

THE EFFECT OF COVER AND FOOD ON SPACE USE
BY WINTERING SONG AND FIELD SPARROWS

A thesis submitted in partial fulfillment of the
requirements for the degree of Bachelor of Science with
Honors in Biology from the College of William and Mary in
Virginia

by

Christopher W. Beck

Accepted for High Honors

Bryant D. Watt

Mackee A. Boyd

James A. Lee
Stewart A. Wore

Williamsburg, Virginia
May 1993

Abstract

The influence of vegetative cover and food on space use by Song (*Melospiza melodia*) and Field Sparrows (*Spizella pusilla*) was examined experimentally within an early successional field. Eight experimental patches were established, representing two replicates of all the combinations of the addition or non-addition of food and/or the placement of a single brush station. The effect of experimental treatments on patch selection was evaluated. Each experimental patch was divided into cut and uncut areas to examine the effect of weedy cover on within-patch distribution. The influence of brush and food on distribution between these areas also was examined. Finally, the effect of brush, food, and weedy cover on patterns of spatial distribution within patches was determined.

A greater number of birds were found in patches with food addition as compared to those without. Between-patch distribution was not influenced significantly by brush stations or brush and food. Within patches, a higher number of birds were found in uncut areas as compared to cut areas. Higher use of cut areas was observed in plots with food and with brush. Proportionately more Field Sparrows than Song Sparrows foraged in cut areas. Weedy cover affected patterns of spatial distribution. In cut areas, birds were concentrated near plot centers, close to cover. In uncut areas, distribution was not skewed toward plot centers. Brush

stations influenced spatial distribution toward woody cover in cut areas, but not in uncut areas.

Within-patch patterns of distribution suggest that: (1) perceived risk of predation may be important in determining distribution; (2) weedy cover may moderate the influence of woody cover on spatial distribution; (3) Field and Song Sparrows may balance the trade-offs between predation risk and foraging rate; (4) difference in distribution between Field and Song Sparrows may allow for coexistence in this system.

Introduction

The study of avian community structure, and especially finch community structure, historically has followed the example of studies of other vertebrate communities by considering resource competition as the primary mechanism promoting coexistence. Several studies have suggested a relationship between the composition of sparrow communities and seed size distribution (Pulliam 1975, 1983). Interspecific partitioning of seeds by size was thought to permit coexistence within diverse sparrow assemblages (Pulliam 1975, 1983, 1985). However, Pulliam (1985) demonstrated that this structure collapses due to broad dietary overlaps among coexisting species when resources are limited to the extent that the consumption of seeds by one species affects the availability of seeds to another species.

Even when resource levels are not limiting for all finch species in an assemblage, resource partitioning within a given habitat may not occur. Five sympatric finch species found in old-field habitats were shown to exhibit an almost 100% overlap in seed size utilization despite significant differences in culmen length among species (Pulliam and Enders 1971). It was suggested that differences in bill size lead to differences in between-habitat distribution. Differences in resource abundance also may explain between-habitat patterns of occurrence because larger species require higher resource densities compared to smaller species (Pulliam 1983).

Pulliam (1983) suggested that species with similar sized culmens may be partitioned spatially with larger species foraging closer to shrubs due to superiority in aggressive interactions among coexisting species. Earlier, Pulliam and Mills (1977) noted spatial partitioning among finch species which forage in plains grassland habitat. Species were shown to forage in concentric rings around tree or shrub cover. Furthermore, they described a positive correlation between distance from cover and predator avoidance behavior. Species close to cover were found to be social and conspicuous in behavior and morphology, while those distant from cover were cryptic. These ideas of predator-influenced spatial partitioning provide an alternative mechanism to resource partitioning for community organization.

As mentioned above, predation is not considered to be the primary mechanism for structuring vertebrate communities. However, predation acts to remove individuals from a population. Lower population numbers result in reduced interspecific competition for resources between coexisting species. In this way, predation can affect the structure of avian communities. Yet, there is a lack of research in this area due to the difficulty in observing and quantifying predation in avian communities. Davis (1973) did show that if Golden-crowned Sparrows (*Zonotrichia atricapilla*) were removed from a system where they coexisted with juncos (*Junco hyemalis*) that juncos would increase their use of areas near

cover previously dominated by Golden-crowns. This result suggests that predation which would remove individuals from the system also may reduce interspecific competition.

The non-lethal effects of predators -- the presence of predators and the risk of predation -- have been shown to affect many behavioral decisions, including the selection foraging sites (Lima and Dill 1990). Several studies have shown that certain species of finches prefer to forage closer to cover (Grubb and Greenwald 1982, Pulliam and Mills 1977, Schneider 1984), whereas other species do not require or even avoid cover (Lima 1990, Lima et al. 1987, Lima and Valone 1991, Pulliam and Mills 1977, Watts 1990).

It has been suggested that these differences in microhabitat selection are related to differences among species in the perceived and the realized (Watts 1990) risk of predation associated with cover and chosen foraging sites (Lima et al. 1987). In addition, it has been proposed that these differences are correlated with morphological and/or behavioral traits (especially escape behaviors) (Lima 1993, Lima and Valone 1991, Pulliam and Mills 1977, Watts 1990). For example, Song Sparrows (*Melospiza melodia*) which forage close to shrub or dense edge cover escape to this woody vegetation when flushed by a predator (Lima 1993). Further, these woody-cover-dependent species exhibit lower wing aspect ratios, longer tails, and lower relative flight muscle mass and heart mass, which allow for short duration, quick,

maneuverable flight, as compared to herbaceous-cover-dependent species that are adapted for more sustained, higher velocity flight (Watts, unpublished data). The results from all of these studies suggest that the risk of predation may contribute to spatial partitioning within finch assemblages. Similarly, correlations have been found between the structure of communities of granivorous desert rodents and the abilities of rodent species to detect and avoid predators (Kotler 1984). These abilities also have been linked to morphological adaptations (Kotler 1984).

In order to evaluate the relative importance of resources and the risk of predation in habitat and microhabitat selection, and their relation to the structuring of communities, these two aspects must be considered simultaneously. Researchers have found that aquatic insects (Sih 1980), fish (e.g. Gilliam and Fraser 1987, Holbrook and Schmitt 1988, Pitcher et al. 1988) and rodents (Bowers 1990) can balance the conflicting demands of foraging and the risk of predation. Prey species will feed in riskier habitats when the compensation in foraging rate is great enough. Gilliam and Fraser (1987) quantified this trade-off by using a simple model which states that an individual will use the habitat with the lowest ratio of mortality risk to gross foraging rate. They found considerable support for the model by experimentally investigating patterns of habitat selection in juvenile creek chubs (*Semotilus atromaculatus*).

Relatively little work has been done to test the trade-off model in avian communities. This likely reflects the difficulty in quantifying habitat-specific mortality rates for bird species. Schneider (1984) did show that White-throated Sparrows (*Zonotrichia albicollis*) give up higher feeding efficiencies in order to feed closer to cover. Black-capped Chickadees (*Parus atricapillus*) have been shown to change their foraging behavior to maximize their feeding efficiency while minimizing time spent exposed to predators (Lima 1985). Finally, Bland and Temple (1990) suggested that Himalayan Snowcocks (*Tetraogallus himalayensis*) switch habitats between winter and summer to forage where the risk of predation is lower at the cost of reduced feeding efficiency.

The aims of the present study were to examine (1) the influence of food and refugia from predators on patch selection in sparrows, (2) the effect of weed cover on patterns of space use, and (3) interspecific differences in cover dependency. It was hoped that trade-off patterns would lend insight into general principles of community structure.

Methods

Site Description

All field work was conducted on a farm just south of Williamsburg, Virginia (37°13'N, 76°46'W). The site was an agricultural field (12.2 ha) that had been fallow for 3-5 yr. The field contained a mixed flora dominated by broomsedge

(*Andropogon sp.*), aster (*Aster sp.*), and golden rod (*Solidago sp.*). It also contained crabgrass (*Digitaria sp.*), poke weed (*Phytolacca americana*), and sweet gum (*Liquidambar styraciflua*). The northern edge was separated from an adjacent plowed field by a bramble edge along a fence (Figure 1). The southern edge was a small deciduous patch with a stream and pond which extended to form part of the western edge of the field. The remainder of the western edge was bounded by a road and another small deciduous patch with a stream in the northwest corner of the field. Another small deciduous patch was located in the northeastern corner of the field. The eastern edge of the field connected to another old field which extended to the south.

Experimental Set-up

Eight experimental plots measuring 40 m x 40 m were chosen within the field in mid-January 1993. Plots were positioned in such a way as to maximize the inter-plot distances, while maintaining wide buffers between plots and the field edge (Figure 1). To the extent possible, vegetational density was controlled for between plots. After all plots were established, vegetation was removed on one half (20 m x 40 m) of each plot to a height of approximately 30 cm using a swing blade and a weedeater. Plots were then marked off at 5 m intervals using white surveyor's flags (Figure 2).

Four different treatments were used, representing all the

Figure 1: A map of the study site. Area=12.2 ha. Scale: 1 cm=27.4 m. The numbered points represent the experimental plots. For treatments, see Figure 4. The blackened areas represent deciduous patches.

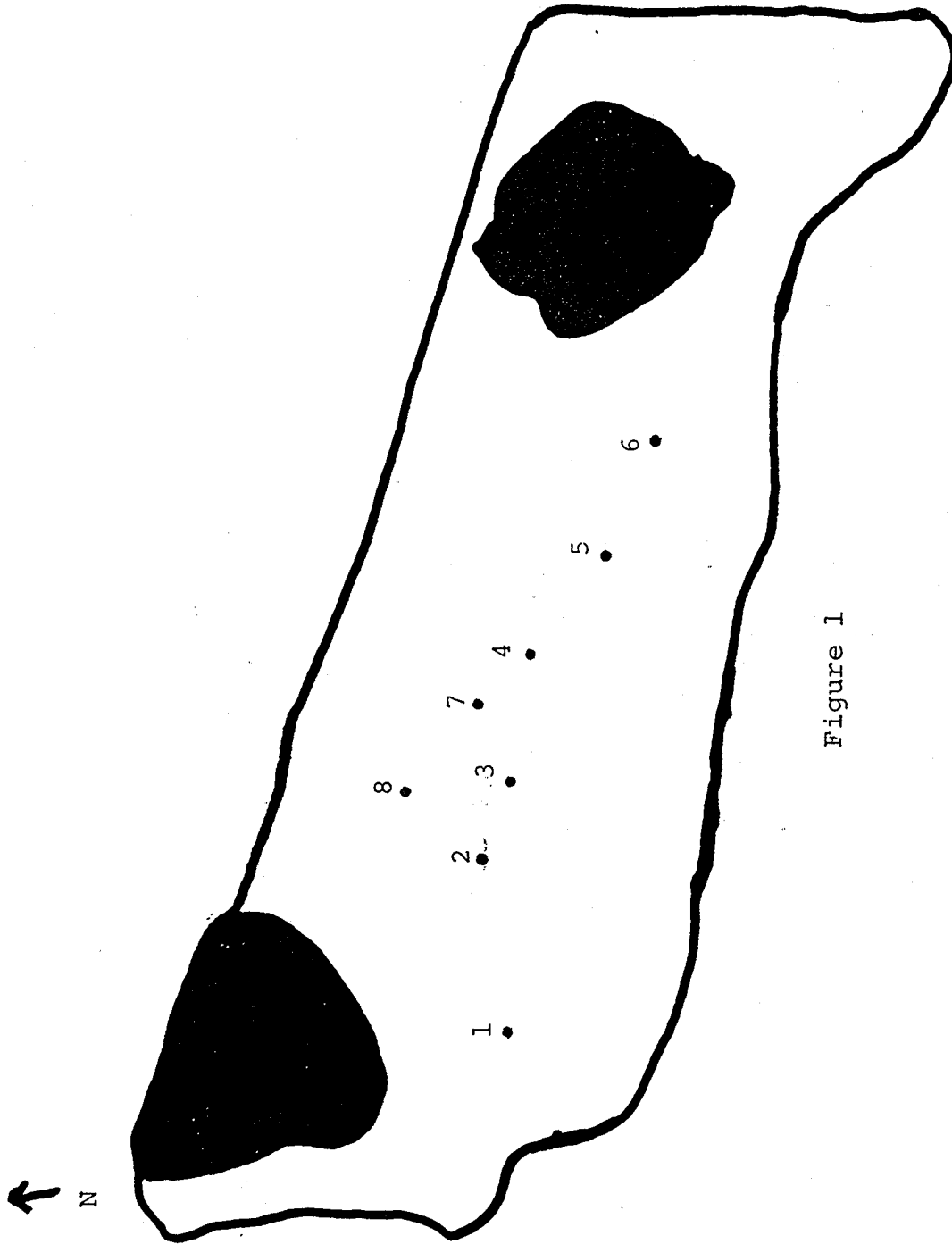
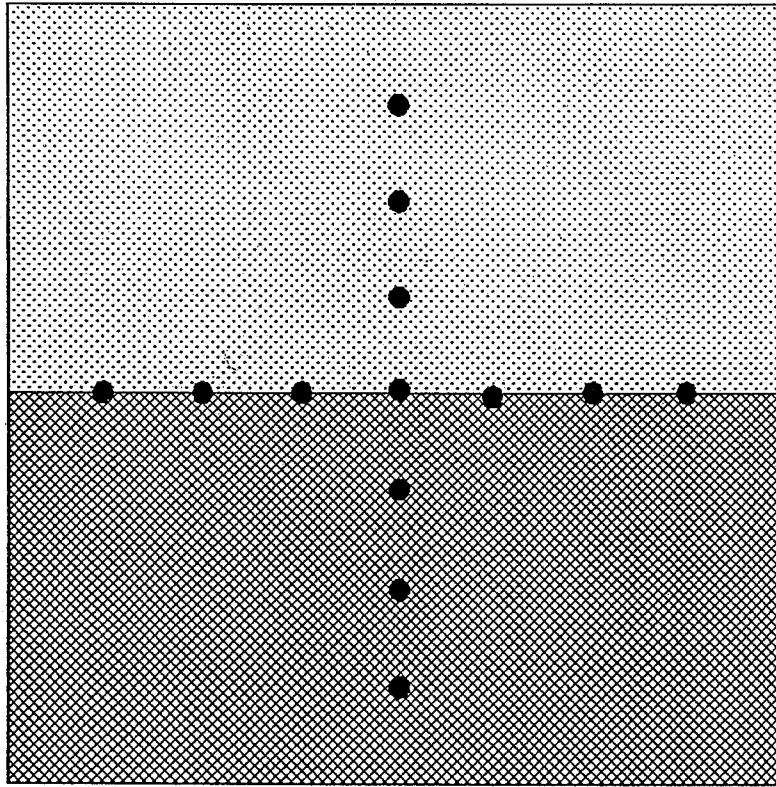


Figure 1

Figure 2: An experimental plot. The plots were 40 m x 40 m with cut and uncut areas (20 m x 40 m). The vegetation was cut to a height of approximately 30 cm in the cut areas. The black circles represent white surveyor's flags which were placed at 5 m intervals. They were used to determine the location of birds on the plots during censuses.



Cut

Uncut

Figure 2

combinations of the addition or non-addition of food and/or the placement of a single brush station (see below for explanation). Plots that received no brush station or food were considered controls. All treatment combinations were assigned randomly resulting in two replicates per treatment (Figures 1, 3, 4).

Brush stations were constructed from 5-7 small saplings (about 2-3 m high) driven into the ground to simulate an isolated tree island. The base of the brush station was filled with branches to the height of about 1 m. Brush stations were placed at the center of plots (see Figure 3). Seed trays, measuring 61 cm x 61 cm, were constructed from 1.3 cm plywood with a 4 cm high edge nailed on all four sides. Trays were placed at 5 m intervals from the center of food addition plots (see Figure 3). One seed tray also was placed on either side of the brush station, or 1 m from the center of the plot in those plots without brush stations, so that there were a total of 4 seed trays on both the cut and uncut halves of food addition plots (Figure 3).

Data Collection

All experimental plots were censused 15 times between 1 and 28 March 1993. No censuses were conducted on days with moderate to heavy rain. Censuses were taken between 0700 and 0800. All sightings of potential predators during census periods were recorded. To census birds in a plot, I walked

Figure 3: The experimental treatments. The black circles represent brush stations. The black squares represent seed trays placed at 0 m, 5 m, 10 m, and 15 m from the brush station or 1 m from the center of food only plots. The stippled area represents the cut area; the cross-hatched area the uncut area.

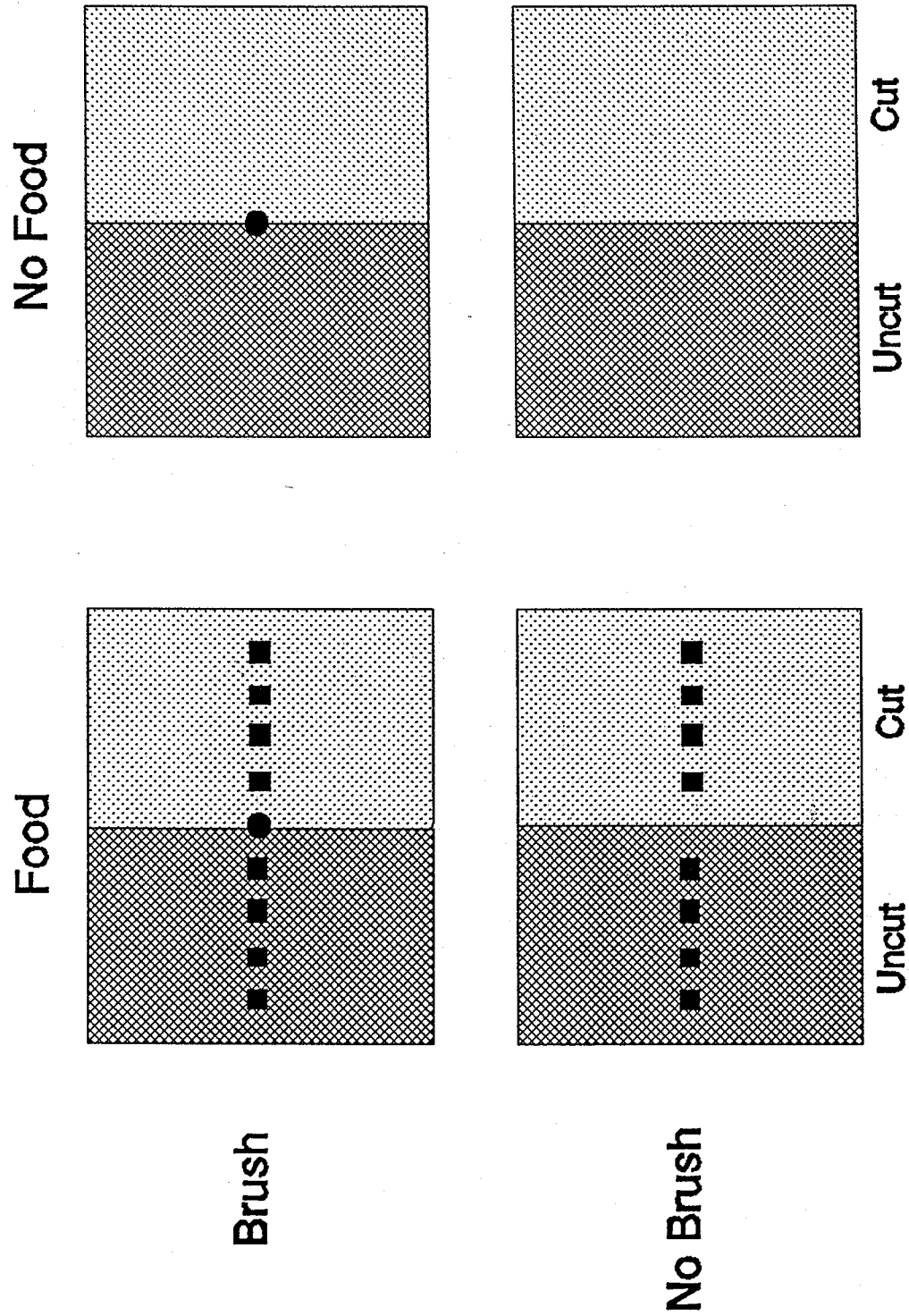


Figure 3

Figure 4: The numbers identify the plot numbers of each treatment type. See Figure 1 for the location of plots within the site.

	Food	No Food
Brush	3, 7	6, 8
No Brush	2, 5	1, 4

Figure 4

along the interface between the cut and the uncut halves of the plot and then walked a zig-zag pattern through the plot in lines parallel to the interface at 5 m intervals. The positions of all birds seen were plotted on a map with concentric circles representing 5 m, 10 m, and 15 m intervals from the center of the plot. This level of resolution allowed for the analysis of both the broader-scale distribution of birds between experimental plots and the finer-scale distribution within the plots.

The sparrows were trained on the seed trays with white millet (*Panicum sp.*) several weeks before the beginning of data collection. Millet was used because it was a commercially available seed preferred by sparrows and had been used successfully with sparrows in similar experiments (e.g. Pearson 1991). Also, the large size of millet allowed for easier reclamation of the uneaten seed. Millet (mean mass=10.4706±0.1561 g) was measured out using the levelled volume of a small plastic container and distributed equally over the entire area of the seed tray. The samples of millet were placed on each seed tray between 0615 and 0645 of the days censuses were taken. Millet left on the seed trays was reclaimed between 1400 and 1600 on the day that the seed was put out, except for 5 March when heavy rains in the afternoon prevented reclamation. The reclaimed food from each tray was put into an individually marked zip-lock plastic bag using a plastic funnel and jug. These reclaimed samples were later

weighed using a Sartorius balance to 10^{-4} g. The depletion for each tray was calculated by subtracting the mass reclaimed from the initial mean mass. The millet was added and reclaimed daily to prevent consumption by rodents during the night. In addition, this method allowed the experiment to be run on a daily basis, which allowed for the removal of confounding factors such as the effects of precipitation and temperature when the data were pooled. However, the total consumption of all of the millet on certain seed trays may have resulted in birds foraging in non-preferred locations and the inability to differentiate the order of preference among the feeding trays which were totally depleted. This prevented calibration of the spatial patterns of within-plot resource depletion to the degree desired.

Data Analysis

The data were analyzed on four different scales. On the scale of the system as a whole, the census data were pooled to determine total and species numbers. The between-plot patterns of patch selection were tested for treatment effects using a two-way ANOVA for census data. A one-way ANOVA was used for the seed depletion data to test for the effect of a brush station on patch selection between food addition plots. Depletion data for all tests were rounded to one decimal place, because of the relatively large standard deviation (± 0.1561 g) in the amount of millet placed on each seed tray.

Chi-square frequency tests were used to test for all within-plot patterns. Patterns of distribution relating to the cut and uncut areas in each plot were examined. The effect of the cut versus the uncut area on the distribution of birds was determined using both census and depletion data. Census data from the control and the food only treatments were pooled and compared to the pooled data from the brush station only and food and brush station treatments to look at the effect of the presence of a brush station on the distribution between cut and uncut areas. This effect also was tested by comparing the depletion data from the food only and the food and brush station sites. Control and brush station only census data were pooled and compared to food only and food and brush station census data to determine the effect of food on the distribution between cut and uncut areas. The effect of the cut and the uncut areas on the distribution of Song and Field Sparrows was tested by comparing census data.

The spatial distribution patterns within each plot were considered, again using chi-square frequency tests. Since the high resource densities associated with the seed trays most likely affected the spatial distribution of birds within the plots, only those birds found within 1 m of a seed tray, and thus considered to be influenced by that tray, were considered for the analysis of the within-plot spatial patterns. Therefore, the birds could be grouped into categories of 1 m, 5 m, 10 m, and 15 m from the center of the plot. The effect

of the cut and the uncut areas on the spatial distribution patterns were tested using both census and depletion data. Census data were used to examine the effect of a brush station on the patterns. Finally, the effect of a brush station on the patterns of depletion in both the cut and the uncut areas were tested.

Results

System-wide Patterns

The results can be considered on four different scales: (1) system-wide, (2) between-plot, (3) cut versus uncut areas within each plot, and (4) the spatial distribution within each plot. A total of 176 sparrows were observed during the study. Only two species were present: Song Sparrows (n=45, 26%) and Field Sparrows (n=131, 74%). The only two avian predators, one American Kestrel (*Falco sparverius*) and one Sharp-shinned Hawk (*Accipiter striatus*), were observed during the censuses. Several other avian predators were seen either during the set up of the study site, during seed reclamation, or over adjacent fields. They include: Sharp-shinned Hawks (2), Red-tailed Hawks (*Buteo jamaicensis*) (2), and an American Kestrel.

Between-plot patterns

The effect of brush stations on patch selection was found not to be significant when the census data was considered

(Tables 1, 2). However, the depletion data showed a significant effect of brush stations on patch selection between food only and food and brush station treatments with higher rates of depletion on plots with brush stations (Tables 3, 4). The addition of food was found to have only a marginally significant effect on patch selection (Tables 1, 2). A greater number of birds were found on food addition plots. Further, the combination of food and brush station also had no significant effect on distribution between plots (Table 1, 2). The lack or marginal significance of food, brush stations, or a combination of the two on patch selection most likely can be explained by the high variance in numbers of birds and in depletion between replicates (Tables 1, 3).

Within-plot patterns

Cut versus Uncut

The presence of herbaceous vegetation, which acts as screening cover for sparrows (Watts 1990), was found to have a significant effect on the within-patch distribution of sparrows. A total of 150 (85%) of the sparrows were found on the uncut areas of patches, while only 26 (15%) were found on the cut areas. This distribution pattern is significantly different from an expected even distribution ($X^2 > 100$, $P < 0.001$) suggesting that the sparrows preferred to forage in weedy cover. Patterns of seed depletion were also different for cut and uncut areas ($X^2 > 100$, $P < 0.001$). Seed trays in uncut areas

Table 1: Total number of birds in each replicate by treatments

	Treatment			
	Brush+Food	Brush	Food	Control
Replicate #1	73	1	43	7
Replicate #2	24	14	14	0
Total	97	15	57	7

Table 2: Two-way ANOVA for the effects of food addition, brush stations, and the combination of the two on patch selection using census data.

Source	SS	DF	MS	F	P
Brush	288.0	1	288.0	0.658	NS
Food	2244.5	1	2244.5	5.127	0.1 > P > 0.05
Brush x Food	128.0	1	128.0	0.292	NS
Error	1751.0	4	437.8		

Table 3: Mean total depletion in grams in each replicate by treatments

	Treatment	
	Brush	No Brush
Replicate #1	74.6	31.0
Replicate #2	62.6	13.5
Mean	68.6	22.2

Table 4: One-way ANOVA for the effect of brush stations on patch selection using seed depletion data.

Source	SS	DF	MS	F	P
Brush	2151.6	1	2151.6	19.195	<0.05
Error	224.2	2	112.1		

were depleted at 1.8 times the rate as compared to those in cut areas. The direction of this depletion pattern was consistent with bird observations.

While both Song and Field Sparrows showed a strong preference for the uncut areas of patches, there was a significant difference in the response of the two species to the cut areas ($X^2 > 100$, $P < 0.001$) (Figure 5). Forty-one (41) of forty-five (45) Song Sparrows (91%) were observed on uncut areas compared to 109 of 131 Field Sparrows (83%), suggesting that Song Sparrows had a comparatively greater affinity for screening cover.

Both food and brush stations had significant effects on the distribution of birds between cut and uncut areas. The addition of food had a significant effect ($X^2 = 8.0$, $P < 0.005$) with more birds found on the cut areas in food addition plots as compared to those without food (Figure 6). The census data showed that brush stations had a significant effect ($X^2 > 100$, $P < 0.001$) on distributions with a higher percentage of birds utilizing the cut areas when brush stations were present (Figure 7). This result is supported by the significantly higher depletion of seed trays in the cut areas of plots with brush stations as compared to those without brush stations ($X^2 > 100$, $P < 0.001$) (Figure 8).

Distance from Center

The effects of cut and uncut areas, brush stations and

Figure 5: The effect of cut and uncut areas on the within-patch distribution of Song and Field Sparrows. A significant difference was found between the responses of the species to cut areas ($\chi^2 > 100$, $df=1$, $P < 0.001$).

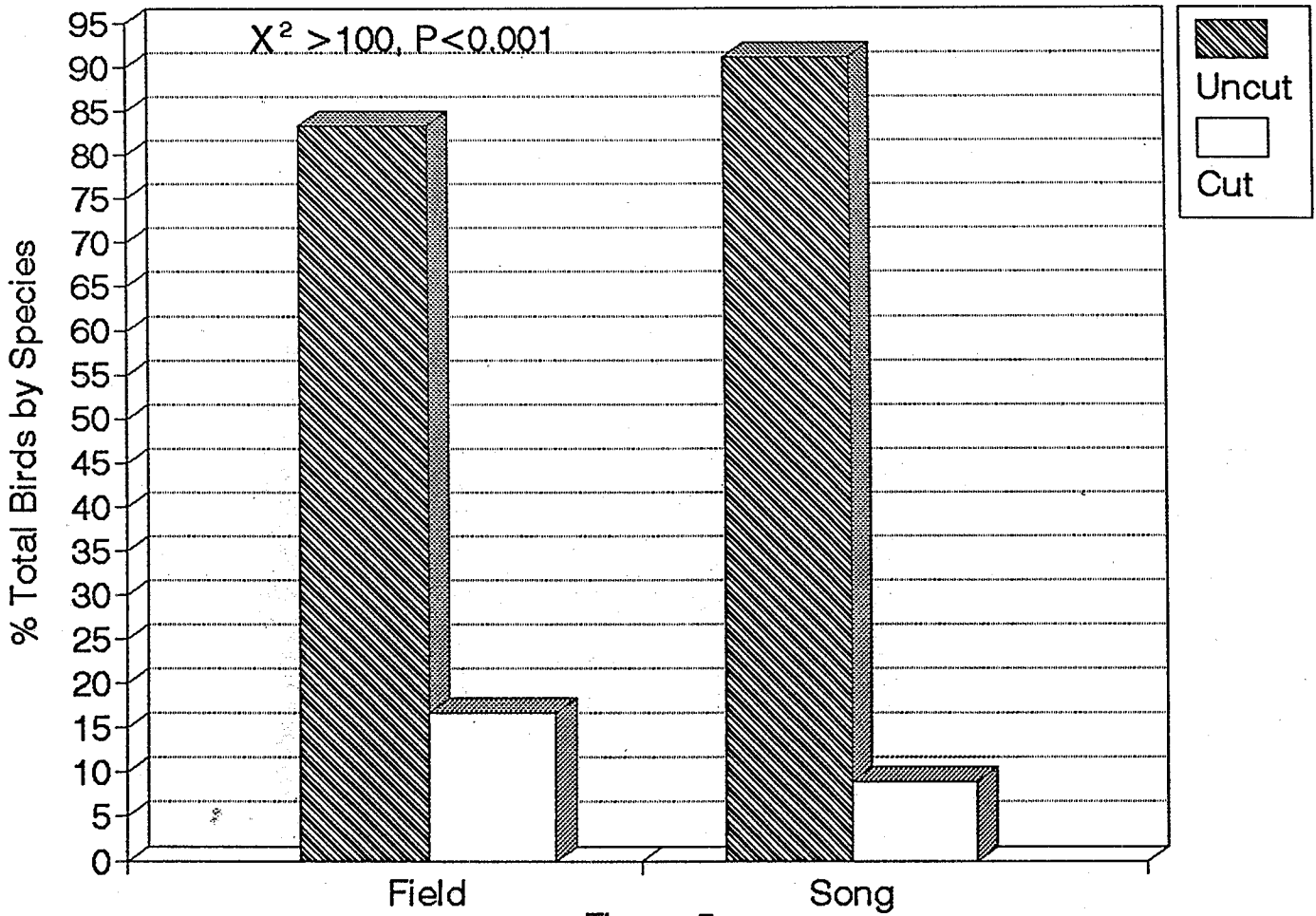


Figure 5

Figure 6: The effect of food addition on distribution between cut and uncut areas. Food addition was found to have a significant effect on distribution between cut and uncut areas ($\chi^2=8.0$, $df=1$, $P<0.005$).

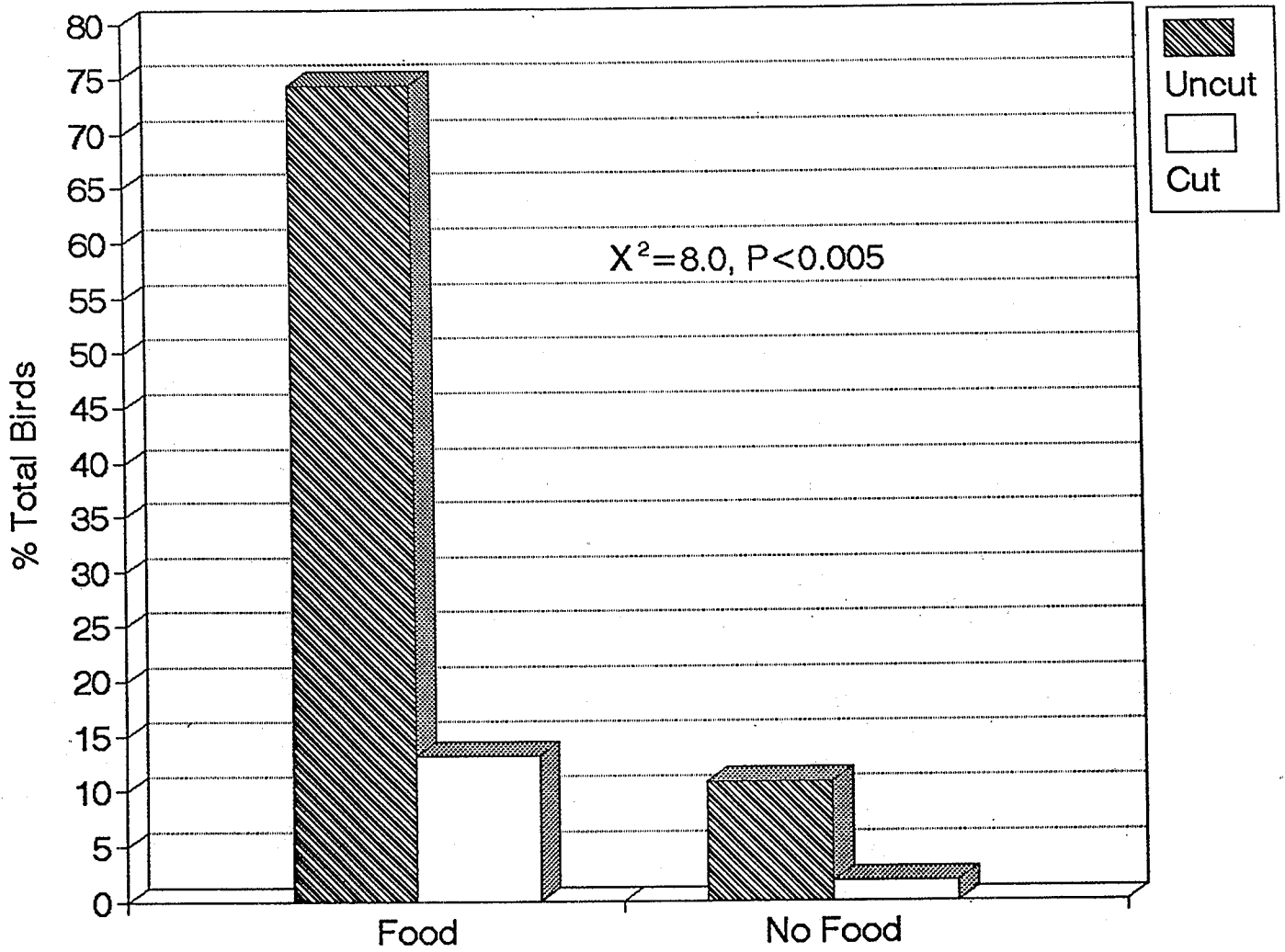


Figure 6

Figure 7: The effect of brush stations on distribution between cut and uncut areas. Distribution between cut and uncut areas was affected significantly by brush stations ($\chi^2 > 100$, $df=1$, $P < 0.001$).

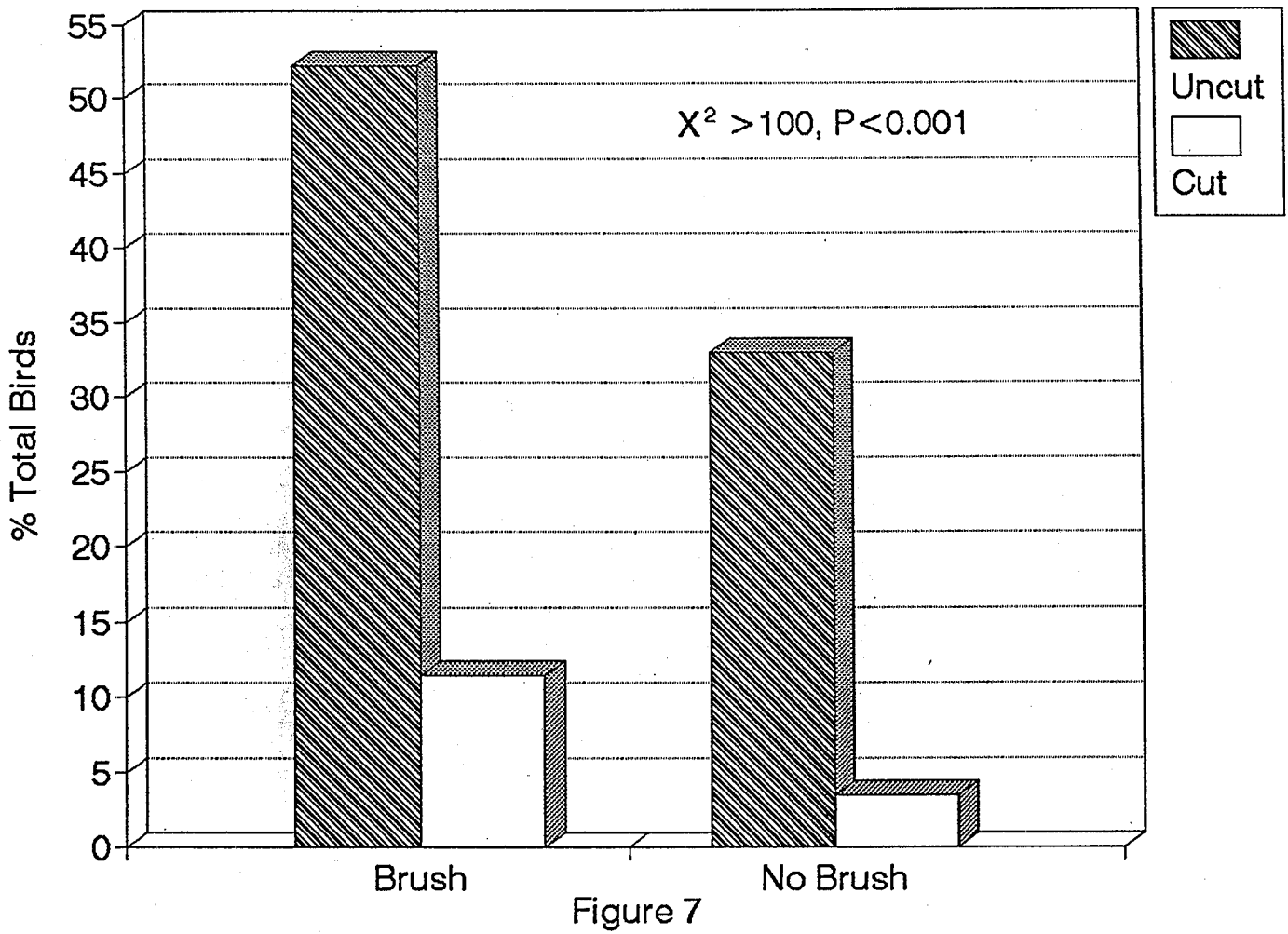


Figure 8: The effect of brush stations on seed depletion between cut and uncut areas. Brush stations significantly affected mean total depletion between cut and uncut areas ($X^2 > 100$, $df=1$, $P < 0.001$).

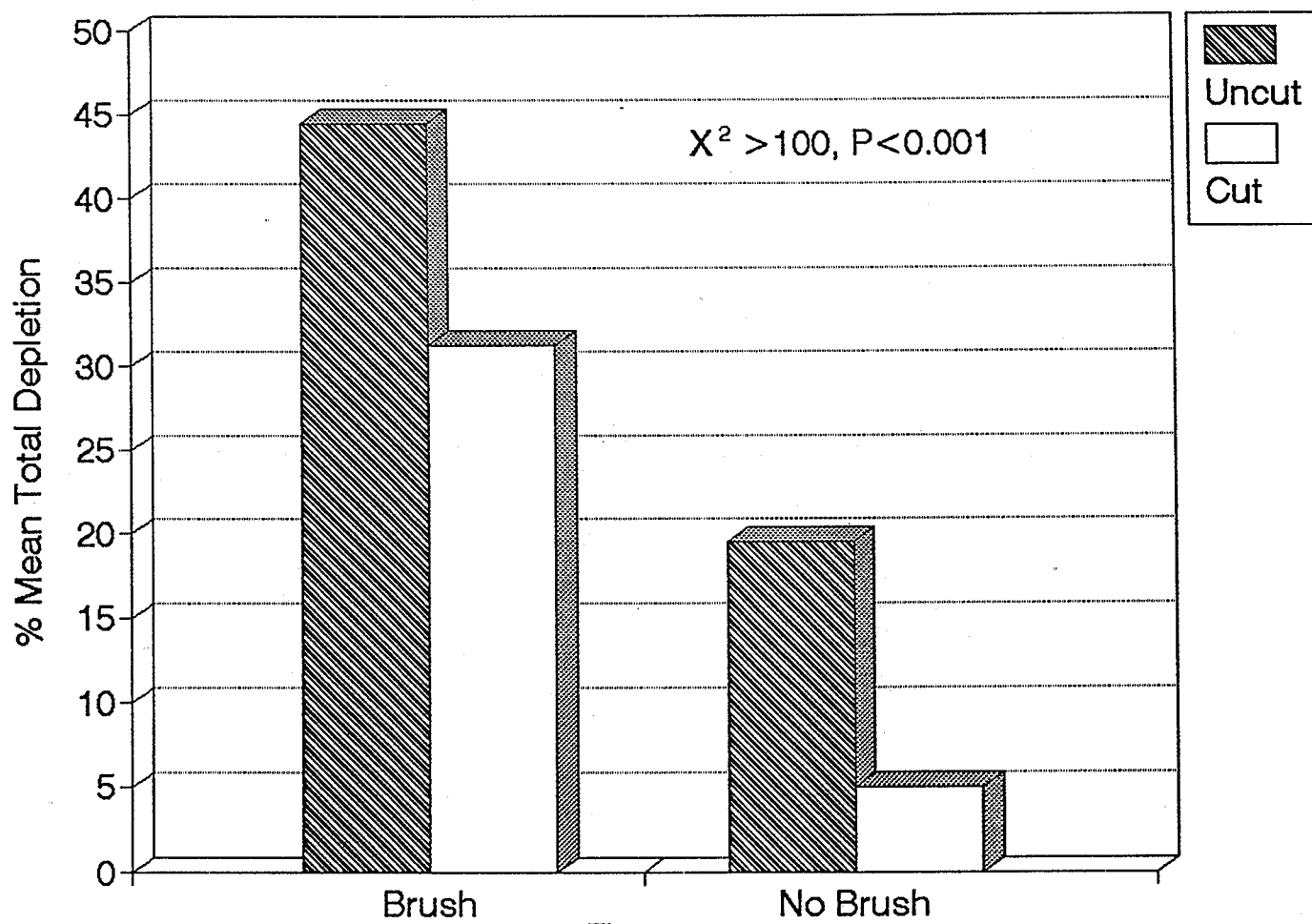


Figure 8

combinations of the two on patterns of spatial distribution of birds within plots were examined. A significant difference was found between the spatial distribution in cut and uncut areas ($X^2 > 100$, $P < 0.001$). In the cut areas, the highest percentage of birds was found associated with the first feeding tray adjacent to the center of the plot (Figure 9). In contrast, birds observed on uncut areas were not concentrated near plot centers. The seed depletion data showed a significant difference in spatial patterns between the cut and the uncut areas ($X^2 = 67.6$, $P < 0.001$). The percentage of mean total depletion was essentially equal for all seed trays on the uncut side, while on the cut side the highest depletion was on the seed tray closest to the center (Figure 10). The differences between the census data and the depletion data in patterns of spatial distribution in the uncut areas suggest changes in patterns of distribution throughout the day.

Brush stations were found to have a significant effect on the patterns of spatial distribution ($X^2 > 100$, $P < 0.001$). However, the patterns did not show a positive skew toward the brush stations (Figure 11). Therefore, it seems that these patterns may have been related to patterns of cover density within the plots. As a result, the statistically significant difference in distribution between plots with a brush station and those without may not have reflected a biologically significant difference between these two treatments. In

Figure 9: The effect of cut and uncut areas on within-patch patterns of spatial distribution. Spatial distribution in uncut areas was significantly different from that in cut areas ($\chi^2 > 100$, $df=3$, $P < 0.001$).

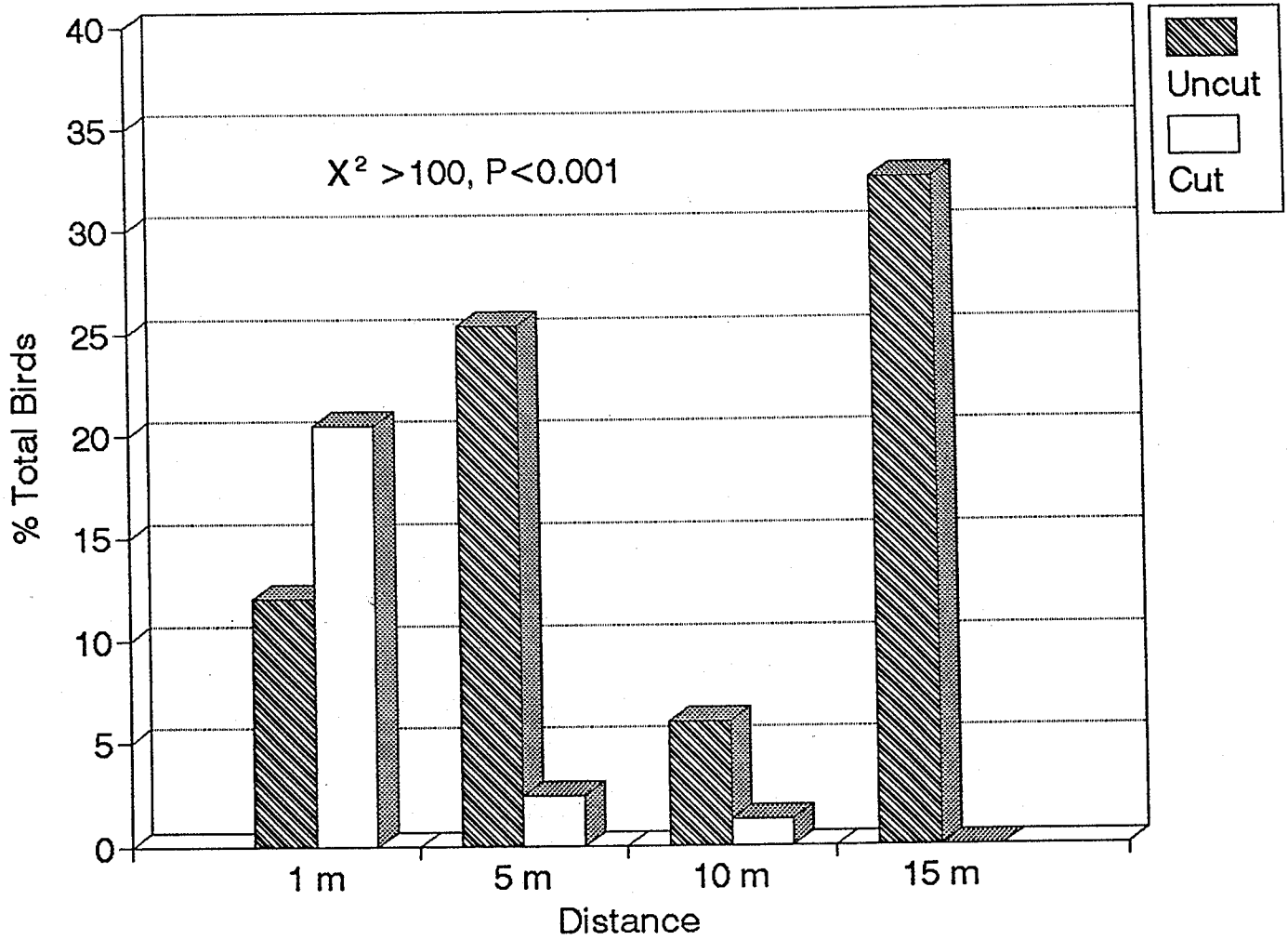


Figure 9

Figure 10: The effect of cut and uncut areas on spatial patterns of seed depletion. Patterns of depletion between cut and uncut area were found to be significantly different ($\chi^2=67.6$, $df=3$, $P<0.001$).

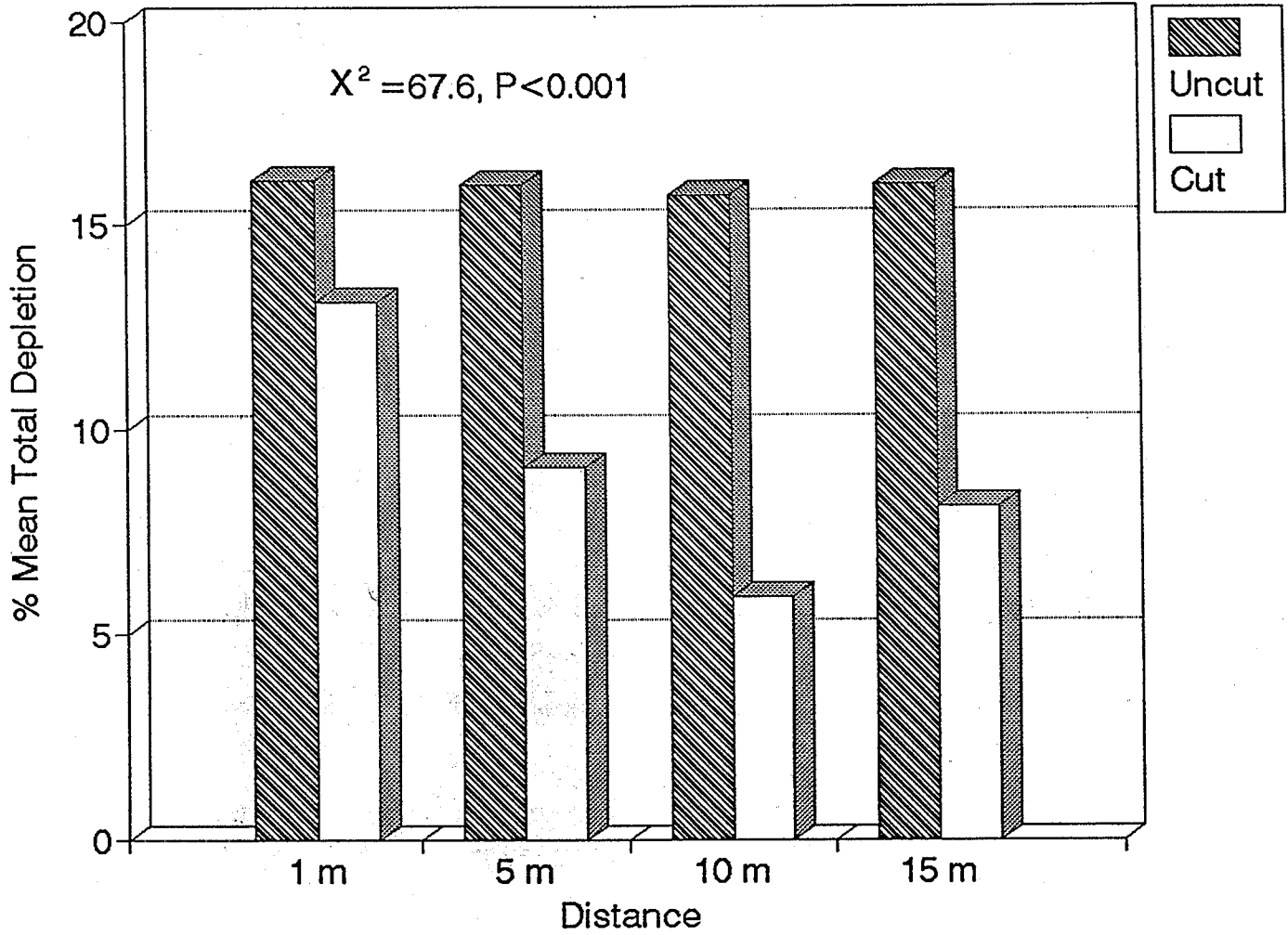


Figure 10

Figure 11: The effect of brush stations on within-patch patterns of spatial distribution. Brush stations were found to have a significant effect on spatial patterns ($X^2 > 100$, $df=3$, $P < 0.001$).

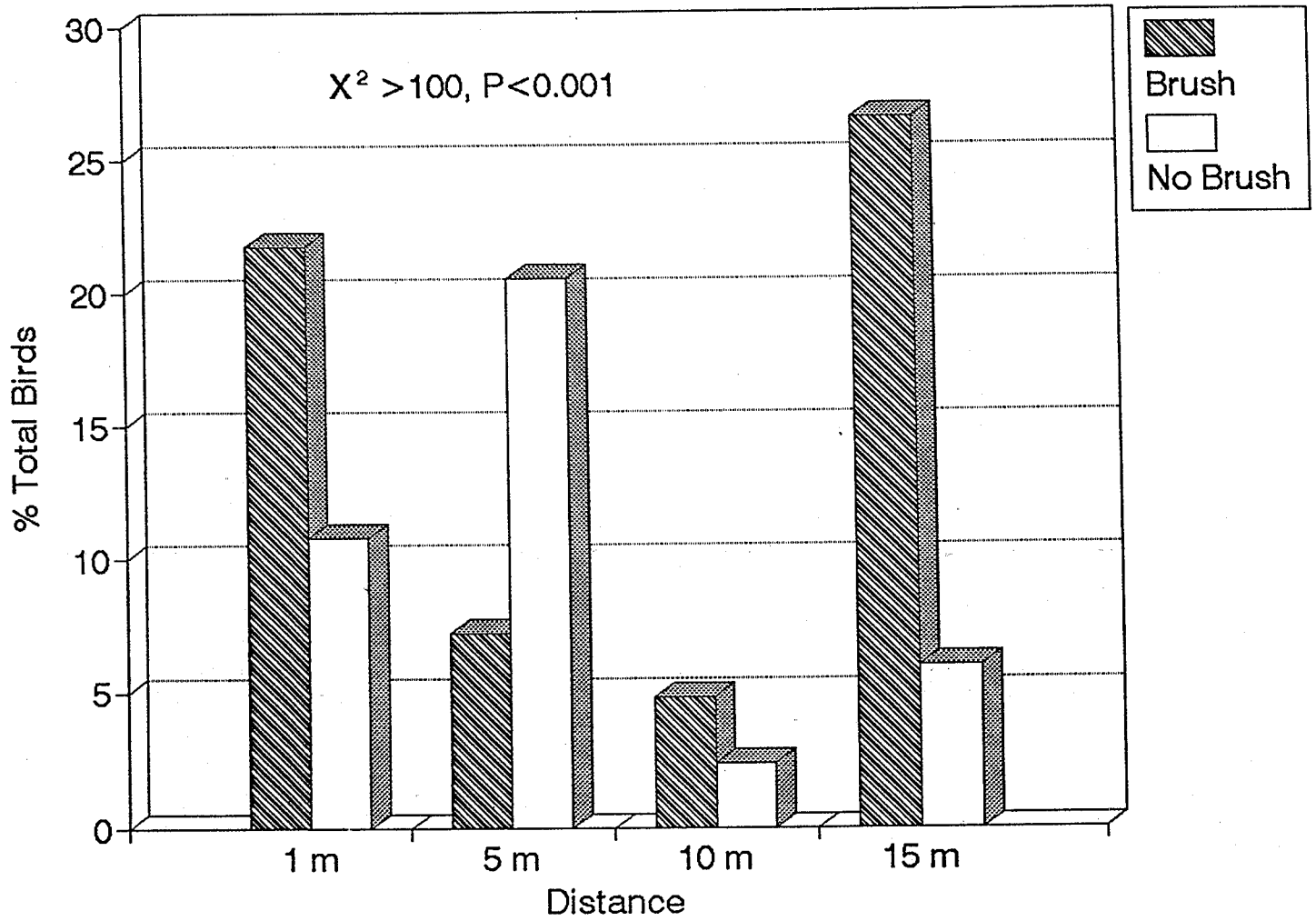


Figure 11

support of this suggestion, the seed depletion data showed no significant effect of brush stations on spatial patterns of depletion in the uncut areas ($X^2=1.5$, N. S.). However, spatial patterns of depletion in cut areas were affected significantly by brush stations ($X^2=19.1$, $P<0.001$). These patterns showed the highest percentage of depletion in cut areas on seed trays adjacent to brush stations (Figure 12). This pattern suggests that the brush stations were used as refuges for birds foraging in the uncut areas.

Discussion

Between-patch Patterns

Several studies have shown that certain species of sparrows prefer to forage close to woody cover (Grubb and Greenwald 1982, Lima 1990, Lima et al. 1987, Pulliam and Mills 1977, Schneider 1984). This suggests that the presence of woody cover may be important in patch selection. Further, it is generally understood that an organism will forage in the patch with the highest resource density, all else being equal (e.g. Gilliam and Fraser 1987, MacArthur and Pianka 1966). However, the between-patch patterns of distribution found in this study do not support these ideas.

Brush stations were found to have no significant effect on patch selection when census data were considered (Tables 1, 2). However, between food only and food and brush station treatments, the depletion data showed a significant effect of

Figure 12: The effect of brush stations on patterns of seed depletion in cut areas. Patterns of seed depletion in cut areas were affected significantly by brush stations ($\chi^2=19.1$, $df=3$, $P<0.001$).

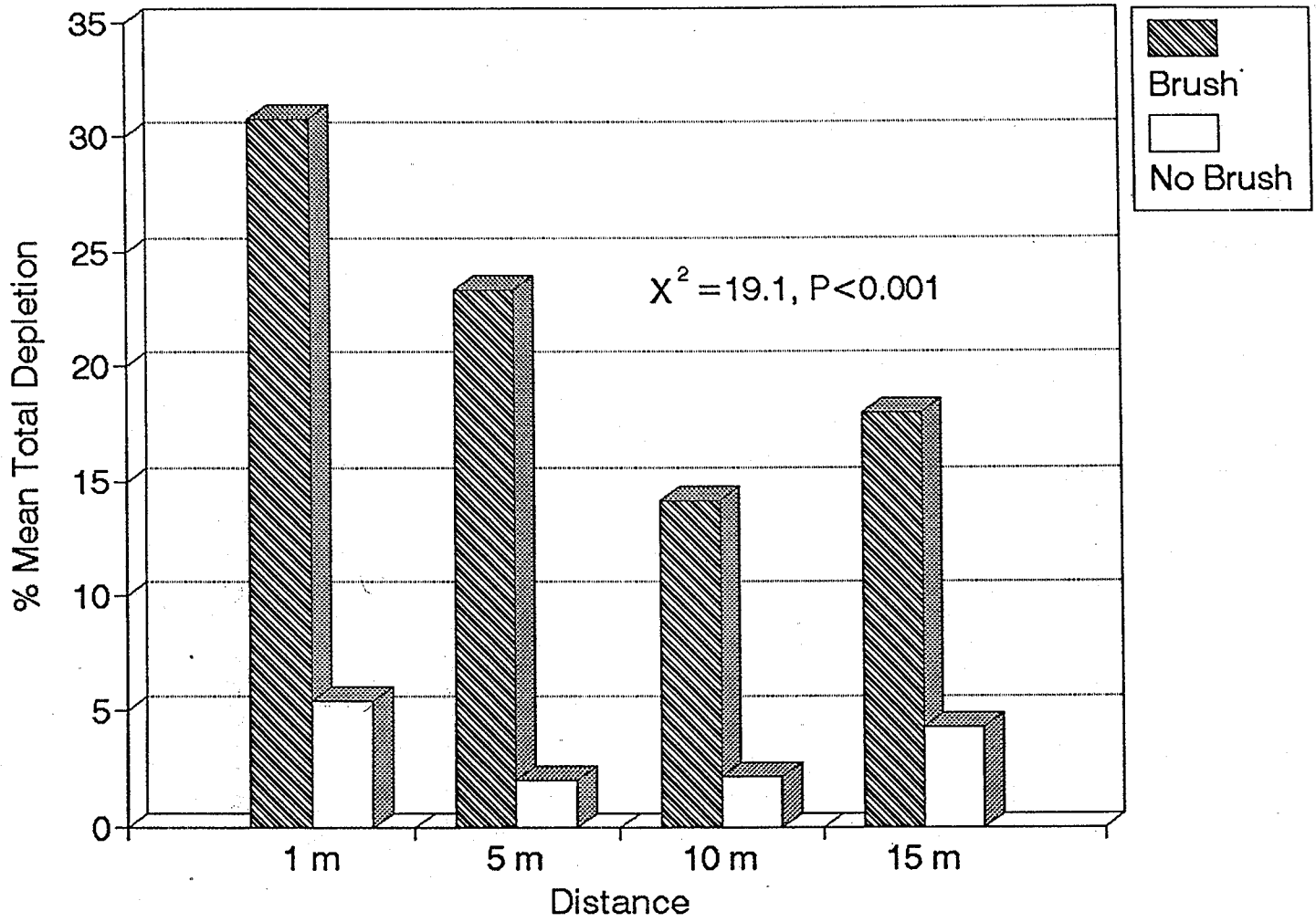


Figure 12

brush stations on patch selection with greater depletion in plots with brush stations (Tables 3, 4). The addition of food had only a marginally significant effect on between-patch patterns of distribution (Tables 1, 2). A higher number of birds were observed on food addition plots. Further, patch selection was not significantly affected by the combination of food and brush (Tables 1, 2).

The lack or marginal significance of food, brush stations, or the combination of the two on patch selection has several possible explanations. First, these treatments actually may have no effect on patch selection for Song and Field Sparrows. However, there was a high variance in the number of birds and in seed depletion between replicates (Tables 1, 3). As a result, the effects of food addition and brush stations on patch selection could not be separated with confidence due to a lack of information. This high variance between replicates could have resulted from differences in proximity to edge, in edge type, and in composition and density of vegetation between plots, despite the fact that these factors were controlled to the extent possible. Alternatively, this level of variation may be inherent to the system. If true, more replicates were needed to be confident of the treatment effect. In addition, the low number of predators may have lessened the importance of woody cover in this system compared to a system with a higher predation risk. Furthermore, the marginal significance of food addition on

patch selection suggests that more than resource densities were determining between-patch patterns of distribution.

Within-patch patterns of distribution between cut and uncut areas show that both herbaceous vegetation acting as screening cover and brush stations used for escape significantly affected patterns of distribution. Across all treatments, the importance of herbaceous vegetation as screening cover in predator avoidance is demonstrated by the significantly higher number of birds observed in the uncut areas. This is in agreement with the observation by Watts (1990) of increased risk of predation in open habitats in both Song and Savannah Sparrows. Watts noted differential use and mortality in open habitats between the two species. Similarly, Field Sparrows were found in cut areas more often than Song Sparrows, suggesting that Field Sparrows have a lower risk of predation in these areas (Figure 5). Seed depletion was also higher in the uncut areas. Grubb and Greenwald (1982) noted a similar pattern. When resource densities were equal along the range of predation risk, House Sparrows (*Passer domesticus*) foraged in the patch with the lowest risk of predation.

In addition to herbaceous vegetation acting as screening cover, brush stations also influenced within-patch distribution (Figure 7). More birds were found in cut areas on plots with brush stations compared to those without. This trend also was seen in patterns of seed depletion (Figure 8).

An increase in the use of cut areas on plots with brush stations suggests that the presence of woody vegetation allows birds to forage in areas of higher risk. Therefore, when woody cover is present, birds may better invade surrounding areas, thereby increasing their foraging range.

Food addition was also found to have a significant effect on the distribution of birds between cut and uncut areas (Figure 6). Significantly more birds were observed on cut areas with food addition compared to those without. By comparing patterns of spatial distribution in census data with spatial patterns of seed depletion, it can be seen that birds only foraged in cut areas when uncut areas were totally depleted. This direction of depletion follows Gilliam and Fraser's model that states that an organism will forage in the habitat or microhabitat in which the ratio of predation risk to foraging rate is minimized. This model also predicts that food addition would have a significant effect on the use of cut areas. If predation risk is equal in all cut areas, birds would forage in those areas with the highest resources.

The importance of proximity to woody cover seems to decline as the density of screening cover increases. It appears that the perceived risk of predation decreases with an increase in screening cover. As a result, birds will forage farther from woody cover in areas of higher density of screening cover. Within-patch patterns of spatial distribution and seed depletion seem to support this idea

(Figures 9, 10). Although brush stations were found to have a statistically significant effect on spatial patterns, the highest percentage of birds were observed 15 m from the brush station (Figure 11). This may suggest that something other than woody vegetation, such as patterns of cover density, was influencing space use.

In support of this suggestion, a significant difference was found in spatial distribution between cut and uncut areas (Figure 9). In uncut areas, there was no clear pattern of spatial distribution; the highest percentage of birds were found 15 m from the centers of plots. This supports the idea that in areas with dense weed cover, close proximity to woody vegetation becomes less important and, thus, birds will forage farther from woody cover. In uncut areas, the lack of a pattern of spatial distribution may suggest a spatial pattern related to densities of herbaceous vegetation, with the highest percentage of birds foraging where the density of vegetation was the highest. In cut areas, most birds were on the seed tray adjacent to the brush station or 1 m from the uncut area on food only plots. The close proximity to either the woody vegetation of the brush station or the herbaceous vegetation of uncut areas would allow for easier escape from predators. Therefore, it appears that in areas with sparse weed cover, patterns of spatial distribution were influenced more strongly by cover for escape.

Spatial patterns of seed depletion also support the idea

that high screening cover density moderates the importance of woody vegetation in determining spatial distribution. In uncut areas, brush stations had no significant effect on spatial patterns of seed depletion. In contrast, in cut areas, spatial patterns of depletion were significantly affected by brush stations (Figure 12). In cut areas, the highest percentage of depletion occurred on seed trays adjacent to the brush stations. The seed trays at 5 m also had higher depletion rates than would be expected if no brush station were present. Importantly, close proximity to herbaceous vegetation, which also acts as a refuge, also had an effect on spatial patterns of depletion in uncut areas of plots without brush stations. The highest percentage of depletion occurred on seed trays within 1 m of the uncut areas and at 15 m (5 m from herbaceous vegetation off of the defined plots).

Several studies have shown that different species of finches respond differently to the presence of cover (Lima 1990, Lima and Valone 1991, Pulliam and Mills 1977, Watts 1990). These different responses have been suggested to reflect interspecific differences in vulnerability to predators. If true, it follows that species may choose among the array of possible habitats those habitats with specific physical characteristics (Lima 1993). One extension of this idea is that the composition of a given habitat may determine

patterns of species coexistence (Lima and Valone 1991).

In this study, cover also was found to affect the distribution of sparrows within patches. More importantly, Song and Field Sparrows showed differential use of cut areas. Watts (1990) suggested that differences in the use of open habitats by Song and Savannah Sparrows may provide a simple, spatial mechanism which promotes coexistence. Differences in the distribution of Song and Field Sparrows may suggest a similar mechanism for coexistence within the current system.

The greater use of cut areas by Field Sparrows may suggest that they are less vulnerable to predation than Song Sparrows in areas with low weed density. This agrees with the observation that Field Sparrows generally are found in moderately dense vegetation, whereas Song Sparrows are found in dense vegetation (Lima 1993). As a result, in a heterogeneous field, only Field Sparrows would be found in moderately dense patches, leading to spatial segregation between the species. Further, this would suggest that at a given density of vegetation Field Sparrows may perceive a lower risk of predation than would Song Sparrows.

It was suggested above that the influence of woody vegetation on patterns of spatial distribution seemed to be moderated by screening cover. Since the density of screening cover relates to the perceived risk of predation and this relationship differs among species, the extent of this moderation may also be species specific. In this case, Song

Sparrows probably would be found closer to woody vegetation than Field Sparrows. As a result, spatial overlap between the two species may be reduced. Unfortunately, the low number of birds utilizing plots did not allow this pattern to be examined. However, Pulliam and Mills (1977) observed different species foraging at different distances from woody cover. This suggests a similar mechanism of species coexistence.

Differences in perceived risk of predation among species at a given density of cover and the relationship of these differences to species coexistence in winter sparrow assemblages need to be examined more carefully. The effect of cover density on patterns of spatial distribution among species could be examined by establishing treatments with different, measured densities of weedy cover. All treatments would have brush stations for woody cover. Differences among species in distribution between and within treatment plots and in the effect of woody cover on distribution may suggest differences in the perceived risk of predation at different cover densities. These differences in perceived risk of predation and distribution among species may suggest a mechanism of habitat selection, of assemblage composition, of species' distribution in a heterogeneous habitat, and of species coexistence similar to the one discussed above.

Acknowledgements

I would like to acknowledge Mr. Montay Smith and Mr. Dudley Waltrip for their generous permission to use their land. I would like to thank Dr. Bryan Watts for his help throughout the entire process of this study, but especially in the writing of the manuscript, and Dr. Stewart Ware for the use of his lab. Amanda Allen, Ivy Hamby, Jennifer Beck, and Tanya Myers were all a great help in the field. Finally, I would like to thank my father, Dr. Robert Beck, who assisted in putting together the figures.

Literature Cited

- Bland, J. D. and S. A. Temple. 1990. Effects of predation -risk on habitat use by Himalayan Snowcocks. *Oecologia* 82:187-191.
- Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's Kangaroo Rat: harvesting rates and predatory risk. *Ecology* 71:2334-2344.
- Davis, J. 1973. Habitat preferences and competition of wintering juncos and Golden-crown Sparrows. *Ecology* 54:174-180.
- Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68:1856-1862.
- Grubb, T. C. and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Animal Behavior* 30:637-640.
- Holbrook, S. J. and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69:125-134.
- Kotler, B. P. 1984. Risk of predation and structure of desert rodent communities. *Ecology* 65:689-701.

- Lima, S. L. 1985. Maximum feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. *Oecologia* **66**:60-67.
- . 1990. Protective cover and use of space: different strategies in finches. *Oikos* **58**:151-158.
- . 1993. Ecological and evolutionary perspectives on escape from predatory attack: survey of North American birds. *Wilson Bulletin* **105**:1-47.
- and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**:619-640.
- and T. J. Valone. 1991. Predators and avian community organization: an experiment in a semi-desert grassland. *Oecologia* **86**:105-112.
- , K. L. Wiebe and L. M. Dill. 1987. Protective cover and the use of space by finches: is closer better? *Oikos* **50**:225-230.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603-609.
- Pearson, S. M. 1991. Food patches and the spacing of individual foragers. *Auk* **108**:355-362.
- Pitcher, T. J., S. H. Lang and J. A. Turner. 1988. A risk-balancing trade off between foraging rewards and predation hazard in shoaling fish. *Behav. Ecol. Sociobiol.* **22**:225-228.
- Pulliam, H. R. 1975. Coexistence of sparrows: a test of community theory. *Science* **184**:474-476.
- . 1983. Ecological community theory and the coexistence of sparrows. *Ecology* **64**:45-52.
- . 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. *Ecology* **66**:1829-1836.
- and F. Enders. 1971. The feeding ecology of five sympatric finch species. *Ecology* **52**:557-566.
- and G. S. Mills. 1977. The use of space by wintering sparrows. *Ecology* **58**:1393-1399.
- Schneider, K. J. 1984. Dominance, predation, and optimal

foraging in White-throated Sparrow flocks. *Ecology* 65:1820-1827.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041-1043.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Company, New York.

Watts, B. D. 1990. Cover use and predator-related mortality in Song and Savannah Sparrows. *Auk* 107:775-778.

----- . 1991. Effects of predation risk on distribution within and between habitats in Savannah Sparrows. *Ecology* 72:1515-1519.