird species sampled on the site. For each study site, a comparison of random shrubs with their nearest neighbor showed no detectable differences in shrub species or shrub condition. Hence, frequencies were com-

TABLE 2
RELATIVE USE (%) OF SONG PERCHES BY SAGEBRUSH-GRASSLAND BIRDS

Perch type	Bird species			
	BS N = 110	VS N = 86	WML N = 96	HL N = 66
Shrub				
Big sagebrush (*Artemisia tridentata*)	93.6	58.1	61.5	69.7
Utah juniper (*Juniperus osteosperma*)	5.5	34.9	35.4	30.3
Utah serviceberry (*Amelanchier utahensis*)	0.9	1.2	0.0	0.0
Coralberry (*Symphoricarpos orbiculatis*)	0.0	1.2	0.0	0.0
Forb				
Prickly poppy (*Argemone corymbosa*)	0.0	1.2	0.0	0.0
Other				
Fence post	0.0	1.2	2.1	0.0
Fence wire	0.0	2.3	0.0	0.0
Wooden stake	0.0	0.0	1.0	0.0

bined in calculating available shrub species and condition values. Frequencies of shrubs used by bird species were analyzed using Chi-square or binomial tests (Conover, Practical Nonparametric Statistics, Wiley and Sons, New York, New York, 1971).

Categorical data analysis was used to determine differences among bird species in the proportional use of type and condition of perches. This statistical procedure uses the logarithm of the frequencies for each class of factors (in this case bird species, perch type, and perch condition) to conduct an analysis of variance (ANOVA) using weighted regression (Fienberg, The Analysis of Cross-classified Categorical Data, MIT Press, Cambridge, Massachusetts, 1977). To test for differences in perch variables by species and site, a one-way ANOVA was conducted with 12 treatments (all combinations of four species and three sites). Multiple comparisons in the form of Scheffé's tests were used to examine differences.

Stepwise discriminant function analysis was used to illustrate differences among bird species with respect to perch preferences. This multivariate statistical method examined the importance of variables for maximally distinguishing between the perch types used by each species. Each of the four perch variables was first transformed to its natural logarithm to satisfy normality assumptions. Perch volume was not included in the discriminant model because the contribution of this variable was nonsignificant (Approximate $F < 1.0$). From formulas in Sokal and Rohlf (Biometry, W.H. Freeman and Company, San Francisco, California, 1969), 99% confidence ellipses were constructed using discriminant scores of the first two functions.

Results.—Virtually all (99.4%) shrubs sampled on NONMAN were sagebrush and 94.4% were living. All shrubs sampled on CHAIN were sagebrush and 83.8% were living. For sagebrush islands on BURN, only sagebrush was found and 95.7% were living. In contrast, only 3.6% of the shrubs in grassland areas of BURN were living and most (97.6%) were sagebrush. Weighting by the respective areas of each stratum, values of availability for BURN were 97.8% sagebrush and 11.0% live shrubs.

Characteristics of shrubs on each site are shown in Table 1. Because shrubs were randomly sampled, differences in size between a shrub and its nearest neighbor were not expected

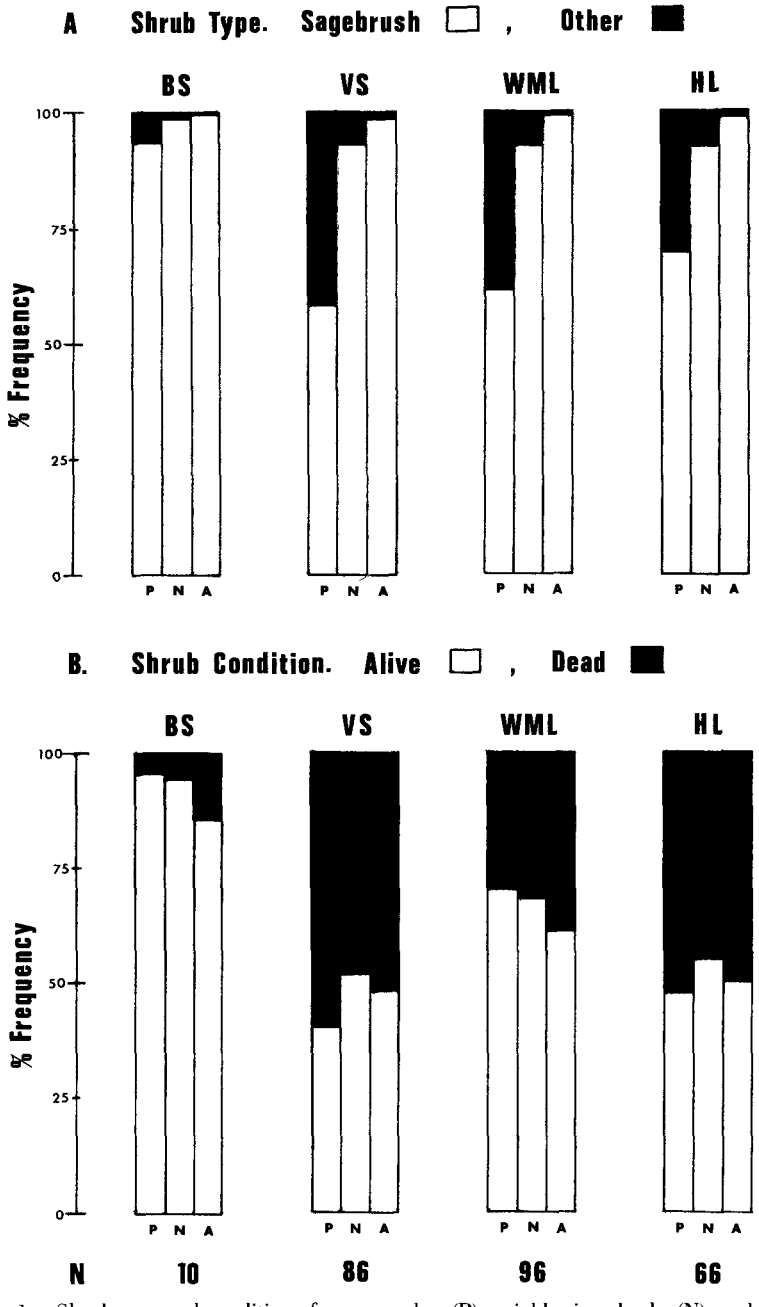

FIG. 1. Shrub type and condition of song perches (P), neighboring shrubs (N), and available shrubs (A) used by four species of sagebrush-grassland birds.

TABLE 3
PERCH CHARACTERISTICS ($\bar{x}$ ± SE) OF SAGEBRUSH-GRASSLAND BIRDS.

Variable	Bird species			
	BS N = 110	VS N = 86	WML N = 96	HL N = 66
Perch height (cm)	84.9 ± 1.9a[a]	101.2 ± 7.2b	122.2 ± 9.0b	77.8 ± 4.5a
Neighboring shrub height (cm)	61.4 ± 1.9	57.0 ± 2.2	55.6 ± 2.3	47.9 ± 2.4
t	9.67***[b]	6.39***	7.50***	6.27***
Perch cover (dm^2)	61.6 ± 5.2a	92.8 ± 28.9ab	130.7 ± 43.6a	39.9 ± 3.9b
Neighboring shrub cover (dm^2)	27.3 ± 2.2	30.9 ± 3.7	30.9 ± 3.6	17.8 ± 1.9
t	6.36***	2.21***	2.29***	6.03***
Perch volume (dm^3)	95.8 ± 10.5a	377.8 ± 229.9ab	785.9 ± 480.0ab	63.2 ± 11.1b
Neighboring shrub volume (dm^3)	31.8 ± 3.7	35.9 ± 5.9	37.7 ± 8.0	17.1 ± 2.2
t	5.90***	1.49 NS	1.56 NS	4.14***
Intershrub distance (cm)	76.8 ± 7.2a	143.1 ± 12.9b	188.7 ± 33.8bc	224.7 ± 37.3c
Shrub density (no./30 m^2)[c]	19.7 ± 0.5a	11.9 ± 1.0b	14.8 ± 0.9c	9.2 ± 1.0d

[a] Dissimilar letters across columns denote nonsignificant differences of perch characteristics between bird species.
[b] Denotes statistical significance (NS $P > 0.05$; * $P < 0.05$; *** $P < 0.001$) of paired *t*-tests between perches and neighboring shrubs.
[c] N = 104 (BS), N = 73 (VS), N = 94 (WML), N = 64 (HL).

unless a bias for encountering larger shrubs existed in the sampling scheme. Paired *t*-tests showed no differences between shrub size variables except for greater mean height of neighboring shrubs on the CHAIN site compared to randomly sampled shrubs.

Three hundred and fifty-eight song perches were recorded being used by Brewer's Sparrows, Vesper Sparrows, Western Meadowlarks, and Horned Larks in this study (Table 2). Shrubs were used 98% of the time. Big sagebrush, the most numerous shrub on each study site, was also the primary song perch used by each species. Perches other than sagebrush (primarily Utah juniper [*Juniperus osteosperma*]), however, were used more frequently than expected based on their availability (Fig. 1A, P vs A). The pattern of use was consistent among all species and highly significant ($P < 0.001$) using binomial tests. This pattern is further substantiated by the fact that perches, compared to the adjacent shrub (Fig. 1A, P vs N), were more likely to be a shrub other than sagebrush. Using Chi-square tests for independence, differences were significant for Vesper Sparrow ($\chi^2 = 28.32$, df = 1, $P < 0.001$), Western Meadowlark ($\chi^2 = 26.53$, df = 1, $P < 0.001$) and Horned Lark ($\chi^2 = 11.10$, df = 1, $P < 0.001$), and Brewer's Sparrow ($\chi^2 = 4.66$, df = 1, $P < 0.05$).

In contrast to a consistent preferential use of juniper perches, no apparent patterns of use were detected for the condition of song perches (Fig. 1B). Living perches were preferred by Brewer's Sparrow (binomial test, $P < 0.01$), but their use by all other species was essentially random ($P > 0.05$). Chi-square tests for independence failed to detect differences between the condition of perches and neighboring shrubs for Brewer's Sparrow ($\chi^2 = 0.09$, df = 1,

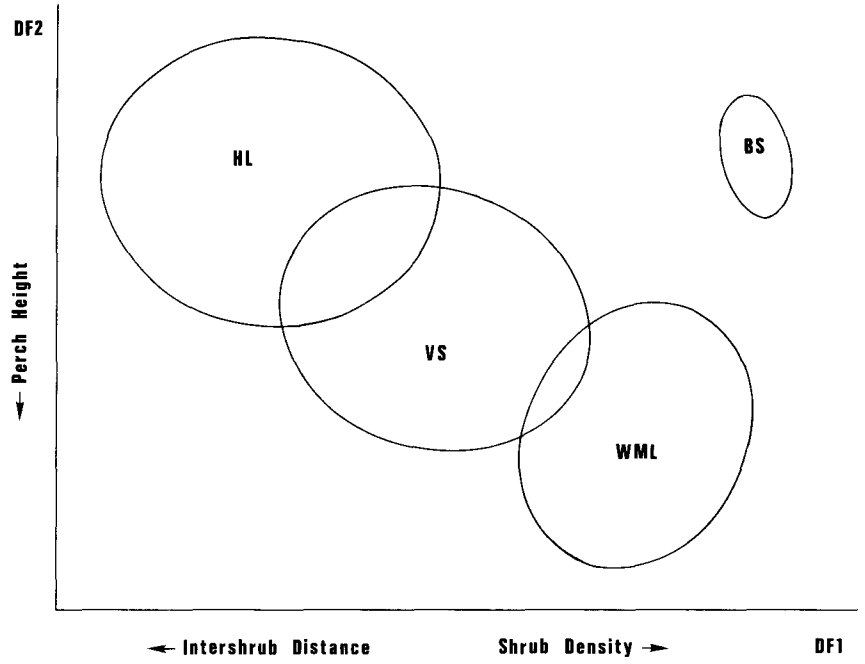

FIG. 2. Bird species ordination using 99% confidence ellipses along the first two discriminant functions (DF).

NS), Vesper Sparrow ($\chi^2 = 2.34$, df = 1, NS), Western Meadowlark ($\chi^2 = 0.10$, df = 1, NS) or Horned Lark ($\chi^2 = 0.75$, df = 1, NS).

Categorical data analysis indicated significant differences in the relative use of perches by all bird species pairs except Vesper Sparrow and Horned Lark. Brewer's Sparrows used relatively more living sagebrush for song display, while other species used a greater proportion of juniper perches along a gradient from Western Meadowlarks to Horned Larks to Vesper Sparrows.

Juniper perches averaged 143 cm in height (N = 100) which was significantly greater ($t = 6.37$, df = 102, $P < 0.001$) than the mean height of 80 cm for sagebrush perches (N = 258). Living shrubs had a mean height of 91 cm (N = 231) which did not differ significantly ($t = 1.87$, df = 153, NS) from the mean of 104 cm (N = 112) for dead perches.

Height, cover, and volume are measures of perch size and, for all species, their mean values exceeded those of the nearest neighboring shrub (Table 3). Paired *t*-tests showed these differences to be significant in all cases except two. Due to the large variation in estimates of volume of perches used by Vesper Sparrows and Western Meadowlarks, differences were not significant.

Scheffé's tests revealed differences in the characteristics of perches used by the four bird species (Table 3). Species or site differences were exhibited by perch height ($F = 4.70$; df = 11, 346; $P < 0.001$), intershrub distance ($F = 10.78$; df = 11, 346; $P < 0.001$), and shrub density ($F = 51.69$; df = 11, 323; $P < 0.001$), but not by perch cover ($F = 1.65$; df = 11,

TABLE 4
SITE DIFFERENCES IN PERCH CHARACTERISTICS

Bird species	Site			Variable				
	NON-MAN	CHAIN	BURN	Perch height	Perch cover	Perch volume	Inter-shrub distance	Shrub density
Brewer's Sparrow	X	X	—	NS[a]	NS	NS	NS	NS
Vesper Sparrow	X	—	X	NS	NS	NS	***	***
Western Meadowlark	X	—	X	NS	NS	NS	***	***
	X	X	—	*	NS	NS	NS	*
	—	X	X	**	NS	NS	***	***
Horned Lark	—	X	X	NS	NS	NS	***	***

[a] Denotes statistical significance (NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) of Scheffé's tests.

346; NS) or perch volume ($F = 1.32$; df = 11, 346; NS). Brewer's Sparrows and Horned Larks both used low perches, but the former species frequented areas of high shrub density while the latter was found in more open areas. Western Meadowlarks used the highest perches and Vesper Sparrow perches had intermediate characteristics. Confidence ellipses derived from discriminant function analysis illustrate the characteristics of the perches used by each species (Fig. 2). Shrub density was the most important variable in discriminating between species followed by perch height and intershrub distance. The characteristics of perches used by Brewer's Sparrows were more distinctive than those used by other species. Considerable overlap occurred in all species, however, and the discriminant function analysis was unable to classify perches very accurately.

Scheffé's tests were also used to examine differences in perch characteristics among the three sites. Because birds were not equally common on all sites, sites with few observations were deleted from the analysis (i.e., Brewer's Sparrow on BURN [N = 4]; Vesper Sparrow on CHAIN [N = 4]; Horned Lark on NONMAN [N = 3]). With some exceptions, each species selected similar-sized perches without regard to site (Table 4). Only Western Meadowlarks used higher perches on NONMAN and BURN compared to CHAIN. Tall junipers were not present on CHAIN unlike the other sites, which may account for this discrepancy. Shrub density and intershrub distance were highly significant for all bird species in contrasts involving the BURN site. These patterns suggest that birds selected similar ranges of perch sizes, but shrub densities and intershrub distances were subject to constraints of the available habitat.

Discussion.—These data suggest that for the four species of birds studied, song perches are not used randomly, but show species-specific selectivity as influenced by availability. Three of the four species are considered grassland residents (Kendeigh, Condor 43:165–174, 1941), but Brewer's Sparrow is sagebrush-dependent (Braun et al., Wilson Bull. 88:165–171, 1976). Hence, the data must be interpreted in light of the habitat preferences of each bird species. In addition, factors other than habitat may be important in the selection of song perches. These include territory size and type, territorial behavior, and body size. Western Meadowlarks had the largest territories, followed by Vesper Sparrows and Brewer's Sparrows. Territories of Horned Larks were difficult to delineate because birds fed outside defended areas. Birds with large territories would have a wider variety of perches from which to sing

given comparable perch densities. Body size may also be a factor because a larger bird would require a stouter perch to support its weight compared to smaller species. Brewer's Sparrows and Vesper Sparrows sing only from elevated perches while Western Meadowlarks and Horned Larks sing during flight and from the ground, the latter to a much greater extent. The conspicuousness of perches and locatability of singing individuals may also be important considerations in selecting a perch in which to engage in territorial song display.

Preferences of birds for juniper perches can best be explained by differences in shrub height. Junipers used as perches were significantly higher than sagebrush perches. No consistent pattern of use was observed between living and dead perches (Fig. 1B), and indeed, living shrubs used as perches did not differ significantly in height from dead perches.

Many authors (Kendeigh 1941; Smith, Wilson Bull. 75:159–165, 1963; Berger, U.S. Natl. Mus. Bull. 237:868–882, 1968; Wiens 1969; Wiens, Ecology 54:877–884, 1973) have noted that selection for high perches occurs, but only Harrison (1977) attempted to test the hypothesis that individuals prefer the highest perches available. Using artificial perches 1.5 and 2.0 m tall, he found that only one (Eastern Meadowlark [*Sturnella magna*]) of six species observed (Vesper Sparrow was included) showed a statistically significant preference for higher perches. Although the artificial perches stood above the surrounding vegetation and were used extensively by all species, he concluded that individuals will use virtually any elevated perch regardless of height. The lack of demonstrable preferences by birds for higher perches (Harrison 1977) may have been due to the wide spacing of perches (80 m minimum distance). At this low density, territorial birds will have few perches to select and the pattern of perch use probably reflects territory use. My data suggest that if two different-sized perches were placed in close proximity (i.e., 1 m), the higher would be used almost exclusively. In 91% of the instances in the present study, the perch selected by an individual was as high as or higher than the adjacent shrub. Smith (1963) found that Grasshopper Sparrows (*Ammodramus savannarum*) abandoned low perches if higher ones were provided.

Nonsignificant differences in perch heights between sites (Table 4) indicate: (1) that sites were similar in vegetation structure; (2) that birds frequented similar microhabitats on each site; or (3) that birds selected similar perches on each site. All were true in certain cases. Bird species using different sites frequented similar habitats and perched on similar-sized shrubs. The CHAIN site was unique in that it lacked the conspicuous junipers favored by Western Meadowlarks. Thus, significant site differences in perch height were comparisons of CHAIN with other sites. No significant height differences were detected in the cases of Brewer's Sparrow and Horned Larks because few territories of these species contained large junipers. However, these birds may not readily use perches exceeding some unknown maximum height.

Factors other than height may play a role in the selection of perches. Utah juniper is a stout shrub and offers good support for perching. Western Meadowlarks, the largest of the birds studied, used Utah juniper more frequently than all other shrubs except sagebrush, and Brewer's Sparrows, the smallest bird, used Utah juniper least frequently. Nonwoody plants were generally not used as song perches suggesting that physical support of an individual is important in selecting perches. Grass stalks were widely available as perches and are used extensively by birds in grassland areas lacking shrubs (Wiens 1969). Dead shrubs offer more support for perching because smaller twigs break off and leave more large diameter twigs compared to living shrubs.

Species patterns in use of perches appear to indicate that partitioning of available perches may be occurring. My observations, however, do not support this hypothesis. Means of perch characteristics showed significant species differences in most cases, but ranges in values overlapped considerably. If confidence ellipses in Fig. 2 were drawn based on standard deviations instead of standard errors, overlap would be extensive. Despite this, no interspe-

cific confrontations were observed during the course of this study although a Vesper Sparrow and a Western Meadowlark perched on a particular large juniper simultaneously on several occasions. The number of perches continuously available to a bird exceeded 200 in the most restricted case and was generally >1000.

Perch-sites, by nature of their high degree of selection by birds, are important components of avian habitat, but are they or could they be potentially limiting? In the present study, 74.0% of perches used by Western Meadowlarks were chosen from a group of the highest shrubs that included only 3.5% of all available shrubs. This pattern is similar but not as dramatic for the other bird species and emphasizes preferences for high perches. It also suggests that shrubs for perching may be a potential limiting resource. Absolute numbers of perches needed by individuals have not been determined for any passerine species to my knowledge, although Lack (1933) and Lack and Vanables (1939) stated that a single tree or shrub used solely as a song perch was necessary in territories of several heathland and woodland birds.

There are several reasons why shrub perches, in most cases, would not be limiting to shrubland and grassland birds. Not all species of birds require a fixed perch for singing (i.e., Horned Lark, Western Meadowlark) and the lack of elevated perches in areas inhabited by true grassland birds may have been a selecting force in the evolution of aerial song displays. Some species (e.g., Western Meadowlark) appear to select the highest available perches in different areas and do not exhibit fixed, narrow ranges in perch heights used. Birds inhabiting grasslands lacking shrubs and requiring fixed perches (e.g., Vesper Sparrow) use grass and forb stalks from which to sing (Wiens 1969) but the same species used shrubs almost exclusively in this study when shrubs were available. In other birds (e.g., Brewer's Sparrow), it is virtually impossible to determine if song perches are limiting because use is confounded with other functions such as nest support and feeding sites. Habitat suitability of an area for shrubland and grassland birds is certainly improved by elevated song perches but the presence of certain species may not be dependent upon them. Abundant song perches should allow males to effectively delineate, patrol, and defend boundaries of their territories.

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Observations of male woodcock on singing grounds.—American Woodcock (*Scolopax minor*) males have been previously reported to use two or more singing sites within a display period (Sheldon, The Book of American Woodcock, Univ. Mass. Press, Amherst, Massachusetts, 1967; Davis, Wilson Bull. 82:327–328, 1970). These observations were speculative, however, since the woodcock involved were unmarked and only appeared to be the same birds. During our study, conducted at the McClintic Wildlife Station, 11 km north of Point Pleasant, Mason Co., West Virginia, birds were color banded and positive identifications made. Woodcock using multiple sites were observed at eight locations between 4 March and 2 April 1979. Individual birds frequently were seen displaying at two or more singing