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HABITAT SELECTION AND TERRITORY SIZE REGULATION  
IN THE VESPER SPARROW (POECCETES GRAMINEUS)

by

J. Michael Reed

B.A. Millersville State College, 1981

Presented in partial fulfillment of  
the requirements for the degree of

Master of Arts

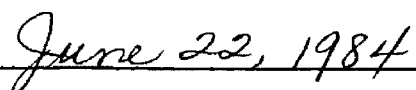
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J. Michael Reed, M.A., June 1984      Zoology

Habitat selection and territory size regulation in the Vesper Sparrow (Poocetes gramineus) (75 pp.)

Director: Dr. Richard L. Hutto



I recorded the size and placement of Vesper Sparrow territories during the breeding seasons of 1982 and 1983 in Missoula County, Montana, to compare an adaptation of the flush method with the spot-mapping method for mapping Vesper Sparrow territories. Each of seven territories was mapped using the flush and spot-map methods. Territorial boundaries were delimited using four standard techniques so that I could determine whether my results were sensitive to the analytical methodology used. The flush method of mapping territories was faster and more representative of the area used by the bird than was spot-mapping.

To investigate the relationship of certain environmental variables with territory size and placement by Vesper Sparrows an adaptation of the flush method was used to map 60 territories. Arthropod densities and 13 variables associated with vegetation structure were measured to determine if any were related to territory size. Territory size was correlated with the number of perches, perch height, vegetation height, and horizontal vegetation density. Since the variables were highly intercorrelated regression analysis was used. Only horizontal vegetation density was significantly related to territory size. Arthropod density was not correlated with territory size, and appeared to be a non-limiting resource.

175 sample points were located at one of the study sites and at each point 11 variables associated with vegetation structure were measured. I compared vegetation variables associated with the following categories: 1) points included within territories vs. those outside territorial boundaries, 2) randomly chosen sample points vs. points within territories and vs. points outside the territories, and 3) points falling within each of six territories. Discriminant function analysis (DFA) showed significant differences in vegetation structure between sample points within and those outside territories. Vegetation structure could be described as a continuum from short, dense vegetation with a high percentage of ground cover in used areas to tall, patchy vegetation in unused areas. Random sample points could be discriminated from points in used areas but not from points in unused areas. The territories were placed in areas with discernibly different vegetation structure. The same four variables were significant in each DFA: horizontal vegetation density, vertical vegetation density, percent ground cover, and mean vegetation height. Horizontal vegetation density had the strongest effect in each analysis.

"It is fairly safe to assume that, if two observers are competent and upright, their contradictory results, no matter on what subject, will prove essential to the final solution of the problem."

Frank Cramer

The Method of Darwin

1896, P. 69

A. C. McClurg and Co., Chicago

This thesis is written in two chapters. The first chapter is entitled "A comparison of the "flush" and spot-map methods for estimating the size of Vesper Sparrow territories." It reports the results of a study to test the applicability of the mapping method I used to map territories. The second chapter has the same title as the thesis ("Habitat selection and territory size regulation in Vesper Sparrows") and contains the primary research for my thesis.

These two chapters are written as papers that will be submitted for publication. Each has its own literature cited.

The research, analyses, and writing for my Master's thesis were truly the learning experience they should have been.



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First of all I would like to thank Douglas S. Laye for providing assistance and companionship during both of my field seasons and for thought-stimulating questions and discussions throughout my work.

I would like to thank Thomas K. Bicak for showing me the ropes of graduate school, and helping me early on, while forming my research ideas. I also thank Nathaniel Schambaugh and Paul Hendricks for reading part of my manuscript and providing helpful insights and advice. Moira Ferguson and Dr. Andrew Sheldon gave me much-needed help teaching me what discriminant analysis is all about. I thank Steve Howe for help with some of the computer work. Dr. Donald Jenni supplied moral support and helpful criticism of this manuscript and helped me think clearly about research. Dr. George McRae also provided helpful criticism for this thesis and gave advice on statistics and on calculating territory sizes.

I thank Dr. Richard Hutto for advice on my manuscripts, interpreting results, guiding my research and thinking, and being patient with me when I know at times he would rather have beaten me.

I also thank Karlen Reed for her support, encouragement, companionship, and for putting up with my moods.

This research was partially financed by the Department of Zoology, the University of Montana.

# A COMPARISON OF THE "FLUSH" AND SPOT-MAP METHODS FOR ESTIMATING

## THE SIZE OF VESPER SPARROW TERRITORIES

### INTRODUCTION

Spot-mapping is commonly used as a census method for birds (Williams 1936, Kendeigh 1944, Emlen 1977, Paul and Roth 1983), and it has also been used to delimit individual territories or "known use" areas (Zimmerman 1971). Spot-mapping involves mapping individual observation points throughout the day, or over a course of several days, so that territorial locations and boundaries may be drawn. A faster method of mapping territories, especially suitable for grassland species, was developed by Wiens (1969). The method (the "flush" method) involves repeatedly flushing an individual a minimum of 20 times and recording its flight path and flush sites. Together, these paths are assumed to fall within territorial boundaries (Wiens 1969). Both methods have been used in grassland research to provide estimates of territory size (spot-map--Zimmerman 1971, 1982; flush--Wiens 1973, 1974; Whitmore 1979, 1981, Rotenberry and Wiens 1980). These two methods have not been compared with respect to their relative accuracy, consistency, or usefulness in estimating territory size.

The objective of this study was to compare the accuracy and efficiency of the spot-map method for mapping territories with that of an adaptation of the flush method, using observations from the Vesper Sparrow (Pooecetes gramineus), a common grassland bird species. I used

four standard techniques of delimiting territorial boundaries to examine the robustness of my results, i.e. whether the results are independent of boundary delimitation technique.

### STUDY SITE AND METHODS

The study site, a 130 ha upland plot, was situated amid the grassy slopes located 0.5 km North of Missoula, Montana (114° 00' W; 47° 48' N; elevation 980m). Vegetation was typified by Idaho fescue (Festuca idahoensis), rough fescue (F. scabrella), blue bunch wheatgrass (Agropyron spicatum), and spotted knapweed (Centurea maculosa).

I mapped seven territories using an adaptation of the flush method, whereby only flush points were used, rather than flush points plus flight paths (Wiens 1969), to delimit territories. I excluded flight paths because flight paths of some individuals crossed known territorial boundaries, as indicated by observation of habitat use and territorial skirmishes. If another Vesper Sparrow territory was invaded during the flushing, the territory owner whose boundary was crossed chased out the encroacher. These chases never occurred when an individual landed at a flush point.

After flush mapping was completed, I set up routes for spot-mapping the individuals that occupied the same territories. Each time I traversed a territory, I recorded the location of any bird seen. This technique differs from the flush method because all points are generated from the first sighting of an individual each time the path is traversed. Researchers have used as few as three repetitions of their systematic paths to delimit a territory (Williams 1936), but the International Standard for Mapping (Robbins 1970) recommends a minimum of eight visits and three sightings for census work in open habitat. To get more information on territory sightings, I repeated each systematic path 38



times and sighted each individual a minimum of 20 times.

From the points generated by both the flush and spot-map methods I estimated territory sizes using four different boundary delimitation techniques:

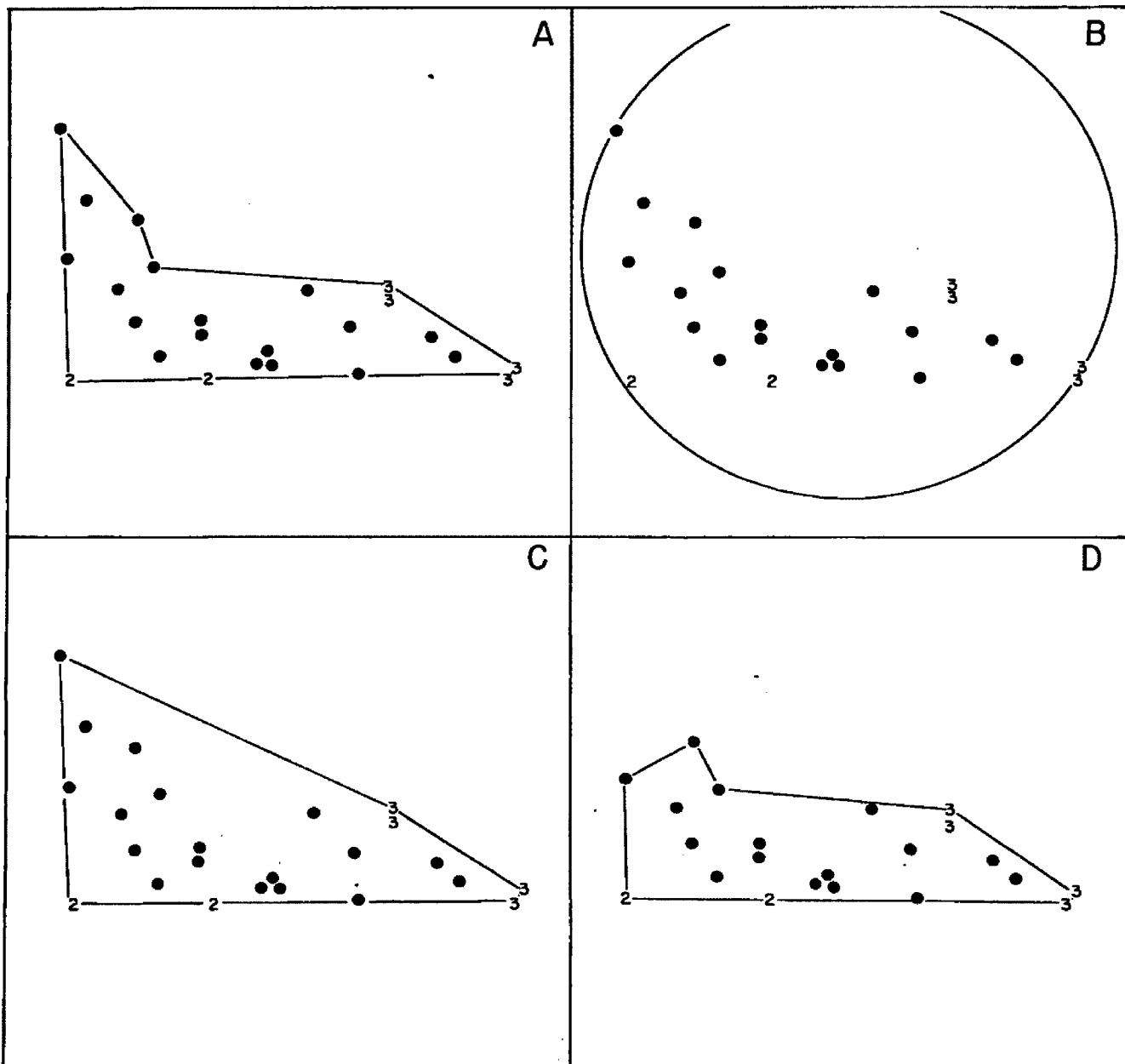
(1) Adjusted Polygon (Figure 1A)--Found by connecting the outermost points with straight lines, except that areas that were not used or defended, for whatever reason, were not included (Mohr 1947 ["minimum home range"], Janes 1959 ["composite method"], Ambrose 1969 ["adjusted home range"], Seastedt and MacLean 1979). The decision about an area's exclusion was made through repeated observations of an individual's presence in different parts of the territory. If an area was consistently unused it was excluded.

(2) Minimum Circle (Figure 1B)--The territory area was calculated by using the two most distant points as the diameter of a circle (Fitch 1958). Such a method may be reasonable for grassland species, as evidenced by the fact that the territory of the Chestnut-collared Longspur (Calcarius ornatus) is approximately circular (Harris 1944).

(3) Maximum Polygon (Figure 1C)--Found by connecting the outer-most of the cluster of points with straight lines (Odum and Kuenzler 1955, Ambrose 1969).

(4) 90% Polygon (Figure 1D)--A maximum polygon is found with the most isolated 10% of the points excluded. Stenger and Falls (1959) calculated a "utilized" territory, excluding the most isolated 5% of the

Figure 1. Plot for territory 2 using the flush method and each of the techniques of delimiting territorial boundaries: adjusted polygon (A), minimum circle (B), maximum polygon (C), and 90% polygon (D). Numbers represent multiple points.



points. I had smaller sample sizes than they, and by excluding 10% I eliminated two points from each territory for both map methods.

To determine the variability in estimating territory size using the flush method, I chose five of the seven territories that were initially mapped and remapped each four times during the following three weeks. I then compared the within-to between-territory variances in territory size. The method used for determining territorial boundaries for this part of the analysis was the adjusted polygon method (for reasons presented in the discussion).

The areas of the polygons were calculated using a digitizer.

## RESULTS

Using the adjusted polygon technique to define the territorial boundaries (Figure 2), the flush method resulted in significantly larger territory sizes than spot-mapping did (Sign test,  $n = 7$  for each method,  $P < 0.01$ ). This result held true regardless of the technique used to delimit territory boundaries (Table 1).

Territory sizes ranged from 0.29 ha (90% polygon, spot-map, territory 1), to 3.04 ha (minimum circle, flush, territory 2). The 90% polygon method consistently resulted in the smallest territory sizes, while the minimum circle resulted in the largest territory sizes (Table 1).

In the repeat-mapping portion of the study, territory sizes ranged from 0.53 ha (territory 3) to 1.13 ha (territory 5) (Table 2). I performed a nested analysis of variance (ANOVA) to determine where the variability in territory sizes was most prominent, and the most significant amount of variability occurred between territories (98.6%), rather than within territories (1.4%) ( $F = 2.60$ ,  $df = 4, 20$ ,  $P > 0.05$ ) (Table 3).

Figure 2. Flush points (left column) and spot-map points (right column) for seven Vesper Sparrow territories. Numbers represent multiple points. Territories are depicted using the adjusted polygon method.

┌───┐ = 20m

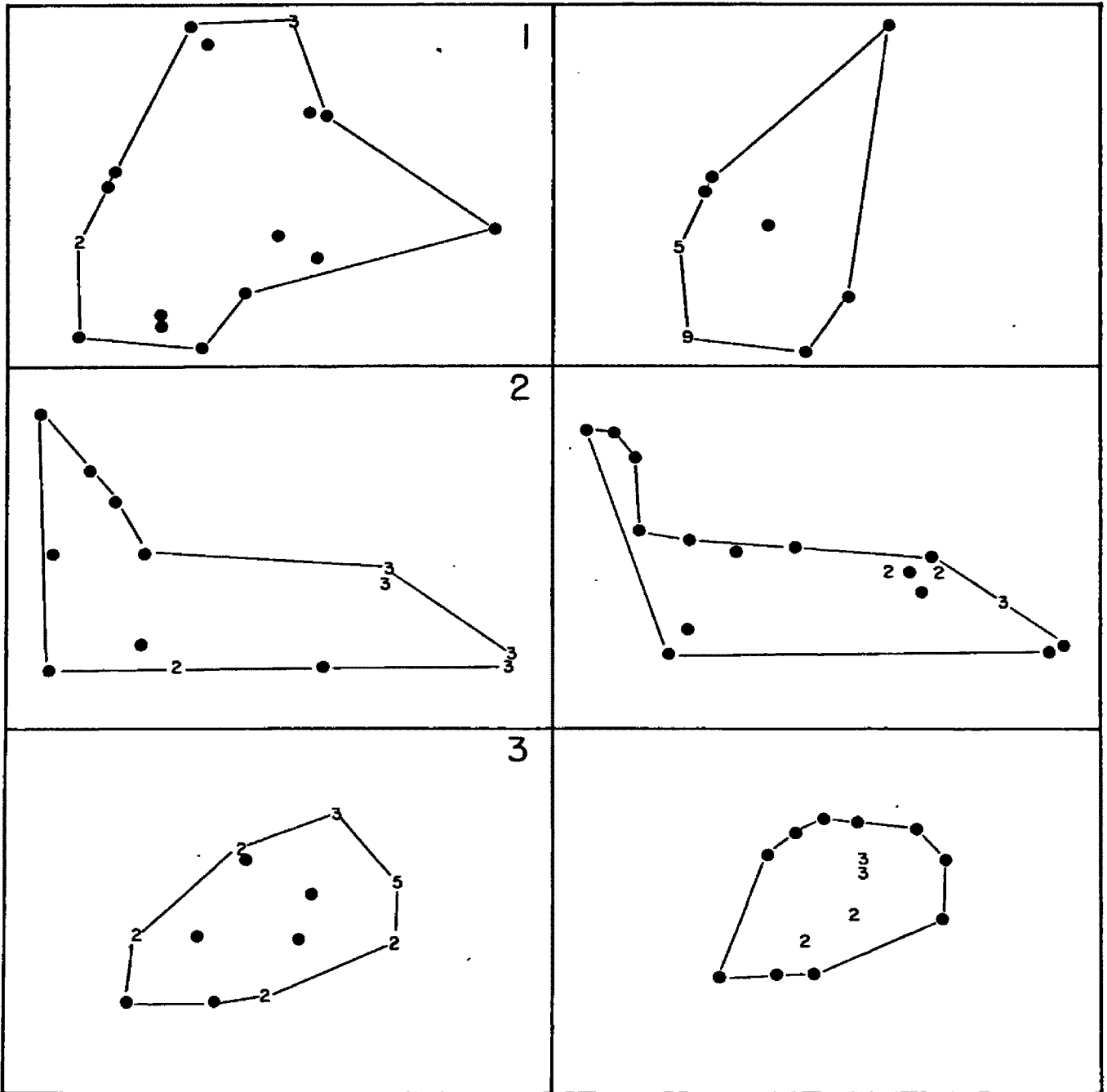


Figure 2. Continued.



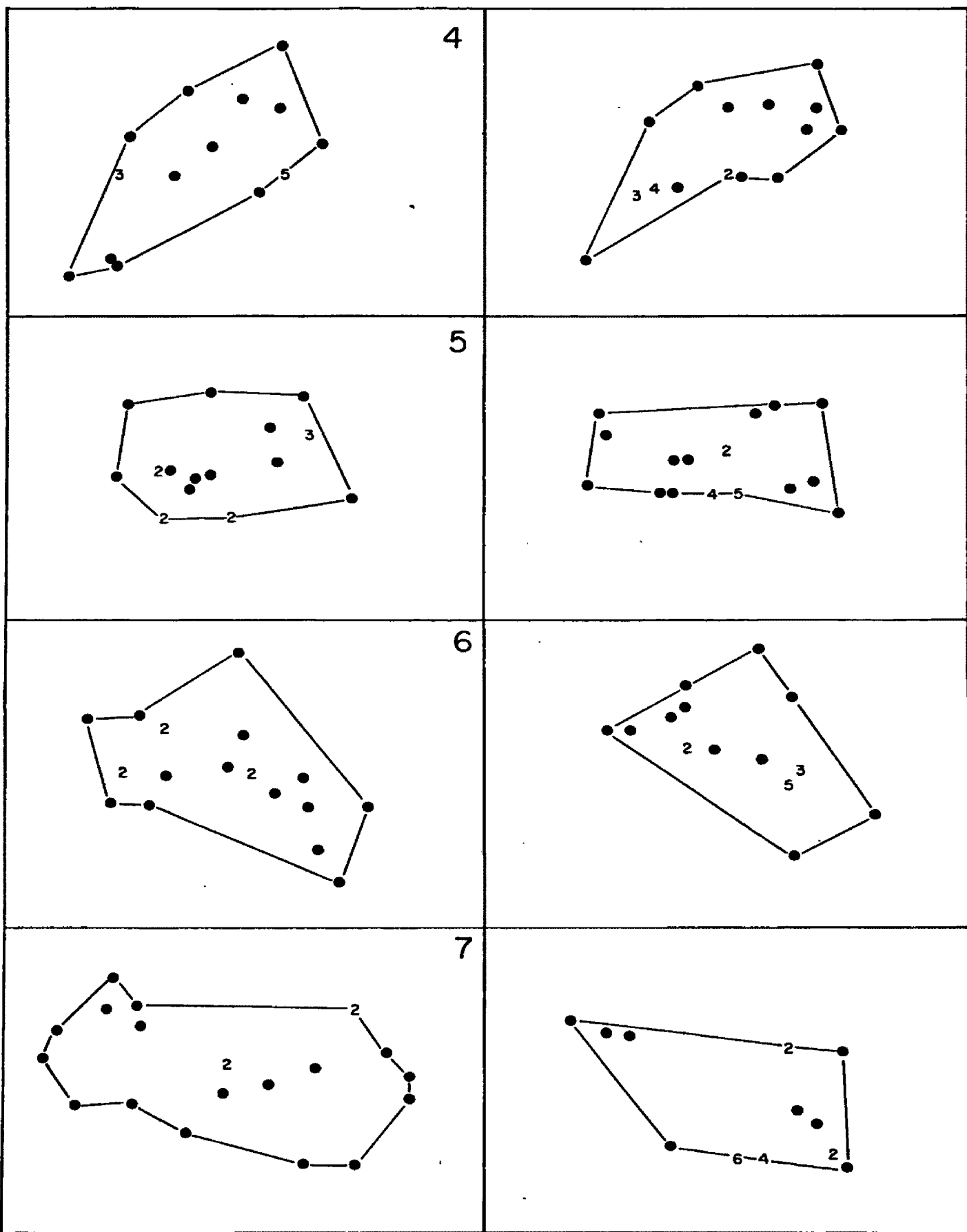


Table 2. The area (ha) of five territories using the flush method to generate points and the adjusted polygon technique to estimate territory size for each of five sample dates.

Territory	Repetition Date				
	6/25	6/28	6/30	7/6	7/10
3	0.61	0.78	0.90	0.76	0.59
4	0.71	0.86	0.71	0.77	0.75
5	0.64	0.39	0.80	0.53	0.62
6	0.94	0.89	0.73	1.00	0.87
7	1.12	1.13	1.05	0.92	0.89

Table 3. Analysis of variance table for data on territory sizes.

Source of Variation	df	SS	MS	F	% of Variation
Between territories	4	0.52	0.13		98.6
Within territories	20	0.26	0.05	2.6	1.4

DISCUSSION

## TECHNIQUES OF TERRITORY SIZE ESTIMATION

Adjusted Polygon--For purposes of discussion I will define "territory" as the area on which an individual bird was consistently found. The adjusted polygon method probably best defines a Vesper Sparrow's territory for the following reasons. It is the only method that I used which allows for researcher interpretation from observations in the field, allowing the exclusion of areas that the individual does not use (e.g., Ambrose 1969, Seastedt and MacLean 1979). From additional field observations and flushing of individuals I am fairly certain that the boundaries shown by the adjusted polygon technique are accurate. Territory borders often followed fence lines or trails for a distance, which altered the territory shape from the expected maximum polygon shape. For example, territory 2 was "L"-shaped. The area avoided by the individual, causing the unusual territory shape, was one of sudden vegetation structure change from mixed grasses to a broad-leafed forbs. Vesper Sparrows had difficulty perching on this vegetation (pers. obs.) and may have avoided it on this basis.

Minimum Circle--The greatest problem with Fitch's (1958) technique is that it assumes an individual's territory is circular. The greater the territory deviates from a circle, the greater the area erroneously interpreted as "territory." The most extreme problem would occur with birds having very narrow territories. For example, a known "L"-shaped

DISCUSSION

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Minimum Circle--The greatest problem with Fitch's (1958) technique is that it assumes an individual's territory is circular. The greater the territory deviates from a circle, the greater the area erroneously interpreted as "territory." The most extreme problem would occur with birds having very narrow territories. For example, a known "L"-shaped

territory (territory 2) produced the greatest deviation between actual and estimated territory size (Table 1).

Maximum Polygon--This technique is probably a bit more accurate than the minimum circle because it excludes some of the area known to be unused. It often yielded the same results as the adjusted polygon technique (Table 1), but ran into errors with territories that had an irregular shape (e.g., territory 2). This technique may include sections of the habitat that are not suitable for the individual, or for some other reason are not used, as part of the territory size estimate.

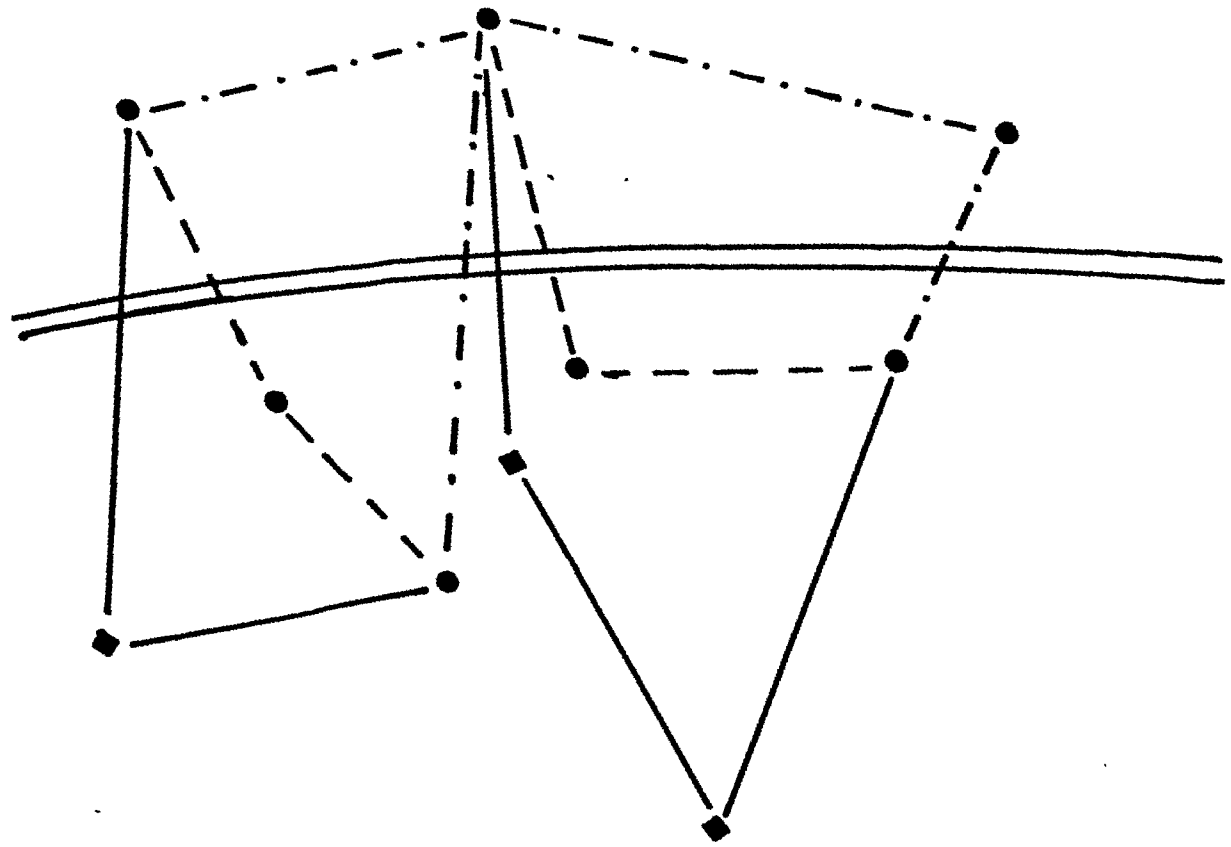
90% Polygon--In addition to the problems associated with the Maximum Polygon technique, it was often the case that one of the points excluded was a perch site. Perhaps this particular problem would be eliminated with additional data.

#### MAPPING METHODS

I feel the modified flush method (Wiens 1969) was better than spot-mapping for mapping territories for two reasons: accuracy and time. The best way to explain why the flush method was more accurate is to go through the hypothetical example illustrated in Figure 3.

The first problem with the spot-map method is that the only way to see an individual is when it is perched or when it is flushed from the ground while walking the path. Vesper Sparrows are very secretive and are virtually never flushed from the ground unless approached within 1.5 m. It was effectively impossible to see an individual on the ground because the vegetation was so obstructive.

Figure 3. Comparison of hypothetical flush-mapped (squares) and spot-mapped (dots) territories.





The modified flush method on the other hand involves repeatedly flushing an individual a minimum of 20 times, and recording the flush points. In all my territories the individual began repeating its flush points before I completed mapping. The "invisible boundaries" that surround the territories seemed very distinct, especially where the territories abutted (Figure 3). When an individual was flushed into an adjacent territory it was chased out by the resident territory holder, resulting in two abutting territories (solid lines), much larger in size than the spot-mapped territories that met at a single perch site.

It may be important to note that the study site did not seem to be "saturated" with individuals, which might have influenced territory size and shape. If the area had been saturated, spot-mapping might have resulted in more points along the territorial borders due to border disputes.

One apparent drawback to spot-mapping is that a very large number of sightings of an individual ( $\gg 20$ ) may be necessary to establish its territorial borders. By chance along an individual is more likely to be seen anywhere in its territory except its borders, since the majority of time is spent centrally (Robbins 1971, Martindale 1982). Feeding and nesting activities are generally centered around the nest site, thus increasing the probability of sighting an individual away from its territorial borders (i.e. towards the territory center). Flush-mapping forces an individual to the edge of its border, and repeated flushing defines a distinct border which probably represents the "familiar area" of an established territory. I believe the flush method gave an

accurate picture of territory sizes and distributions, while spot-mapping gave information on centers of conspicuous activity within the territory.

The flush method has the added advantage of being less time-consuming than spot-mapping, particularly when many sightings are required for detailed territory-border results using the latter method. Flushing a Vesper Sparrow 20 times generally took little more than 10 min. while the information needed by spot-mapping took much longer and can take hours of continuous observation time (Odum and Kuenzler 1955)--or at least a week of regularly walking a systematic path (Robbins 1970).

There is one situation in which the flush method is ineffective for mapping territories. The flush method is not useful when mapping a species that will leave its territory when flushed. Potter (1972) had this trouble mapping Savannah Sparrow (Passerulus sandwichensis) territories and had to use spot-mapping. A situation in which spot-mapping may be as effective as flush mapping is when the species under observation is large enough that the vegetation does not obstruct its detection, e.g. Long-billed Curlews (Numenius americanus). In such cases the individual can be seen on the ground at some distance from the systematic path, which increases the possibility of seeing the individuals at the borders most distant from the path.

#### VARIABILITY

After remapping territories, I found much less variation in territory size within than between territories. This finding, coupled

with an assumption that individual territory sizes remain constant with time, indicates that the flush method is a relatively precise method of measuring Vesper Sparrow territory size.

There is evidence however, that grassland bird species' territories increase in size during the breeding season (Risser et al. 1982:225). Results from individual territories in this study (Table 1) indicate that although fluctuations did occur in Vesper Sparrow territory size, there was no noticeable trend in direction of change. It may be that territories set up later in the season differ in size from those established earlier due to reasons associated with changes in prey densities, but individual territories established earlier did not appear to increase with time.

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## HABITAT SELECTION AND TERRITORY SIZE REGULATION

## IN THE VESPER SPARROW

INTRODUCTION

Most bird species of higher latitudes are migratory, and most also defend breeding territories in the spring. This means that every spring the individuals falling within each of the above characteristics have two important decisions to make:

- 1) Exactly where should the territory be established; and
- 2) How large a territory should be defended?

When considering habitat selection on a broad scale, the answer to the first question probably involves a rigid evolutionary programming (e.g. woodland birds do not breed on the tundra). However, except for the most site-tenacious species (e.g. Pied Flycatcher (Ficedula Hypoleuca), Greenwood 1980), at least some flexibility on a finer scale may be involved.

If a habitat is perfectly homogeneous in all resources, then one would expect territories of a given species to be randomly placed (provided that the habitat is unsaturated) and to be equal in size. Within a habitat, however, locations differ in vegetation structure, plant species, prey density, light intensity, soil moisture, mineral content, and many other factors. If any of these parameters affect survival or reproductive success, natural selection would favor those individuals that locate their territories in the best sites, or

microhabitats, and those that adjust the size of their territory to maximize an economic benefit to cost ratio.

Nonrandom microhabitat selection by species within an area has been reported in many bird communities (e.g. Vander Wall and MacMahon 1984, and references). Additionally, different bird species have been found to select specific sites within a habitat on the basis of ground moisture (Tryon and MacLean 1980), plant species (Holmes and Robinson 1981, Meents et al. 1982), and vegetation structure (Lack 1933, Miller et al. 1966, Wiens 1973, Lance 1978, McKittrick 1979, Meents et al. 1981, Whitmore 1981).

In fact, based on reproductive success, certain habitats are considered to be "optimal" for a given species (Orians 1969, Weatherhead and Robertson 1977, George et al. 1979). This does not mean, however, that all individuals of a given species will breed in the habitat for which they are best suited. For example, Zimmerman (1971) found that Dickcissels (Spiza americana) occupy both old-field and prairie habitats. The old-field was "preferred" by males because the habitat heterogeneity allowed multiple nest sites within a territory, while the prairie sites did not (Zimmerman 1971). Even though reproductive success for males was higher in the old-field, individuals still bred in the prairie habitat because the old-field was saturated with individuals. So instead of not breeding, individuals bred in suboptimal habitats.

Vegetation structure may affect territory size through the amount of protective vegetation for nesting (Knapton 1979), or amount of visually obstructive vegetation (Ewald et al. 1980). It is also possible that vegetation parameters may act secondarily as a cue for

prey abundance later in the season (Willson 1966, Cody and Walter 1976, Myers et al. 1979), and that territory size is ultimately related to food supply. In fact, prey density has been proposed to affect territory size directly. Studies of insectivorous birds (Stenger 1958, Cody and Cody 1972, Morse 1976) and herbivorous birds (Lederer 1977, Salomonson and Balda 1977) have revealed negative correlations between territory size and food abundance. Sunbirds adjust their territory sizes on a day-to-day basis to provide just enough food to survive (Gill and Wolf 1975). The Cactus Finch (Geospiza scandens) adjusts its territory size to cactus area, which affects food supply and, consequently, territory quality and mating success (Millington and Grant 1983).

In contrast, Hinde (1956) asserted that except for a few rare instances there was no evidence that territories of birds are limited in size by prey abundance. Brown (1969), Krebs (1971), and Franzblau and Collins (1980) all found no correlation between territory size and prey abundance. In grasslands, Evans (1964), Wiens (1974), and Folse (1982) reported prey to be "superabundant", and that prey abundance should therefore not be expected to restrict territory sizes.

Some of these questions have been addressed toward Vesper Sparrows (Pooecetes gramineus), which occur in a variety of geographic regions (Whitmore 1979, Wray and Whitmore 1979, Rotenberry and Wiens 1980a,b, Wiens and Rotenberry 1981, Rodenhouse and Best 1983, Best and Rodenhouse 1984) and which are known to breed in grassland, meadow, cropland, and shrubsteppe habitats.

Working on a regional scale (i.e. 16 sites from many areas across the western United States) with grassland and shrubsteppe species,



Rotenberry and Wiens (1980a) found that if Vesper Sparrows were present at a site, their densities were correlated with habitat structure. However, habitat structure was not a good predictor of whether Vesper Sparrows would be present at a given site (Wiens and Rotenberry 1981). On what I will call a "semi-regional" scale (i.e. nine sites in S.E. Oregon and N. Nevada) Rotenberry and Wiens (1980b) found Vesper Sparrow distributions to be independent of habitat structure.

It may be that neither the regional nor semi-regional scale of resolution is fine enough to detect local-scale (i.e. one or two sites) interactions between the habitat and individual sparrows. At the local level, Wray and Whitmore (1979) found reproductive success in Vesper Sparrows to be directly correlated with different measures of habitat structure. Rodenhouse and Best (1983) found an association between some measures of habitat structure and nest placement, and they also found an association between measures of habitat structure and territory site selection in croplands (Best and Rodenhouse 1984).

Habitat structure was a good indicator of Vesper Sparrow density if the Sparrows were present at a given site (Rotenberry and Wiens 1980a). This could be due to a limitation of sparrow density because the amount of suitable habitat is limited, or because habitat "quality" affects territory size. Certain habitat-structure characteristics appear to be "preferred" by Vesper Sparrows and such parameters have the potential to affect both territory size and territory placement (Wray and Whitmore 1979, Best and Rodenhouse 1984). In this paper I investigate the effect of several environmental variables on both

microhabitat selection (territory placement) and territory size in Vesper Sparrows. Specifically, I ask whether several aspects of vegetation structure and food density influence territory size, and whether territories are situated nonrandomly with respect to vegetation structure.

### STUDY AREA

My study sites were in upland grasslands in central, western Montana, 1.4 km north of Missoula (Missoula County, 114° W, 47° 48' N; elevation 980m). Dominant grass species included Idaho fescue (Festuca idahoensis), rough fescue (F. scabrella), and blue bunch wheatgrass (Agropyron specatum). The most common forb in the study area was spotted knapweed (Centurea maculosa), an exotic that often dominated large areas (>0.5 ha). Taller plants were commonly used as perch sites for Vesper Sparrows. Many birds had shrubs or fences within or bordering their territories, and some had a tree at their border.

## METHODS

The study was conducted during the spring and summer months of 1982 and 1983. Research in 1982 centered on the question of territory size regulation, and in 1983 I concentrated on habitat selection.

In 1982 I mapped 60 Vesper Sparrow territories and measured vegetation parameters and arthropod abundance within the approximate center of each territory.

In 1983 I set up five plots on one study site, each of which consisted of a 7 X 5 grid of sample points with 25m between each point. The grids were set up along a previously marked census route, and were placed to overlap areas that included Vesper Sparrow territories during the year before. I then mapped Vesper Sparrow territories (Figure 4) and determined which grid points fell within territories ("used") and which lay outside territories ("unused"). At each point I measured vegetation characteristics in each of the four major compass directions. No territory overlapped grid 2 so it was excluded from the analysis.

Territory Mapping--I mapped territories both years using an adaptation of the "flush" method (Wiens 1969; Chapter 1). Instead of including both flush points and flight paths in the territory, only flush points were included. Flight paths of individuals sometimes occurred outside known territory boundaries. This was best demonstrated where territories abutted. Typically, when chasing an individual, it would fly as far as a particular point and then turn around. Its neighbor, when chased towards the same border, would fly only to that

same point and turn around as well. Sometimes the individual would continue into the other's territory and the owner would chase out the intruder. No chases occurred from a flush point, so I concluded that flush points were included in the territory, while flight paths often were not. A minimum of 20 flush points were located for each bird. Each individual began returning to earlier flush points before 20 points were recorded.

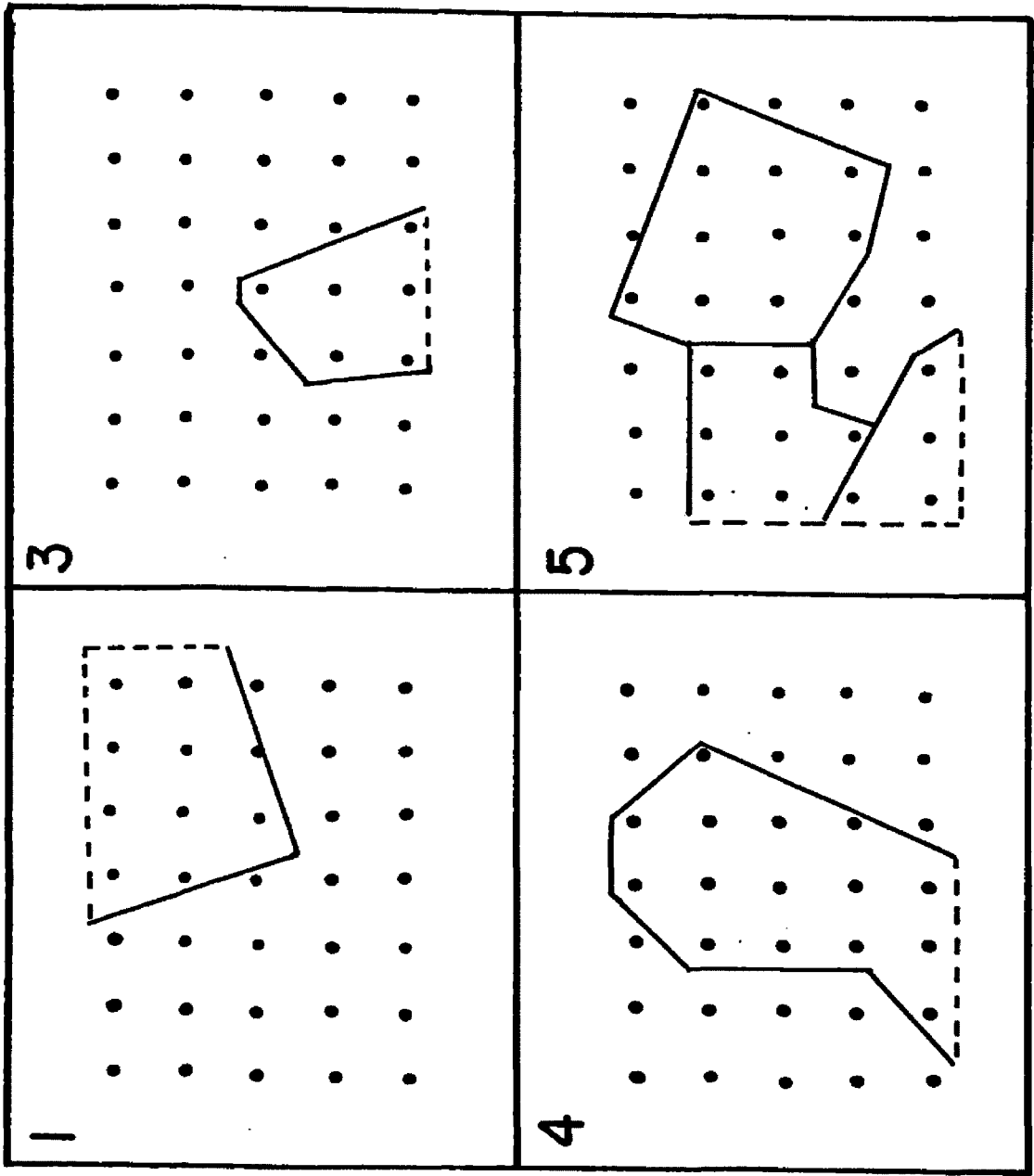
The flush points were connected to form the territory using the "adjusted polygon" method, in which a polygon is formed by connecting the outer points, excluding areas from which individual was not flushed (Janes 1959, Ambrose 1969, Seastedt and MacLean 1979).

#### Vegetation Measurements

Ground Cover--Grinnell and Miller (1944) and Wray and Whitmore (1979) found Vesper Sparrow densities to be correlated with ground cover, while Rotenberry and Wiens (1980a) and Best and Rodenhouse (1984) found forb cover to be correlated with Vesper Sparrow densities. Consequently, I measured percent vegetation cover, percent forb cover, and percent grass cover because of their potential importance in providing the basis for microhabitat selection.

1982 - I randomly placed a 0.25 m<sup>2</sup> frame on the ground within each territory, and estimated each of the percent coverages by eye. This was repeated four more times in each territory. The coverage estimates for each of the five frame placements were then averaged for each territory for analysis.

Figure 4. Grids with territories overlain. Rows and columns of grid are 25m apart. Dashed lines indicate portions of territories extending beyond grid boundaries.



1983 - At each grid point four 5-m cords were placed on the ground in the four cardinal directions, with the grid point as the origin for each cord. Percent coverages were then estimated by eye along each of the cord-transects. The values for each cord were then summed into a composite value for analysis.

Vegetation Height--Because vegetation height is potentially important as a means by which grassland bird species divide resources (Cody 1968), I made the following measurements:

1982 - The mean vegetation height (cm) was calculated from 15 measurements taken at 1 m intervals along a transect running through the center of the territory. The variance of this measurement was used as an indicator of vegetation height variability.

1983 - Vegetation height (cm) was recorded, using a meter-stick, at the grid point and at 1 m and 5 m from the grid point in each of the four cardinal directions. These values were analyzed as separate measurements and also were averaged to determine a mean height.

Vertical Vegetation Density--Vertical vegetation density was estimated only in 1983. I determined this by lowering a thin vertical rod through the vegetation at the grid point and counting the number of hits by the vegetation. The number of hits equaled the vertical vegetation density. Wray and Whitmore (1979) found this measurement to be correlated with reproductive success in Vesper Sparrows.

Horizontal Vegetation Density--1982 - At the approximate center of each territory I placed a 1m X 1m board on edge and estimated the amount of the board obstructed by vegetation. To make density estimation more accurate, the board was divided into a 1 dm<sup>2</sup> checkerboard



pattern, and the percent of each square covered by vegetation was estimated. The squares were then added together to find total board cover. These measurements were made with the observer looking from 10 cm above the ground (approximate Vesper Sparrow eye-height), and 75 cm above the ground (to simulate view from a perch). The observer made estimates at distances of 1 m, 5 m, and 10 m from the board. After rotating the board 180° (on its vertical axis), this procedure was repeated.

1983 - A 4 X 10 dm board, again painted in a checkerboard of 1 dm<sup>2</sup>, was placed narrow end down at 1 m and 5 m distant from the grid point. Cumulative board cover was estimated in the same manner as in 1982. The observer was stationed at the grid point and was looking with eye level at 75 cm from the ground. This height was chosen because in 1982 it yielded the greatest variability in measurement (see results) and therefore has the greatest potential for discrimination among grid points (Anderson 1981).

Vegetation volume--I calculated vegetation volume for analysis to determine if it was independently correlated with microhabitat selection. Vander Wall and MacMahon (1984) found the presence and density of insectivorous bird species to be correlated with vegetation volume.

1982 - Volume = percent ground cover times territory size times mean vegetation height.

1983 - Volume = percent ground cover times mean vegetation height.

Perches--Perches are important to Vesper Sparrows for singing (Wiens 1969, Rodenhouse and Best 1983). Identification of potential perches was subjective, based on what I had seen Vesper Sparrows use.

They include shrubs, trees, fences, forbs, rocks, and mounds of bare ground. Even though rocks and mounds were lower than the mean vegetation height, the area immediately surrounding them was typically free of vegetation.

1982 - The number of potential perches on each territory was counted and the territories were divided into three groups by perch number:  $\leq 4$ , 4-7, and  $> 7$  perches. Mean perch height was divided into three groups based on perch height relative to the surrounding vegetation height: 0.7-1.5x mean vegetation height, 1.5-3x, and  $> 3x$ .

1983 - The height of the potential perch (dm) nearest the grid point was measured, as was distance to nearest perch (m), and perch type.

Litter--In several studies of grassland birds litter depth has been measured and found to be important in occupancy selection by Vesper Sparrows (Whitmore 1979, 1981, Wray and Whitmore 1979). In my study area vegetation was either alive or standing dead, so there was essentially no litter.

#### Arthropod Sampling

Arthropods were sampled in 1982 only. In each territory I made 50 sweeps with an insect net. I swept as close to the ground as possible and typically scraped the ground with the net. The number of arthropods captured per sweep was used as a measure of arthropod density. I calculated a measure of arthropod availability to the birds by the equation: number of arthropods per sweep in each territory times vegetation volume.

### Effects of Time

There is evidence that the territory sizes of some grassland bird species increase through the breeding season (Risser et al. 1982). In 1982 I kept track of the date I measured each territory to determine if this trend occurred in Vesper Sparrows.

I also recorded the time of day that measurements were made to determine if territory size measurements were directly related to time of day independent of arthropod densities.

## RESULTS

### Habitat Selection

The data for the grid points in used and unused areas (Appendix 1) were subjected to stepwise discriminant analysis to determine which variables, if any, were important in discriminating the two categories of the grid points: those falling within and those falling outside of the territories. The values from measurements taken at 1 m had the greatest variability and revealed the greatest difference between used and unused areas. The same was true for 5 m for measurements of horizontal vegetation density (Table 4). Because of this variability, they had the greatest potential to discriminate between grid points falling within used and unused areas (Anderson 1981).

Maximum discrimination between used and unused grid points was based on four variables: vegetation height at 1 m, percent vegetation cover (=percent ground cover), horizontal vegetation density at 1 m, and vertical vegetation density (Table 5). Vegetation height and horizontal vegetation density varied inversely with percent ground cover and vertical vegetation density. Horizontal vegetation density had the greatest effect within the function. The distribution of points from used and unused areas along the discriminant function axis (Figure 5) can be interpreted as a continuum from tall, patchy vegetation in unused areas (-3, centroid = -0.359), to short, dense vegetation with a relatively high percent ground cover in used areas (+3, centroid = 0.608).

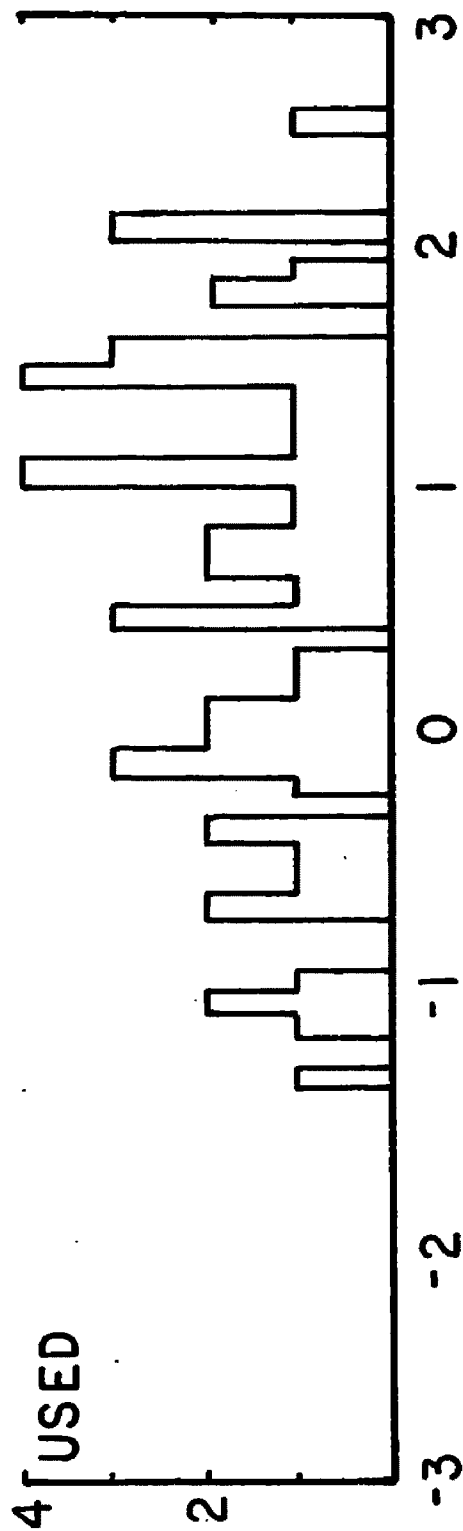
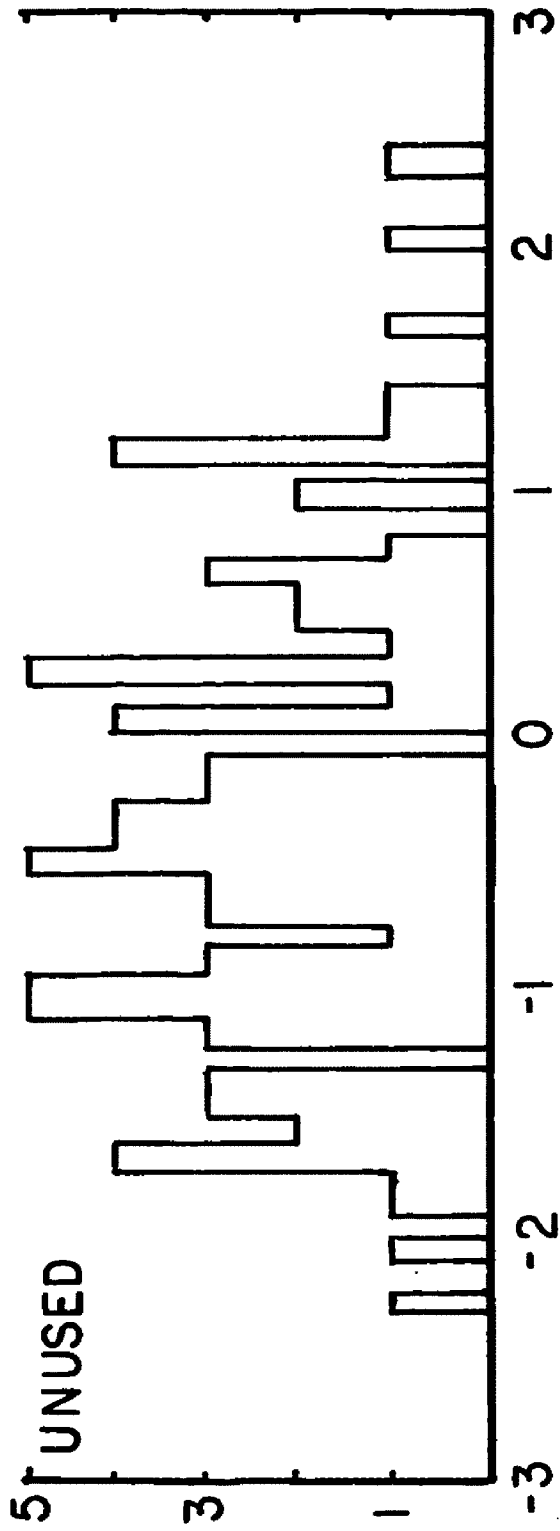
Table 4. Mean values and standard deviations of continuous variables used in the discrimination of points from used and unused areas.

Variable	Used	Unused
Vegetation Height (cm)		
Grid Point	20.23 (13.1)	22.67 (18.5)
Mean at 1 m	24.01 (10.9)	31.26 (12.3)
Mean at 5 m	28.97 ( 9.5)	34.47 (10.8)
Ground Cover		
Cover	351.26 ( 29.1)	343.25 (36.7)
Grass	163.93 (108.1)	145.81 (89.5)
Forb	235.05 (108.9)	254.00 (89.4)
Vertical Vegetation Density	3.49 (1.8)	3.54 (2.3)
Horizontal Vegetation Density		
1 m	505.63 (275.7)	633.27 (333.7)
5 m	1710.45 (758.2)	2163.85 (984.5)
Perch		
Height (dm)	9.00 (3.9)	9.37 (2.4)
Distance to nearest (m)	9.32 (6.4)	8.06 (5.5)

Table 5. Variables that provided maximum discrimination ( $P < 0.05$ ) among points from used and unused Vesper Sparrow microhabitat, and standardized canonical discriminant function coefficients (SCDFC).

Variable	Wilk's Lambda	P	SCDFC
Vegetation Height at 1 m	0.913	0.0004	-0.2498
%Vegetation Cover	0.867	0.0001	0.6408
Horizontal Density at 5 m	0.827	<0.0001	-0.7731
Vertical Density	0.819	<0.0001	0.7000

F R E Q U E N C Y



To test the significance of the discriminant analysis I used the linear function in a classification analysis. In this test, grid-point-variable values from each grid point are plugged into the linear equation, and then each point is classified as used or unused based on which centroid they are nearest. Results show that 69% of the 140 points were classified correctly (Table 6). This is significantly more than the 55% correct classification expected by chance sorting (proportional chance criterion, Hair et al. 1979:102-103) ( $\chi^2 = 11.09$ ,  $df = 1$ ,  $P < 0.005$ ).

I tested the hypothesis that values of variables from grid points found within a territory were not significantly different from those of grid points chosen at random. I selected 52 grid points at random (equal to the number of grid points falling into used habitat) and compared them to grid points in used and unused areas. These comparisons were made using direct discriminant analysis involving the four variables in Table 6.

Discriminant analysis successfully discriminated between grid points from used areas and those chosen at random ( $P < 0.02$ ). The classification test showed significantly more cases classified correctly (61%) than expected by chance sorting (50%) ( $\chi^2 = 6.26$ ,  $df = 1$ ,  $P < 0.025$ ) (Table 7). Analysis could not discriminate between random and unused grid points ( $P > 0.1$ ), however, and the classification results (54%) were not significantly different from that expected by chance sorting (55%) ( $\chi^2 = 0.10$ ,  $df = 1$ ,  $P > 0.5$ ) (Table 8).

Each of the six territories could also be successfully discriminated from the other five on the basis of the same four



Table 6. Classification analysis for grid points from used vs. unused areas. Significantly more were classified correctly than expected by chance ( $\chi^2 = 11.09$ ,  $df = 1$ ,  $P < 0.005$ ).

Actual	N	Classified as:	
		Used	Unused
Used	52	34	18
Unused	88	26	62

Table 7. Classification analysis for points from used areas vs. randomly selected grid points. Significantly more points were classified correctly than expected by chance ( $\chi^2 = 6.26$ ,  $df = 1$ ,  $P < 0.25$ ).

Actual	N	Classified as:	
		Used	Unused
Used	52	32	20
Random	52	21	31

Table 8. Classification analysis for points from unused areas and randomly selected grid points. No more points were classified correctly than expected by chance. ( $\chi^2 = 0.10$ ,  $df = 1$ ,  $P < 0.5$ ).

Actual	N	Classified as:	
		Used	Unused
Unused	88	48	40
Random	52	25	27

variables. Classification analysis resulted in 44% classified correctly, significantly greater than expected by chance sorting (19%) ( $\chi^2 = 20.3$ ,  $df = 5$ ,  $P < 0.005$ ) (Table 9). The first discriminant function explained 72% of the variability (Table 10), and four functions were required to explain 100% of the variability.

A possible explanation for discrimination success between points in used and unused areas, and between territories, is that adjacent grid points may be more similar than non-adjacent points. This would result in discrimination as an artifact rather than by biological cause. To look at variability between adjacent points and non-adjacent points I chose two sets of 36 grid points. One set was chosen at random, and the second set consisted of the middle-most point and the eight surrounding points in each of the four grids. These represented random and clumped points respectively. The variability of each of the four variables important in discrimination was similar, but the clumped points tended to be more variable than the random points (Table 11).

### Territory Size Regulation

Territory Size--Vesper Sparrow territories ranged in size from 0.25 - 5.09 ha, with a mean size of 1.65 ha ( $n = 60$ ) (Table 12).

Vegetation Relationship--Territory sizes were compared with vegetation-structure measurements using correlation and regression analysis. Territory sizes and their respective vegetation measurements are listed in Appendix 2. Five vegetation-structure measurements were significantly correlated with territory size

Table 9. Classification analysis comparing grid points from within each of six territories. Significantly more points were classified correctly than expected by chance ( $\chi^2 = 20.28$ ,  $df = 5$ ,  $P < 0.005$ ).

Actual	N	Classified as:					
		1	2	3	4	5	6
1	10	4	4	2	0	0	0
2	6	2	4	0	0	0	0
3	15	2	2	5	1	4	1
4	10	0	1	1	4	2	2
5	7	0	1	1	0	4	1
6	4	1	0	0	1	0	2

Table 10. First discriminant function for between-territory comparisons.

The function accounts for 72% of the variability in the discriminant function analysis.

	Coefficient of Variability
Vegetation Height (lm)	.2359
Vertical Density	-.5957
% Ground Cover	-.1932
Horizontal Density	1.1003

Table 11. Variability of the four variables important in the discriminant analysis. Values are the standard deviations for 36 random points and 36 clumped points.

	Clumped	Random
Vegetation Height (1m)	11.4	11.2
Vertical Vegetation Density	1.5	2.2
% Ground Cover	32.8	28.4
Horizontal Vegetation Density	1009.4	998.0

Table 12. Summary statistics for territory sizes and vegetation structure measurements of the territories (excluding perch height and number). N = 60.

	Grand Mean	SD	Range		r**
			Minimum	Maximum	
Territory Size (ha)	1.65	1.10	0.25	5.09	
% Cover	80.78	12.37	27	100	.24
% Grass Cover	28.58	14.53	5	69	.10
% Forb Cover	52.27	13.84	18	89	.11
Relative Perch Height	2.23	0.5	1	3	.28*
Number of Perches	2.47	0.7	1	3	.26*
Mean Vegetation Height (cm)	25.30	8.04	20.0	52.0	.31*
Variance of MVH	284.78	118.80	87.0	718.0	.11
Horizontal Vegetation Density-10cm					
1 m	1771.3	1201.8	90	6100	.09
5 m	8400.0	3857.9	1400	17100	.06
10 m	14692.5	3888.6	6000	20000	.13
Horizontal Vegetation Density-75cm					
1 m	466.5	1301.8	20	10200	.39*
5 m	1623.3	1183.3	330	5100	.01
10 m	3555.3	1755.0	950	8700	.10

\*P<0.05

\*\* r = the correlation coefficient from correlation between a given variable and territory size.



correlated with date ( $r = -.38, P < 0.002$ ) (Figure 8), and positively correlated with time of day ( $r = 0.56, P < 0.001$ ). Arthropod numbers were significantly correlated with time of day ( $r = .37, P < 0.005$ ).

Figure 6. Territory size vs. Arthropod density.  
 $r = -.06, P > 0.30.$

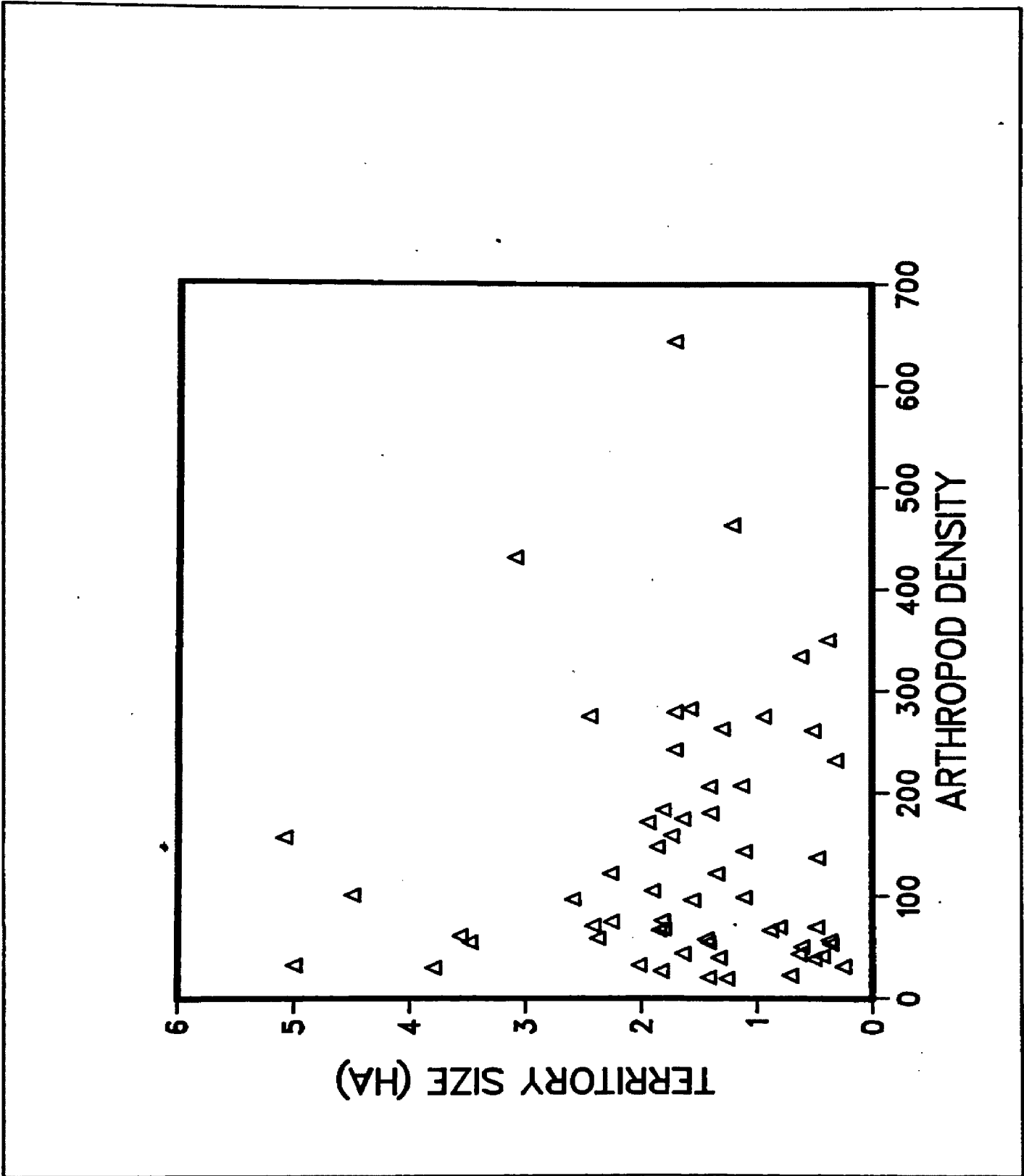


Figure 7. Territory size vs. Day of measurement.  
 $r = .30, P < 0.05.$

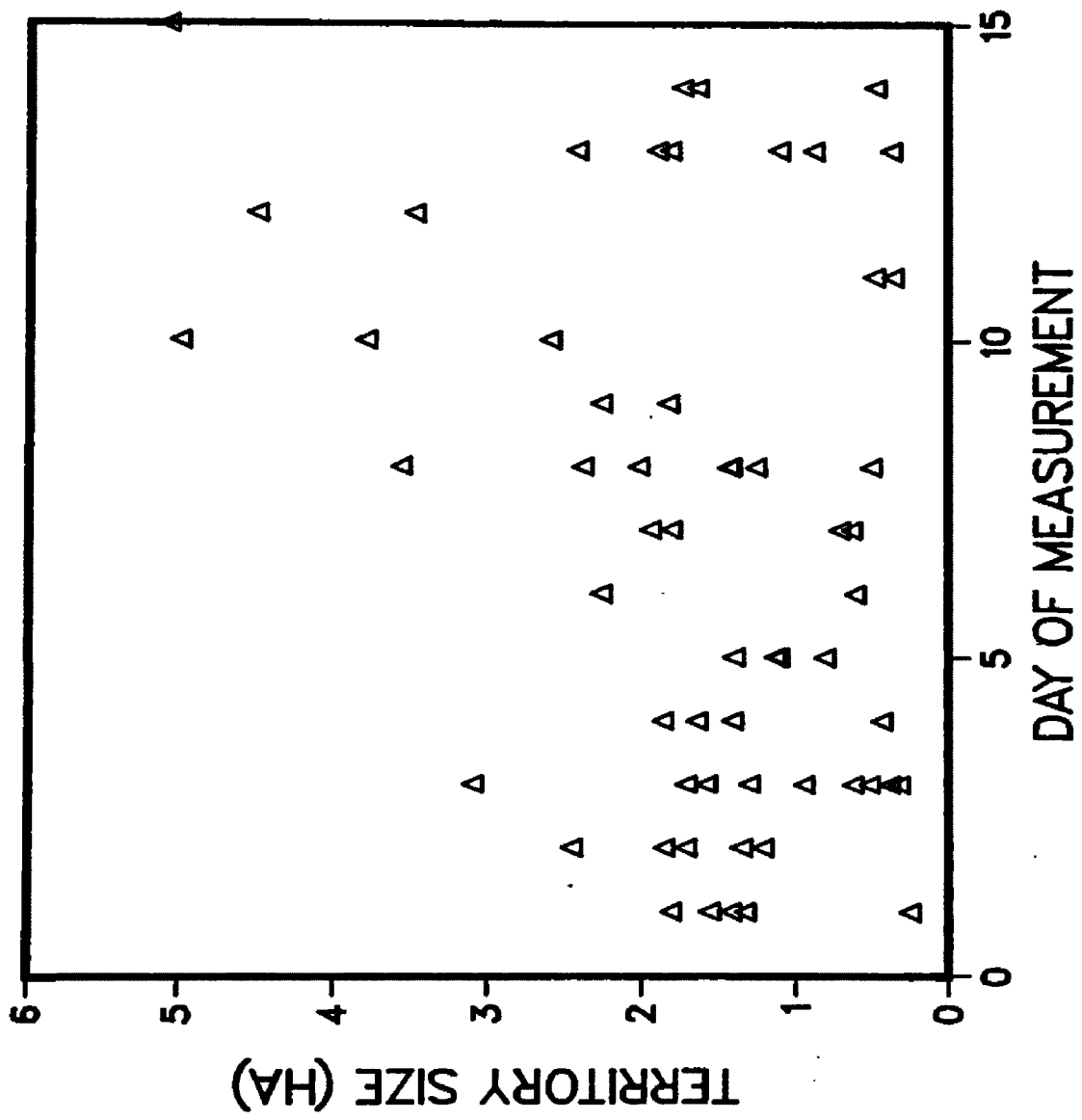
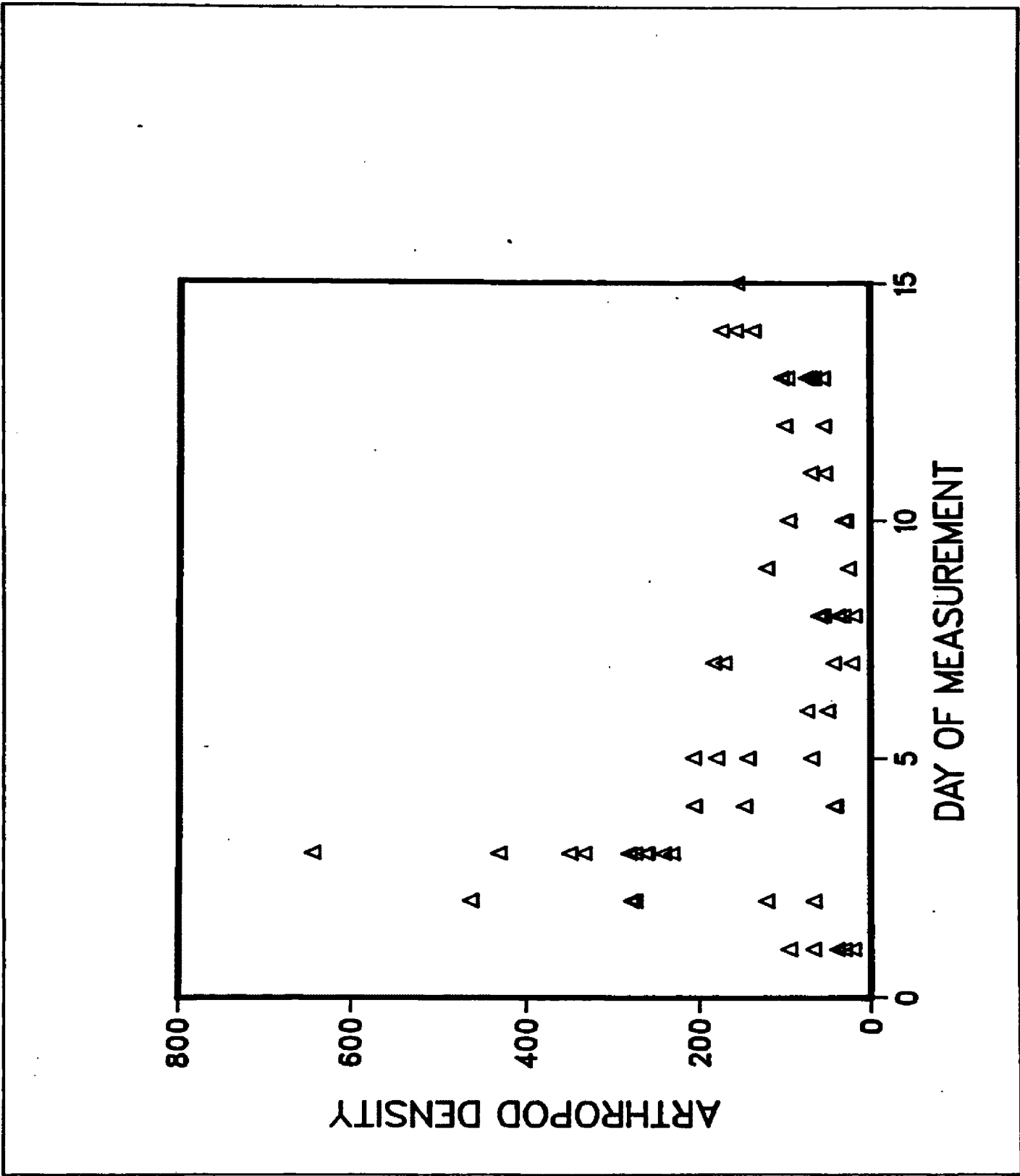


Figure 9. Residuals from arthropod density vs. Time and date plotted against standardized territory size.



## DISCUSSION

### Habitat Selection

Patterns at the Population Level--Vesper Sparrows were found in areas where the vegetation was short and dense, with a relatively high percentage of ground cover, and were not found in areas where the vegetation was tall and patchy. This distribution might be expected on the basis of their feeding habits. During the breeding season, a minimum of one-third (Bent 1968) to over 50% of an adult's diet and nearly 100% of a juvenile's diet (Evans 1964) consist of arthropods. Vesper Sparrows do much of their foraging on the ground but also capture flying insects. Low, dense vegetation would probably provide greater availability of food for both types of foraging. Crawling arthropods would be more accessible to a sparrow when they are on low rather than high vegetation. Shorter vegetation, which is more uniformly distributed, would probably be easier for the Vesper Sparrow to maneuver around during flight than would taller, patchy vegetation.

This is only one possible explanation of my results. Other explanations may include such things as: 1) lower vegetation may be less visually obstructive, allowing easier detection of predators or conspecifics, or 2) the higher amount of ground cover may be needed for proper nest concealment (Wray and Whitmore 1979).

Wray and Whitmore (1979) found that high percent litter cover, vertical vegetation density, and percent ground cover near the nest were associated with high reproductive success of Vesper Sparrows.



They felt this type of cover hid nests from predators, because nests found in "less preferred" habitat were all lost presumably due to predation. Two of their three structural measures are the same as those that I found to be important in discriminating used from unused areas. Their work, in an area with higher Vesper Sparrow densities, indicates the presence of a continuum of vegetation structure along which reproductive success varies. I found a similar continuum defining habitats chosen for territory sites and those avoided.

Grid points in used areas could be discriminated from randomly chosen grid points. This result is consistent with the hypothesis that individuals are not positioning territories at random with respect to the measured vegetation parameters. Recent studies have stressed the importance of habitat selection by bird species, particularly in explaining community structure (e.g. Karr and Roth 1971, Wiens 1983, Vander Wall and MacMahon 1984). My results demonstrate that Vesper Sparrows exhibit a specific vegetation-structure affinity. However, these results do not discriminate between the possibilities that this affinity is a result of specific site selection or interspecific competition.

There are several possible explanations for the lack of discriminating success between unused and random grid points. The study area may not have been "saturated" (Wiens 1974) with Vesper Sparrows. In fact, in 1983 the study site had fewer territories than it did the year before (pers. obs.). In other words, based on vegetation structure the site could have supported more individuals in "optimal" territories. This "unsaturated" condition resulted in some grid points being unused which could have been used.

Another explanation is that a second species with similar resource requirements was limiting Vesper Sparrow distribution in the area. This would result in some grid points being unused which would have been used in the absence of the competing species.

The final explanation I offer is that approximately three-fifths of the grid points are classified as unused. A random sample of grid points would contain a greater proportion of unused than used points. Discrimination between random and unused points would favor a type II error - not discriminating between the two samples when in fact they differ.

Inter-Individual Variation--The niche variation hypothesis (Van Valen 1965) states that individuals in an area utilize separate subsets of the available resources, rather than each individual being a generalist and using all of the resource types available. This differential use of resources is a result of behavioral and/or morphological differences between individuals. My results are consistent with the niche variation hypothesis. I could discriminate each territory on the basis of vegetation measurements taken from grid points within each. The first function of the discriminant analysis explained explained a high percentage (73%) of the observed variation (Table 10). Since territories could be distinguished from one another, it appears their residents utilize distinct subdivisions of the acceptable habitat.

That territories were significantly different from one another may be due to adjacent grid points being more similar than non-adjacent points. Although I have shown this possibility to be unlikely, if it were true, it would not affect the conclusion that the individuals

use distinguishable subdivisions of the acceptable habitat. Such differences would not be the result of differences in the "preferences" of individuals. Rather, they would be the result of chance differences in the vegetation structure associated with each territory. In any case, since grid points were scattered throughout each territory, I can be confident that the vegetation structure of each territory was significantly different, for whatever reason.

### Territory Size Regulation

Vegetation--Several aspects of vegetation structure were positively correlated with territory size. Horizontal vegetation density, the most important variable in the discriminant analysis, was also the only measure that was significantly correlated with territory size in regression analyses. I found territory placement to be associated with some aspects of vegetation structure. My data also indicate territory size to be associated with vegetation structure. Horizontal vegetation density increased in unused areas and was also greater in larger territories. Vegetation structure similar to that affecting territory placement on my study site affected reproductive success in another study (Wray and Whitmore 1979). Whether due to nest site availability (Knapton 1979, Wray and Whitmore 1979), visually obstructive vegetation (Ewald et al. 1980), or a less direct effect, it appears that as vegetation becomes taller and patchier it is "less preferred" by Vesper Sparrows. As a result, territories associated with this vegetation type are larger.

This relationship between vegetation structure and territory size and placement does provide evidence that vegetation structure affects Vesper Sparrow density. Rotenberry and Wiens (1980a,b) and Wiens and Rotenberry (1981) provide evidence that Vesper Sparrow population densities may be affected by vegetation structure. However, their evidence is conflicting. It is likely, from my results, that Vesper Sparrow densities are affected by vegetation structure through influencing both territory size and the amount of suitable habitat.

Arthropods and Time--Territory sizes vary with the date they were measured, and the increase in size with time was highly significant (Figure 7). Of the variables correlated with date, I believe arthropod densities might be a potentially important influence on territory size. Arthropod densities are highly negatively correlated with the date (Figure 8). Although the relationship resembles the rectangular hyperbolic one described by Cody and Cody (1972) for Wrens (Troglodytes troglodytes), when my own plot of territory size vs. arthropod density was redrawn using a semi-log scale the correlation was not improved, as would be expected if the relationship were truly hyperbolic. Arthropod densities were not significantly correlated with territory size, but this relationship may have been clouded by the effects that date and time of day may have had on arthropod densities. To remove any effect that date and time may have had, I regressed these variables and the square of each (in case there was a simple curvilinear relationship) on arthropod densities. I then plotted the residuals against standardized territory size (Figure 9), and no relationship became apparent. I therefore conclude that arthropod densities do not





affect territory sizes of Vesper Sparrows and that they are a non-limiting resource. In fact, as territory size increased the density of arthropods increased. These results are consistent with those of Evans (1964), Wiens (1974), and Folse (1982) who reported arthropod prey to be "superabundant" (i.e. non-limiting).

There remains the question of territory size increasing with date. In another study (Chapter 1) I found that individual territories do not increase in size during the breeding season. A possible explanation for the trend of increased territory size is that territories set up later in the year (perhaps as a consequence of individuals losing their first nest, or late nesters) are placed in less preferred habitat. This would result in larger territories later in the breeding season.

CONCLUSION

These results indicate that vegetation structure played a significant role in where Vesper Sparrows place their territories. They seemed to select areas nonrandomly, choosing sites which had low, dense vegetation with relatively high percent ground cover. This result was expected from previous research. Vegetation structure also may affect territory size. Horizontal vegetation density was the most important of the variables I measured in both habitat selection and territory size regulation. Vesper Sparrow population densities may be affected by vegetation structure through limiting available habitat and affecting territory sizes. Arthropods appeared not to limit territory size.



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Vegetation measurements for grid points. Perch types: (1) forb, (2) rock, (3) tree, (4) mound, (5) fence; Use: 0 = no, 1 = yes;

Vert. Veg. Den. = Vertical Vegetation Density; Horizontal Vegetation Density = cumulative % cover; Perch height = cm.

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
1	01	0	04	11	08.75	18.75	368	032	325	0085	0780	11	1	10
1	02	0	05	26	22.00	18.50	375	025	380	0740	2050	01	1	07
1	03	0	04	15	22.75	20.75	337	063	290	0880	1740	12	1	08
1	04	0	02	17	18.25	26.75	376	024	344	0290	1350	06	2	02
1	05	0	01	01	02.50	20.75	386	014	334	0160	0650	14	1	09
1	06	0	06	14	12.75	13.75	354	046	384	0350	1650	02	1	05
1	07	0	04	30	22.25	31.50	372	028	360	0450	1110	03	1	08
1	08	0	04	08	07.50	20.00	324	076	367	0230	1000	04	1	09
1	09	0	04	14	19.00	18.75	345	055	377	0580	1640	03	1	09
1	10	0	03	22	20.75	26.00	370	030	394	0560	2430	09	1	10
1	11	0	05	18	15.50	27.25	373	027	382	0430	1930	07	1	08
1	12	0	02	21	16.75	23.75	373	027	381	0410	2200	04	1	11
1	13	0	04	46	33.25	20.25	374	026	394	0680	1530	17	1	08
1	14	0	03	10	34.75	22.75	378	022	377	0570	1360	01	1	09
1	15	0	02	28	28.75	32.75	361	039	381	0470	1840	13	1	05
1	16	0	00	00	06.25	26.75	370	030	349	0220	1400	11	1	09
1	17	0	01	05	13.00	28.50	365	035	385	0430	1660	04	3	35

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
1	18	0	02	03	24.50	26.75	324	076	382	0420	2070	01	1	11
1	19	1	04	22	22.25	33.75	254	146	380	0280	1770	05	1	10
1	20	1	02	05	36.00	26.00	280	120	269	0240	1200	01	1	07
1	21	0	02	10	28.75	27.25	375	025	381	0390	1410	25	3	09
1	22	1	00	00	26.75	30.25	363	037	337	0280	0910	11	1	11
1	23	1	03	09	28.50	29.75	352	048	291	0310	0980	07	2	02
1	24	1	03	17	39.25	39.50	361	039	360	0470	1450	20	3	13
1	25	1	03	50	16.50	37.50	341	059	331	0440	1190	17	1	08
1	26	0	03	33	15.25	21.25	284	116	305	0250	0940	07	1	09
1	27	0	04	08	12.25	09.25	109	291	349	0200	0700	07	2	03
1	28	0	04	34	27.25	26.50	202	198	354	0390	0840	18	2	03
1	29	0	05	35	16.75	30.75	286	114	360	0730	2780	18	2	04
1	30	0	05	23	23.00	30.25	278	122	325	0280	2290	18	2	05
1	31	0	10	42	31.50	32.25	320	080	368	0810	2710	08	1	07
1	32	1	10	17	24.25	33.50	336	064	374	0590	2420	15	3	10
1	33	1	06	07	18.50	26.25	269	131	322	0260	1550	09	1	09
1	34	1	04	18	10.75	18.50	267	133	324	0140	0570	06	1	07
1	35	1	02	05	12.50	42.25	388	012	254	0330	0800	25	1	10
2	01	0	02	15	20.75	32.50	310	090	334	0390	2620	25	3	19
2	02	0	04	11	14.75	36.50	273	127	357	0600	2510	25	3	19
2	03	0	03	15	23.25	32.50	295	105	318	0610	0950	25	1	07

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
2	04	0	06	13	19.75	12.75	343	057	342	0310	1510	10	1	07
2	05	0	02	11	11.25	27.75	261	139	341	0170	0950	12	1	07
2	06	0	03	11	19.00	35.00	324	076	354	0580	2050	13	1	05
2	07	0	03	10	06.75	21.50	297	103	364	0430	1680	06	1	04
2	08	0	04	13	20.75	40.50	155	245	376	0660	0980	08	0	10
2	09	0	04	09	12.00	30.75	236	164	358	0470	1800	06	1	07
2	10	0	05	20	06.75	18.75	297	103	332	0200	1850	14	1	08
2	11	0	03	21	18.25	24.75	297	103	276	0450	1840	13	1	09
2	12	0	04	16	17.25	22.25	336	064	322	0250	0920	16	1	08
2	13	0	01	04	27.50	25.75	263	137	320	0380	1440	12	1	09
2	14	0	07	30	15.75	19.00	169	231	390	0220	1290	12	3	24
2	15	0	03	14	25.25	15.00	259	141	366	0480	1200	15	1	07
2	16	0	01	02	36.75	27.75	230	170	258	0390	0580	12	1	09
2	17	0	03	28	05.00	20.50	265	135	348	0240	1360	16	1	05
2	18	0	04	21	22.50	29.00	312	088	342	0650	1810	10	1	06
2	19	0	04	12	10.50	15.00	187	213	374	0250	1020	12	1	08
2	20	0	02	07	36.00	17.00	249	151	352	0790	0670	09	1	08
2	21	0	04	19	25.25	28.75	288	112	352	0250	1180	14	1	08
2	22	0	02	09	08.75	22.75	281	119	356	0180	2030	10	1	07
2	23	0	04	27	16.25	26.50	299	101	348	0430	1560	11	1	11
2	24	0	02	10	13.00	19.25	292	108	354	0360	1420	09	1	08

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5m	Forb	Grass	Cover	1 m	5 m			
2	25	0	05	11	26.75	21.50	292	108	366	0460	1500	08	1	07
2	26	0	01	06	11.75	21.50	238	162	342	0550	1340	11	1	05
2	27	0	03	10	15.75	26.25	275	125	306	0580	1500	05	1	07
2	28	0	02	10	18.50	33.00	276	124	338	0550	1720	06	1	09
2	29	0	00	00	03.75	11.00	176	224	222	0150	0310	07	1	08
2	30	0	02	10	08.25	15.50	250	150	274	0130	0780	07	1	04
2	31	0	03	33	12.75	21.50	209	191	358	0350	1100	12	1	04
2	32	0	06	27	21.00	27.00	278	122	386	0690	2510	05	1	06
2	33	0	03	11	07.25	10.25	318	082	372	0360	1370	12	1	08
2	34	0	04	12	24.00	17.50	313	087	354	0320	1080	16	1	08
2	35	0	02	17	09.00	23.75	253	147	354	0200	1390	11	1	09
3	01	0	09	33	37.25	33.00	292	108	354	1290	2520	17	1	10
3	02	0	03	07	14.00	23.00	172	228	320	0140	0980	19	2	05
3	03	1	02	05	14.75	18.75	133	267	340	0240	0980	14	2	05
3	04	1	02	07	21.50	14.50	156	244	310	0340	0630	11	1	10
3	05	1	04	12	25.75	21.25	041	359	336	0430	1590	09	1	08
3	06	0	02	16	12.25	23.50	044	356	322	1080	0480	14	1	10
3	07	0	02	04	19.25	21.25	047	353	340	0150	0530	08	1	09
3	08	0	01	10	11.00	25.75	085	315	358	0240	1120	07	1	08
3	09	0	03	11	04.50	19.25	039	361	322	0170	0440	25	1	08
3	10	0	04	17	44.25	34.25	152	248	334	0690	1220	12	1	06



Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
3	11	1	03	13	16.00	20.25	040	360	328	0240	1210	11	1	10
3	12	0	05	32	18.75	24.75	114	186	326	0270	1150	13	2	06
3	13	0	02	19	11.25	17.50	102	298	345	0310	0770	12	2	05
3	14	0	03	24	32.75	32.25	095	305	306	0710	1600	06	1	08
3	15	0	02	05	10.25	23.75	157	243	332	0200	1380	04	1	09
3	16	0	02	07	17.25	30.75	128	272	298	0360	2000	25	4	05
3	17	0	03	13	37.25	19.50	046	354	342	0380	0510	13	1	08
3	18	0	04	33	24.75	24.50	038	362	360	0470	1230	02	1	10
3	19	0	02	05	17.50	15.50	103	297	346	0420	0700	25	1	09
3	20	0	04	20	14.75	18.25	041	359	358	0390	0820	25	1	08
3	21	0	03	10	13.75	19.75	143	257	374	0320	1410	09	1	09
3	22	0	02	08	13.75	15.75	221	179	378	0540	1560	20	1	09
3	23	0	04	35	16.75	22.50	069	331	360	0230	0920	06	1	07
3	24	0	03	08	17.75	21.25	055	345	342	0580	0770	20	1	08
3	25	0	04	37	23.25	28.25	104	296	312	0310	1340	03	2	03
3	26	0	04	09	19.50	17.50	150	250	364	0400	2390	09	1	09
3	27	0	03	26	36.00	33.25	171	229	332	0730	2110	05	1	13
3	28	0	03	09	16.00	20.00	112	288	312	0330	0930	15	1	12
3	29	0	04	31	29.75	26.25	227	173	366	0380	1640	13	1	09
3	30	0	02	31	26.00	32.25	159	241	302	0400	1780	08	1	07
3	31	0	03	30	21.25	23.50	163	237	346	0350	1230	06	1	10

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
3	32	0	05	15	21.25	33.25	147	253	340	0570	0990	14	1	06
3	33	0	02	06	21.00	38.75	116	284	346	0400	1900	08	1	10
3	34	0	03	10	23.00	22.00	140	260	380	0320	1030	10	1	11
3	35	0	04	32	20.50	43.50	243	157	388	1180	2910	07	1	09
4	01	0	01	05	31.00	39.50	121	279	334	0310	1410	05	5	10
4	02	0	04	29	35.50	24.25	329	071	360	0790	1760	05	5	10
4	03	0	02	22	04.00	21.75	117	283	286	0120	0770	05	5	15
4	04	1	05	30	37.75	39.25	133	267	380	0610	1810	05	5	10
4	05	1	02	07	56.25	27.50	205	195	386	0780	2580	05	5	10
4	06	0	05	29	34.25	49.25	244	156	400	1050	3450	05	5	10
4	07	0	03	20	36.00	28.00	292	108	400	0830	2600	05	5	10
4	08	0	06	32	41.00	24.50	293	107	374	0980	2120	01	1	10
4	09	1	05	34	31.00	31.75	305	095	388	0810	2090	10	1	09
4	10	1	05	72	38.00	29.50	276	124	364	0900	1790	04	1	12
4	11	1	04	29	27.00	28.75	210	190	370	0790	1260	11	3	12
4	12	1	02	13	29.00	14.00	201	199	318	0340	0730	08	1	07
4	13	0	05	32	42.00	28.00	200	200	334	0400	1000	16	1	11
4	14	0	04	38	37.25	34.25	271	139	390	0650	2600	05	1	13
4	15	0	04	11	35.00	36.00	205	195	380	0540	2440	10	3	08
4	16	0	02	07	22.75	57.75	256	144	368	0500	3260	04	1	09
4	17	1	03	32	07.50	11.50	279	121	260	0250	0780	10	1	08

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
4	18	1	06	25	33.25	35.00	263	137	366	0830	3380	03	1	10
4	19	1	05	41	24.00	39.25	296	104	376	0800	4450	01	1	09
4	20	0	05	31	22.00	34.50	283	117	356	0520	1430	06	1	11
4	21	0	05	61	27.50	34.50	337	063	368	0490	2400	02	1	09
4	22	0	08	46	58.75	52.25	318	082	400	1450	3290	01	1	10
4	23	0	01	05	33.25	51.00	236	164	388	0330	1720	08	1	11
4	24	1	03	10	37.25	34.75	259	141	362	0390	2920	04	1	14
4	25	1	03	10	55.25	57.75	223	177	386	1790	3140	06	1	10
4	26	1	06	50	28.50	36.00	101	299	272	0530	1890	04	1	09
4	27	0	04	33	22.75	51.00	146	254	308	0190	1790	10	1	09
4	28	0	07	22	32.25	34.00	186	214	358	0330	1880	14	1	11
4	29	0	09	28	42.25	40.75	132	268	340	0590	2310	08	1	12
4	30	1	12	33	40.25	47.75	088	312	287	0730	2650	13	1	11
4	31	1	02	06	45.75	37.50	170	230	294	0550	1860	25	1	08
4	32	1	01	03	29.00	31.25	251	149	278	0330	1830	16	3	08
4	33	0	03	30	31.75	45.00	284	116	370	0650	2600	17	3	11
4	34	0	05	64	19.50	42.25	338	062	392	0830	2630	03	1	10
4	35	0	04	22	30.50	36.00	296	104	352	0280	2160	01	1	09
5	01	1	05	63	49.25	59.00	277	123	384	1110	4140	05	1	10
5	02	0	04	19	32.25	46.00	154	246	396	0480	2770	07	3	09
5	03	0	03	10	27.75	27.50	300	100	354	0750	1710	11	1	12

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
5	04	1	01	05	18.00	33.50	239	161	316	0420	2360	04	1	08
5	05	1	06	28	59.00	50.00	159	241	382	1230	2890	04	1	10
5	06	0	04	14	41.00	25.00	366	034	364	1250	4320	05	1	12
5	07	0	01	03	15.25	24.75	318	082	330	0620	1640	04	2	03
5	08	1	00	00	37.00	33.50	349	051	348	0740	2420	08	2	03
5	09	1	02	19	46.50	34.75	338	062	354	0640	2240	03	1	13
5	10	1	03	55	48.25	40.25	231	169	360	1020	2990	07	1	09
5	11	1	00	00	13.50	13.50	118	282	312	0270	1070	13	1	07
5	12	1	07	29	40.75	41.00	363	037	394	1170	4710	03	1	11
5	13	1	04	56	29.25	45.25	113	287	334	0970	2660	03	1	12
5	14	1	08	32	52.75	53.75	150	250	364	0980	3160	02	1	10
5	15	1	02	15	37.25	45.50	278	122	390	0480	2740	09	1	09
5	16	1	03	20	41.00	29.50	267	133	380	1090	3100	05	1	10
5	17	1	02	06	43.50	29.50	285	115	374	0480	2120	11	1	08
5	18	1	02	10	36.25	33.25	310	090	348	1070	2750	04	1	10
5	19	1	03	33	25.25	38.50	316	084	366	0600	3030	09	1	11
5	20	1	02	18	30.75	33.25	349	051	360	0840	2360	03	1	08
5	21	0	02	18	25.50	34.00	326	074	344	0710	2020	14	1	10
5	22	0	04	32	34.75	31.00	326	074	358	0620	2550	03	2	03
5	23	1	02	04	29.75	50.00	331	069	334	0620	2620	05	2	04
5	24	1	05	61	28.50	35.50	352	048	338	0780	2430	06	1	13

Grid #	Grid Point	Use	Vert. Veg. Den.	Grid pt.	Vegetation Height		Cumulative % Cover			Horizontal Vegetation Density		m to Perch	Perch Type	Perch Ht.
					Mean 1 m	Mean 5 m	Forb	Grass	Cover	1 m	5 m			
5	25	0	02	03	40.25	32.75	276	124	318	0380	1940	10	1	13
5	26	0	03	16	34.75	28.25	281	119	314	0510	1790	08	1	12
5	27	1	03	16	24.50	37.75	349	051	364	0850	1790	03	1	11
5	28	1	03	16	20.00	29.00	283	107	358	1040	2580	05	1	14
5	29	1	03	38	25.00	38.50	281	119	332	0470	1830	10	1	10
5	30	1	02	52	35.75	39.75	292	103	360	0590	2250	08	1	10
5	31	1	04	21	21.00	43.25	337	063	354	0450	3870	03	1	09
5	32	0	02	25	10.50	32.25	356	044	304	0440	2420	05	1	10
5	33	0	01	11	25.00	33.50	308	092	294	0340	1730	11	1	12
5	34	0	02	15	44.25	40.75	293	107	316	0590	2000	05	1	12
5	35	0	03	20	12.00	42.50	242	158	328	0660	1590	02	2	05

Territory sizes and vegetation measurements for each territory. Mean Height of Vegetation (cm) = MHV; Number of Perches = PN; Perch Height (cm) = PH.

Territory Size (ha)	Mean % Cover			MHV	Variance of MHV	Horizontal Vegetation Density						PN	Day #	Time of Day	
	Grass	Forb	Cover			10 cm high			75 cm high					Time	PH
						1 m	5 m	10 m	1 m	5 m	10 m				
0.25	52	24	076	24	218	1250	05650	09300	00100	1600	2870	2	01	1317	2
1.56	26	68	094	33	718	1500	07500	10050	00290	2200	3950	2	01	1347	2
1.81	25	56	081	28	242	6100	12000	19700	01090	2950	3800	3	01	1140	3
1.42	09	18	027	20	461	0090	05300	08700	00020	0400	2800	1	01	1345	3
1.33	32	38	070	47	169	2900	14200	18200	00960	3800	7100	3	01	1212	2
1.85	50	37	087	19	174	1150	06450	16300	00150	0850	2850	2	02	1420	2
1.71	41	39	080	26	413	0600	03100	08800	00250	0650	2750	2	02	1448	2
1.35	28	43	071	26	238	1350	05400	12300	00300	1350	2600	2	02	1442	2
2.45	27	61	088	31	460	0650	11500	18000	00070	0350	8700	2	02	1452	2
1.21	46	47	093	26	326	2100	09300	16700	00090	1550	3000	2	02	1504	2
1.71	29	53	082	30	574	1350	07600	15500	00110	0560	2200	2	03	1507	2
0.51	36	47	083	22	204	1450	07100	15200	00100	1150	3300	2	03	1525	2
1.71	25	64	089	32	319	1400	13600	19900	00170	1300	5000	3	03	1431	2
0.62	20	58	078	30	341	1700	10600	16400	00600	2650	3300	3	03	1450	2
3.09	36	50	086	32	349	1700	05650	16900	00200	1100	3900	3	03	1551	2
0.38	31	58	089	24	203	1150	09800	13900	00250	1100	3300	1	03	1604	2
0.32	28	44	072	36	535	1750	05800	12300	00320	1170	1950	1	03	1541	2

Territory Size (ha)	Mean Cover			MHV	Variance OF MHV	Horizontal Vegetation Density						PN	Day #	Time of day	PH
	Grass #	Forb	Cover			10 cm high			75 cm high						
						1 m	5 m	10 m	1 m	5 m	10 m				
1.58	34	44	078	19	143	0410	05000	16200	00110	0440	1450	2	03	1620	2
1.30	27	60	087	21	202	0620	09200	12200	00100	0400	1300	1	03	1630	2
0.94	36	57	093	28	291	4400	14000	18400	00850	3700	4800	3	03	1644	2
1.41	20	36	056	22	238	0550	04200	08000	00070	0500	1900	3	04	1405	3
0.43	20	57	076	13	251	0660	02400	06000	00060	0470	1050	3	04	1426	3
1.86	19	70	089	28	310	1650	08800	14500	00850	2500	4000	3	04	1456	3
1.64	54	49	100	25	311	0700	07900	12600	00250	2500	4650	3	04	1512	3
1.40	44	48	092	24	190	2250	08950	17100	00570	1800	3600	2	05	1131	2
1.11	10	65	075	24	381	3100	11800	19700	00550	2300	4800	3	05	1112	2
0.81	27	57	084	21	170	0400	08200	14700	00080	0330	2450	3	05	1107	2
1.13	14	82	096	26	328	1050	08000	19100	00330	1900	4800	3	05	1101	3
2.26	26	50	076	25	206	1100	07300	18800	00100	0850	2800	3	06	1123	3
0.61	35	46	081	15	130	1400	12100	16100	00180	0750	3500	2	06	1119	2
1.94	14	58	072	24	473	1100	08100	15600	00220	0650	2100	3	07	1335	2
1.81	12	62	074	27	328	1800	08000	19900	00400	2000	5000	2	07	1351	2
0.71	46	39	085	16	252	2750	06300	15700	00250	1450	2850	1	07	1424	2
0.63	43	27	070	10	087	1100	03600	07500	00090	0350	0950	2	07	1409	2
1.44	33	47	080	15	178	0700	03400	07500	00080	0550	1100	1	08	1226	2
2.02	52	41	093	16	157	0650	06100	10200	00080	0550	1850	3	08	1244	2
3.56	13	56	069	21	287	1100	03600	14200	00140	0950	4000	2	08	1225	2
2.38	11	63	074	25	401	3450	06300	09400	00100	1350	3050	3	08	1214	2

Territory size (ha)	Mean Cover			MHV	Variance of MHV	Horizontal Vegetation Density						PN	Day #	Time of day	PH
	Grass	Forb	Cover			10 cm high			75 cm high						
						1 m	5 m	10 m	1 m	5 m	10 m				
1.26	38	48	086	19	371	0250	03700	13000	00100	0500	2200	3	08	1204	2
0.50	24	62	086	22	195	1250	08200	14200	00130	1800	3100	3	08	1208	2
1.42	42	46	088	18	164	0950	04100	08900	00250	0800	1850	3	08	1313	3
1.83	23	55	078	11	124	1350	04150	07000	00160	0550	1750	3	09	1323	2
2.26	17	67	084	28	385	0850	15300	19100	00200	0600	1550	3	09	1333	2
2.59	11	89	100	43	363	2750	14700	20000	00550	3800	6500	3	10	1401	1
5.00	23	75	098	52	249	4150	17100	19400	10200	5100	7000	3	10	1419	3
3.79	69	31	100	43	374	1600	06200	14900	00220	1000	3450	3	10	1341	2
0.48	05	69	074	31	285	3050	11500	18900	00530	2150	6500	2	11	1330	2
0.36	12	52	064	25	205	2550	01400	17700	00820	2700	4800	2	11	1340	2
4.50	30	57	087	23	303	1700	04800	13800	00250	1150	2800	3	12	1146	3
3.48	55	38	093	32	315	2250	12400	15500	00680	2450	5100	3	12	1135	3
1.82	06	49	055	19	321	0500	03250	11800	00090	0380	1250	3	13	1239	3
2.42	09	65	074	25	326	0700	05700	10300	00110	1000	2000	3	13	1231	3
0.37	14	51	065	25	242	2750	13600	16400	00300	2100	6000	3	13	1225	2
0.88	15	76	091	24	213	2650	15200	18700	00350	5050	7000	3	13	1215	3
1.11	45	33	078	22	218	2050	12900	15100	00270	3350	5300	3	13	1152	2
1.90	16	67	083	29	212	4750	13100	17400	00300	2750	5300	2	13	1208	2
1.64	33	44	077	32	283	3150	09900	17100	00550	2250	2200	3	14	1231	1
1.74	50	40	090	16	146	2500	09800	17100	00550	2550	3650	3	14	1248	2
0.47	13	58	071	30	369	3150	14200	17900	00450	3500	5800	2	14	1219	2
5.09	34	45	079	18	166	2250	09000	15800	00400	0850	2850	2	15	1252	3