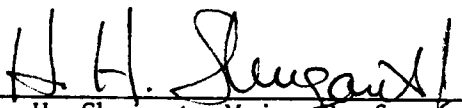
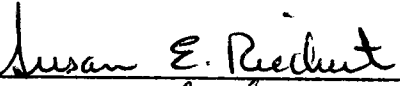
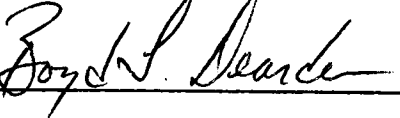


To the Graduate Council:

I am submitting herewith a dissertation written by Thomas M. Smith entitled "Variation in Territory Size of the Ovenbird (Seiurus aurocapillus): The Role of Habitat Structure." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.


H. H. Shugart, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:


Vice Chancellor
Graduate Studies and Research

VARIATION IN TERRITORY SIZE OF THE OVENBIRD
(SEIURUS AUROCAPILLUS): THE ROLE OF
HABITAT STRUCTURE

A Dissertation
Presented for the
Doctor of Philosophy
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Thomas M. Smith

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ABSTRACT

The concept that structural habitat cues are proximal factors for territory size is explored by examining the intrapopulation variation in territory size among ovenbirds (Seiurus aurocapillus). Initial territory size was determined during the first weeks of the breeding season and variables describing the structure of the vegetation within these territories were measured. Prey abundance within territories was monitored both within and among breeding seasons and correlated with both territory size and habitat structure. Similar data were also collected on areas of the study site not occupied by ovenbirds.

There is a negative correlation between prey abundance and territory size with territory size decreasing as prey abundance per unit area increase. A comparison of prey abundance between territory sites and areas unoccupied by ovenbirds reveals a significant difference in prey abundance per unit area. Linear multiple regression of prey abundance with variables describing the habitat structure of territory sites indicates that differences in habitat structure account for 73 percent of the variation in prey abundance among territories. Analysis also indicates that those features of the habitat which best discriminate between territories and unoccupied sites are the same habitat variables which correlate with variation in prey abundance.

A comparison of territory size with predicted prey abundance on the basis of habitat structure shows territory size is more strongly correlated with habitat structure (i.e. predicted prey abundance) than

actual or sampled prey abundance, suggesting the use of habitat structure as a proximal factor for territory size. Those territories which showed the greatest difference between predicted prey abundance on the basis of habitat structure and actual or sampled prey abundance were tested for their fit to the two models: territory size—prey abundance, territory size—habitat structure. Results show that the model defining territory size as a function of habitat structure is significantly correlated with territory size, whereas, territory size was not found to be significantly correlated with actual prey abundance for the territories included in the analysis.

In an analysis of the role of intraspecific competition on territory size, the relationship between territory size and distance to the nearest neighboring territory was analyzed. Results show that the distribution of territories in the study area is not significantly related to either prey abundance or habitat structure and that distance to nearest neighbor accounts for only a small portion of the variation in territory size.

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CHAPTER I

INTRODUCTION

Avian Territoriality: Selection and Function

The role of territorial behavior in avian species has long been a subject of intensive study among ecologists. However, the adaptive function of territoriality has remained an area of controversy (Wilson 1975, Verner 1977). One hypothesis, the food value theory (Wilson 1975), postulates that the function of territorial behavior is to space pairs of birds over an area to ensure an adequate food supply for the successful rearing of young (Stenger 1958). This theory implies that territory size is related to the abundance of prey available to birds within the territory. Numerous studies have demonstrated that territory size is inversely related to food abundance (Pitelka et al. 1955, Stenger 1958, Moss 1969, Holmes 1970, Clarke 1970, Maher 1970, Watson and Moss 1970, Stimson 1973, Slaney and Northcote 1974, Simon 1975, Gass et al. 1976, Salmonson and Balda 1977). Although this hypothesis appears to have earned a general level of acceptance, there have actually been few attempts to identify the mechanisms through which this relationship occurs. Two hypotheses have been postulated. The first is that individuals directly monitor prey abundance and adjust territory size to ensure sufficient resources for their energetic needs (Armstrong 1965, Stimson 1973, Brown 1975, Simon 1975, Cass et al. 1976, Salmonson and Balda 1977). Under the second hypothesis, an individual

defends an area as large as possible, but territory size is limited by intraspecific competition for habitat (Hinde 1956, Lack 1966, Krebs 1971, Schoener 1971, Dunford 1977). Areas of higher quality (i.e. prey abundance) would attract more competitors and result in a higher cost per unit area in defense. Thus, the increased pressures of competition would result in smaller territories in areas of higher quality habitat.

These hypotheses are considered mutually exclusive, each postulating a different mechanism for the territory size-prey abundance correlation. The "direct monitoring hypothesis" suggests that birds "directly" monitor food abundance and adjust territory size to provide sufficient resources, whereas, the "intraspecific competition hypothesis" suggests that the territory size-prey abundance correlation is an "indirect" result of increased competition for more favorable habitat (i.e. areas of higher prey abundance). Much of the evidence in support of these hypotheses comes from field studies designed to look at intraspecific variation in territory size.

Support for the "direct monitoring hypothesis" is usually of two sorts: correlations between prey abundance and territory size, and experimental data on changes in territory size when prey abundance is altered within the territory boundary. Gass et al. (1976), in a field study of female and immature rufous hummingbirds (Selasphorus rufus), found that feeding territories are closely regulated in size to maintain reserves of energy per individual. The territories contained two plant species with widely differing pollen production rates, but territories were found to have similar daily caloric productivity regardless of

their plant composition. Salmonson and Balda (1977) found that yearly variations in the size of winter feeding territories of the Townsend's Solitaire (Myadestes townsendi) were correlated to annual differences in food productivity on the study area. The strongest evidence for the "direct monitoring hypothesis" has come from manipulative experiments. Featherstone (1966) found that territory size in breeding ovenbirds increased when prey abundance within the territory boundaries was experimentally decreased with the use of insecticides.

Evidence in favor of the "intraspecific competition hypothesis" has been in the form of correlations of territory size with indices of intraspecific competition, such as territory intrusion rate or population density of conspecifics. Krebs (1971) found that territory size in the great tit (Parus major) was not correlated with the amount of food on the territory, but was negatively related to the number of neighbors and the population density. Myers et al. (1979) in a study of territory size among sanderlings (Calidris alba) found that territory size varied inversely with prey abundance, but multivariate analysis suggested that the inverse correlation resulted indirectly. Apparently the areas of higher prey density attracted a greater number of intruders, thus raising the cost of territory defense. Myers et al. found that the negative correlation between territory size and prey density was not statistically significant when the effects of food on intruder pressure were eliminated. Furthermore, when intruder pressure declined seasonally, without a decline in food availability, territory size increased. Both Gibb (1956) in his study of territoriality in the

rock pipit (Anthus spinoletta) and Ewald and Carpenter (1978) in their investigation of the territorial responses to energy manipulations in the Annas hummingbird (Calypte anna), found that as food availability increased there was a corresponding increase in intrusion rate.

Ewald et al. (1980) in a study of territory size in Western gulls (Larus occidentalis) found that spatial variation in intrusion rate per unit area best explained variation in territory size. They also found that territory size was positively correlated with the amount of visually obstructive vegetation. This correlation was apparently a result of gathering spots occurring in areas with little cover. This relationship led Ewald et al. to state, "In many cases variation in physical structure may influence territory size by influencing other variables (e.g., intrusion rate, availability of breeding sites) as well as obstructing vision or movement." This concept of the relationship between habitat structure and territory size has been widely recognized in the literature. Erickson (1938) found that differences in territory size for the Wrentit (Chamaea fasciata) were correlated with variation in the density of brush; Miller (1931) found that the loggerhead shrike (Lanius ludovicianus) maintains territories on sand dunes or areas of bare ground two to three times larger than in wooded areas; Howell (1952) found that the yellow-bellied sapsucker (Sphyrapicus varius) maintained larger territories on open slopes than in dense groves; and results of a study by Odum (1941) showed that the larger territories of the black-capped chickadee (Parus atricapillus) contain considerably more open or sparsely wooded area. Orians (1961) reported that territories of

red-wing blackbirds (Agelaius phoeniceus) increased in size after marshes were burned and then decreased as they revegetated.

Wiens (1973), in one of the first extensive studies on the role of habitat structure on territory size in avian species, explored the interterritorial variation in grasshopper (Ammodramus savannarum) and savannah (Passerculus sandwichensis) sparrows in southern Wisconsin. Wiens found that no single vegetation feature, among those measured, was closely related to patterns of variation in size of grasshopper sparrow territories. In the savannah sparrow analysis, however, interterritory variation in the percent cover of grass accounted for most of the variation in territory size. These studies suggest a relationship between habitat structure and habitat quality, resulting in an inverse relationship between habitat quality and territory size similar to that with prey abundance.

There are many reasons to suspect the ecological importance of structure to birds (Wiens 1969, Cody 1968), ranging from its importance in providing song perches, to its role in providing adequate nesting sites or suitable foraging areas. Various studies have shown that specific structural attributes of the habitat are prerequisite for its occupancy by a certain species. Oelke and Klopfer (1970) found that catbirds (Dumetella carolinensis) respond to the size and shape of leaves, while both Wiens (1969) and Cody (1968) have shown that bobolinks (Dolichonyx oryzivorus) select those parts of prairies where the accumulation of litter near the ground is low. However, to determine the role of habitat structure on territory size it is necessary to

identify the mechanism by which structural features of the habitat influence habitat quality.

Morse (1976) in a study of the variables affecting the territory size of breeding spruce-woods warblers found that differences in size of black-throated green warbler (Dendroica virens) territories in red and white spruce forests did correlate closely with differences in their preference for these two types of foliage and presumably, with their differing efficiencies in exploiting these substrates when similar amounts of food were available in both. This finding suggests a relationship between vegetational structure and habitat quality in terms of foraging efficiency and ultimately, individual fitness of the territory holder. However, various authors (Miller 1931, Howell 1952, Stenger and Falls 1959) have suggested that correlations between territory size and habitat structure may result from differing levels of prey abundance corresponding to the habitats occupied. Studying sylviid warblers in Sweden, Cody (1978) found that vegetation height provided an index to prey abundance which correlated to territory size. However, to determine the role of the habitat structure-prey abundance relationship on territory size, it is necessary to define both the role of habitat structure on prey abundance and the resulting effect of this relationship on the habitat selection process.

Hilden (1965) first suggested that birds may respond to proximate factors related to prey abundance rather than directly monitoring resources. If this is the case, territory size should conform to expected food abundance, but not necessarily to that found in any given

year. Seastedt and MacLean (1979) studied the intrapopulation variation in the size of territories of Lapland longspurs (Calcarius lapponicus) to compare the size and composition of territories with habitat productivity measured in the same season and over a sequence of seasons taken to indicate average conditions. The authors found that the size of breeding territories was positively correlated with prey abundance during the 1975 breeding season, however, when prey abundance was averaged over a series of years to provide an index of "expected" food density of the habitat comprising the territory, a negative correlation between prey abundance and territory size was found. Territories that contained a large portion of the most favored feeding habitats were, on the average, smaller than territories which contained a large portion of poor habitat. Seastedt and MacLean stated, "The fact that this relationship applies most strongly to average or expected food density indicates that the birds respond to the habitat configuration of the area rather than assessing food density directly." This concept, which I shall from now on refer to as the "structural cues hypothesis," suggests that birds may cue to features of the habitat which are correlated to prey abundance, rather than directly monitoring food resources per se. The "structural cues hypothesis" is a third possible mechanism for the inverse relationship between territory size and prey abundance other than the direct monitoring of resources or intraspecific competition. If birds are selecting territory sites on the basis of structural habitat cues which are correlated to expected prey productivity, then territory size may be a function of

expected prey abundance based on habitat structure. To date this hypothesis has received little attention. The study by Seastedt and MacLean (1979) was conducted in an area in which the habitat could easily be classified into distinct categories (i.e. wet, mesic, dry) and the relationship between prey abundance and habitat structure easily interpreted. A need exists to explore this concept in structurally more complex systems.

This study explores the relationship between habitat structure and prey abundance in the habitat selection process of the ovenbird to test the "structural cues hypothesis." To accomplish this goal it is necessary to meet three objectives: (1) To determine the relationship between territory size and prey abundance, (2) To determine the role of habitat structure on the distribution of ovenbirds on the study area, and (3) To determine the variation in both prey abundance and territory size as it relates to changes in habitat structure.

The Ovenbird: Life History and Background Research

The ovenbird is a member of the Parulidae family. Its breeding range is from the Gulf of St. Lawrence and north-east Canada south to eastern North Carolina, northern Georgia, Arkansas and Kansas. The species winters from Florida and southern Louisiana into the tropics of Mexico, northern South America, Central America and the islands of the Caribbean.

During the breeding season, the territory, which is defended by the male, is used by the pair for mating, nesting and as a feeding ground

for the adults and young (type A of Nice's (1941) classification). Territories are established by male ovenbirds almost immediately upon arrival. Upon selection of a mate, the female takes no part in the defense of the territory, but restricts her activities within its boundary. Hann (1937), in his extensive study of the life history of the ovenbird, found that the male takes no part in the building of the nest (a period of approximately 5 days) or the incubation process (12 days). However, the male plays an active role in the feeding of young during the nestling stage (8 days).

The ovenbird feeds by gathering invertebrate prey from the surface of the forest floor litter. Ovenbirds typically forage by walking slowly and continuously along the forest floor, picking invertebrates from the litter surface. Ovenbirds rarely pursue prey and do not work the substrate with either bill or feet. Foraging essentially takes the form of a two-dimensional search path. Males usually fly to the forest floor from a song perch in a tree several meters above the ground to begin foraging. Search paths vary in distance and can last from a few seconds to more than an hour. In a series of studies with both hand reared and wild birds, Zach and Falls (1976a, 1976b, 1976c, 1977, 1979) described the foraging behavior of ovenbirds in relation to the distribution of the food supply. Results showed that the amount of search path in patches (i.e. foraging area) increased exponentially with prey density and the authors proposed that differences in renewal and depletion rates of prey are important determinants of foraging behavior of ovenbirds. Zach and Falls also found that areas used for foraging

had more prey than areas not used for foraging and that ovenbirds distributed search effort patchily in response to their food supply. Birds learned patch locations and made successive visits to these locations.

Stenger (1958) studied the food habits of ovenbirds in southern Canada (Algonquin Provincial Park, Ontario) and concluded that most invertebrate groups are eaten according to availability. Similarly, Zach and Falls (1978) found that captive ovenbirds ate virtually all invertebrates that occur in or near the leaf litter, but they prefer relatively large prey types requiring little handling time.

Stenger (1958) investigated the variation in territory size among ovenbirds inhabiting Algonquin Provincial Park in Ontario and its relationship to prey abundance. Results showed a significant inverse relationship between prey abundance per unit area inside the territories and territory size. However, a later study by Zach and Falls (1979) in the same study area failed to reveal a correlation between prey availability and territory size. The authors found that although ovenbirds defended song territories, birds foraged extensively beyond the boundaries of their song territories. These foraging areas were neither defended nor mutually exclusive and there was extensive overlap among birds.

In a study of the territorial behavior of ovenbirds, Stenger and Falls (1959) found a general relationship between the structure of the habitat on the study plots and the size of territories contained within the plots. The authors reported that territory size increased as canopy

height and density increased, as brush and ground cover decreased, and as the forest changed from an early seral stage with many intolerant trees, to a late stage in development characterized by fewer, but more tolerant trees. The authors speculated that this pattern was the result of either differences in prey abundance among the various habitat types or the behavioral needs of the ovenbird.

CHAPTER II

STUDY AREA

The study was conducted on the Walker Branch Watershed, located on the United States Department of Energy Oak Ridge Reservation in eastern Tennessee, at a latitude 35°58' N and longitude 84°17' W. The watershed catchment includes 97.5 ha. with elevation ranging from 285 to 375 m. The terrain is predominantly sloping; slopes range from 1 to 50 percent, with 45 percent of the slopes greater than 25 percent. Underlying bedrock is Knox dolomite, a cherty, dense to coarsely crystalline limestone. Soils are predominantly red-yellow podzolics (typic paleudults) of widely varying depth. These soils are deeply weathered, infertile and well drained.

The Walker Branch Watershed lies within the Ridge and Valley Physiographic Province and the Oak-Chestnut Forest Region (Braun 1950). Since the disappearance of the chestnut (Castanea dentata), the vegetation of the watershed can be qualitatively described as an oak-hickory assemblage. Prior to 1942 there was selective timber removal and approximately 25 percent of the watershed was cleared for subsistence agriculture and pasture. The only disturbances since 1942 have been the maintenance of a perimeter access road and the establishment of a 2.5 ha. loblolly pine (Pinus taeda) plantation.

As part of a watershed study, 298.08 ha. (1/5 acre) permanent plots were established for vegetation analysis (Curlin and Nelson 1968). Fifty-three woody plant taxa were reported on these plots. Based on the

basal area density data for the 12 species which contributed greater than $0.25 \text{ m}^2/\text{ha.}$ to the mean basal area of the watershed, Grigal and Goldstein (1971) conducted an integrated ordination-classification analysis of the 290 nonplantation plots. Although species composition varies continuously on the watershed, four forest stand (plot) types were identified: oak-hickory (Quercus spp. and Carva spp.), chestnut oak (Quercus prinus), pine (Pinus spp, predominantly P. echinata) and yellow poplar (Liriodendron tulipifera).

The territories studied can be classified into two major habitat types; deciduous and mixed conifer-deciduous. The overstory of the deciduous habitat type is dominated by a mixed-oak assemblage comprised of white oak (Quercus alba), black oak (Quercus velutina) and southern red oak (Quercus rubra). On drier sites chestnut oak (Quercus prinus) and black gum (Nyssa sylvatica) predominate. Other major species present include tulip poplar (Liriodendron tulipifera), hickory (Carya spp.) and maple (both Acer rubrum and A. saccharum). The shrub layer is essentially nonexistent with the woody understory being primarily seedling and saplings of the overstory species. In canopy gaps, tulip poplar forms a dense understory.

In the mixed conifer-deciduous habitat type, the dominant conifer is Virginia pine (Pinus virginiana) with the exception of one territory which was located at the edge of a loblolly plantation. Dominant deciduous species include tulip poplar and maple, however, the entire array of species found in the deciduous habitat type are generally present to some degree in either the overstory or understory layer. In

areas where conifer species dominate, the understory and shrub layer is generally less dense than in the deciduous habitat type. The litter layer is a combination of deciduous and conifer species and in many areas a thick mat of honeysuckle (Lonicera japonica) is present in the herbaceous layer.

CHAPTER III

FIELD METHODS

Territory Size

The Walker Branch Watershed was censused during the spring of 1980 to determine the number and location of ovenbirds territories. Censusing was conducted using the spot map technique of Kendeigh (1944). The breeding territories of 23 pair of ovenbirds were mapped and the size of each territory determined. These territories represented a subset of the breeding population on the watershed and were selected to represent the array of habitats chosen as territory sites on the study area. When a male ovenbird was observed singing, that spot was marked in the field and located on a gridded map of the study area. Observations were made during the first several weeks following the arrival of male birds to the watershed (late April) during the hours of 6:00 to 10:00 EST. A minimum of 100 observations were made for each territory. Data from all observation periods were combined and the central 95 percent of the observation points were enclosed by straight lines to form a polygon defining the total utilized territory (Stenger and Falls 1959) and the area of the polygon determined. This method was used in order to make direct comparisons between this study and the work previously reported by Stenger (1958), Stenger and Falls (1959) and Zach and Falls (1979).

Vegetation Structure

Five .02 ha. (.05 acre) sample plots were randomly located in each of the 23 ovenbird territories. Plot size was selected to be large enough to include the sphere of influence of a large canopy tree yet still allow for repeated observations within a single territory. Location of the plots within the territories was determined by randomly selecting compass coordinates and distances run from a point at the center of the territory. Table 1 contains a list and description of those variables for which data were collected for each plot. In addition, 100 plots were randomly located in areas of the watershed not occupied by ovenbirds. Ground cover within each plot was determined by randomly locating three circular 1 m^2 plots within each .02 ha. vegetation plot. Cover values for each of the three subplots were averaged to give a single percent ground cover measure for each vegetation plot. A total of 215 vegetation plots were sampled over the period of the study.

Prey Abundance

To assess the dynamics of prey abundance from year to year, 25 vegetation plots (.02 ha.) were sampled for forest floor litter invertebrates during the weeks of late April and early May of 1979-1981, corresponding to the arrival of male ovenbirds onto the watershed. Samples were also collected from the same vegetation plots during the months of April-June 1980 to provide a measure of the dynamics of invertebrate prey within a single breeding season. In addition, samples

Table 1. Mnemonic and Description of Habitat-Variables
Measured for Each of the .02 ha. Vegetation Plots

Mnemonic	Description
GRCV	Ground cover—average of 3-1 m ² plots.
SHL5	Density of shrubs less than 1.5 m in height.
SHG5	Density of shrubs greater than 1.5 m in height.
CNPY	Canopy Cover (see James 1971).
TR1	Density of trees 2.54 - 7.62 cm. dbh
TR2	Density of trees 7.62 - 15.24 cm. dbh
TR3	Density of trees 15.24 - 22.86 cm. dbh
TR4	Density of trees greater than 22.86 cm. dbh
RCBA	Relative basal area of conifer species on the sample plot.

of forest floor litter invertebrates were collected from each of the 115 sample vegetation plots contained within the 23 territories during 1980.

Five 0.1 m^2 litter samples were collected from each vegetation plot. These samples were collected using a 0.1 m^2 circular metal frame, sharpened to cut through leaves and stems when driven through the litter layer. All surface organic matter from within the frame was placed in a plastic bag. Invertebrates were extracted by hand sorting and placed into an ethyl alcohol solution and were later air dried with weights and number of individual recorded.

Sample weights were adjusted so as to exclude those invertebrates which were not included in the diet of the ovenbird on the watershed as determined by a preliminary qualitative analysis of stomach contents of 58 birds over the period of the study.

CHAPTER IV

RESULTS AND DISCUSSION

Territory Size and Prey Abundance

A total of 47 ovenbird territories were located on the watershed and adjacent areas (Figure 1). Both the ground nesting habits and foraging behavior of this species preclude the use of steep slopes as territory sites, therefore limiting much of the watershed as suitable breeding habitat. The distribution of birds on the study area is patchy, with the majority of territories being located on ridgetops or areas of the watershed where the topography is less rugged

Size of the 23 territories sampled ranged from 1300 m^2 to 3800 m^2 with an average territory size of 2666 m^2 (standard deviation of 853 m^2). Birds were found to forage exclusively within the territory boundaries. There is usually a buffer zone between the territories of neighboring birds, however, interterritory spaces varied in size.

Prey abundance within territories was calculated by averaging the density estimates from the 5 randomly selected vegetation plots within each territory. Prey densities ranged from .0175 to .4213 grams per 0.1 m^2 with an average density of .1967 (standard deviation of .1037) for the territories sampled. Regression analysis of territory size with prey abundance indicates that 44 percent of the variation ($r^2 = .44$) in territory size is explained by differences in prey abundance among territories. Results of Pearson product moment correlation analysis show a significant negative correlation ($r = .66$, $p \leq .001$) between prey

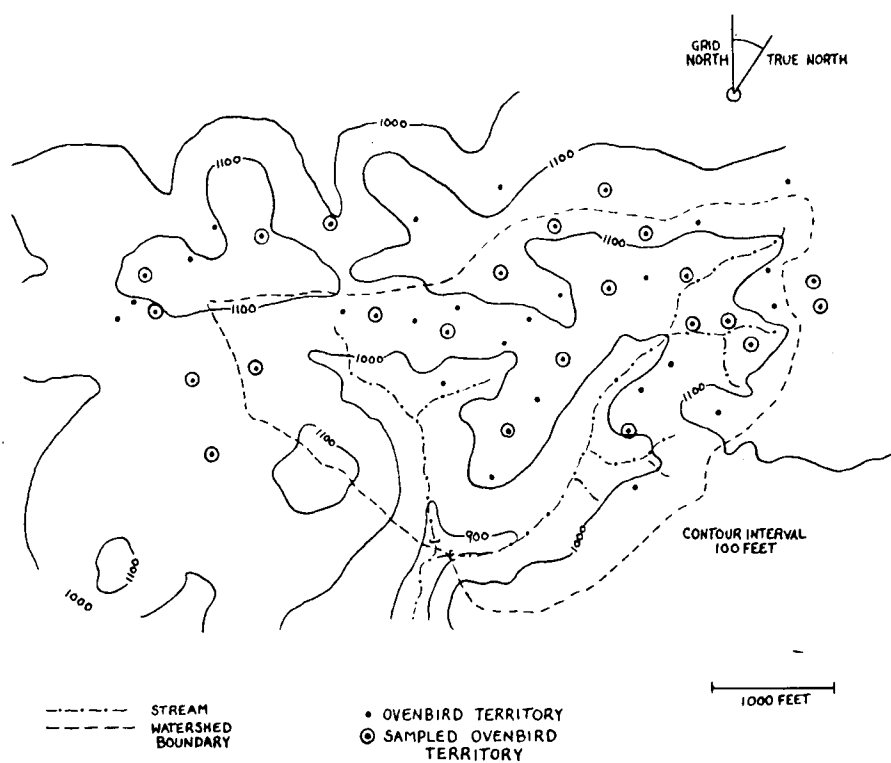


Figure 1. Map showing the location of ovenbird territories on the Walker Branch Watershed and boundary areas.

density per unit area and territory size. Territory size decreases as the abundance of prey per unit area within the territory increases (Figure 2).

Results of the analyses support the findings of Stenger (1958) that the size of ovenbird territories show an inverse correlation with prey density. This result appears robust in that the two studies were at the northern and southern extremes of the eastern breeding range of the ovenbird and were in two quite different vegetation types. Findings also support the food value theory and suggest that at least one function of territorial behavior in the ovenbird is to ensure an adequate food supply for the energetic needs of the territory holder.

Results fit the cost-benefit model of territory size put forth by Brown (1969), a hypothesis based on the idea that as territory size increases, the costs of defense likewise increase. Territory size is then a trade off between costs and benefits, ideally with territory size being an optimization (or maximization) of the benefits to costs ratio. A number of field studies have addressed the cost-benefit approach to territory size by quantifying the costs of territory defense as well as the food value associated with the territory. Carpenter and MacMillen (1976) found that by directly quantifying the costs and benefits associated with territoriality in the Hawaiian honeycreeper (Vestiaria coccinea) they could successfully predict the changes from territorial to nonterritorial behavior when the costs exceeded the benefits. This same threshold effect of the cost-benefits ratio may explain the discrepancy in the findings of Stenger (1958) and

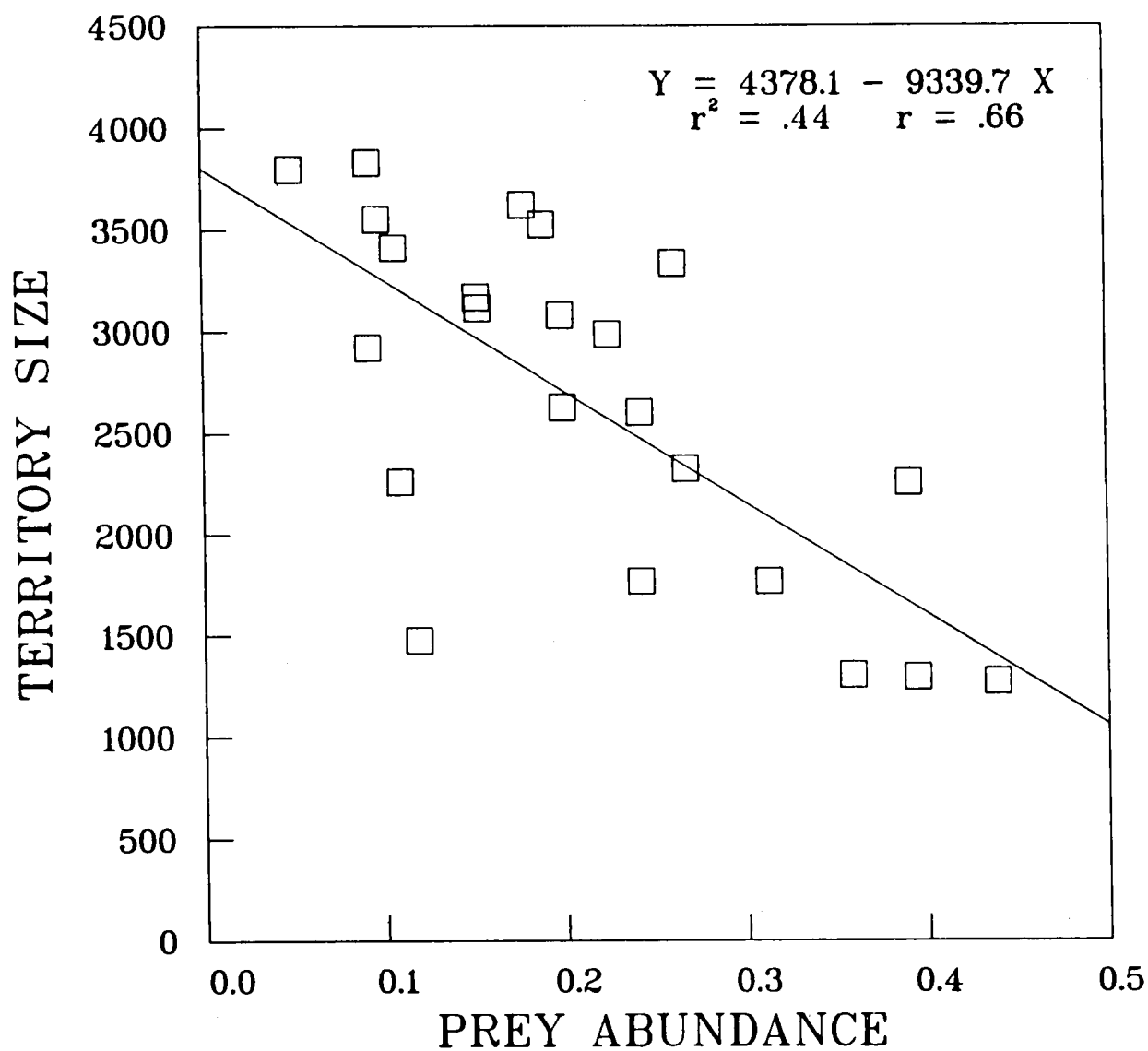


Figure 2. Regression of territory size with prey abundance for 23 territories sampled on the study area. Prey abundance is expressed in g/.1m² and territory size in m².

Zach and Falls (1979) in their studies of the territorial behavior of ovenbirds in Ontario (see p. 10). Zach and Falls found that male ovenbirds defended song territories, but that foraging areas extended beyond territory boundaries and were not defended or mutually exclusive. However, the prey abundance values reported by Zach and Falls are far less than those reported by Stenger. If these values are truly representative of prey abundance during the two time periods, the lack of foraging area defense might be a function of the cost inefficiency of defending an exclusive foraging area. However, when territories serve a multiple purpose (Nice 1941), such as in the ovenbird (Hann 1937), complete breakdown of territorial behavior would not necessarily be expected, explaining the defense of song territories in Zach and Falls results.

Habitat Selection

Most studies of bird habitat selection proceed by identifying structural correlates of species' distribution, either within a particular location of the species range or over its entire geographic distribution. Although care should be taken in the interpretation of correlates of distribution, so as not to assume their causal nature, it does not preclude their use as either predictive models or as a means to understand the nature of actual cues used by the bird in the habitat selection process when coupled with information on species life histories or correlates to individual fitness (e.g., nest sites, foraging sites, prey abundance, etc.). Frequently there are many

measurable vegetational features that could potentially be used in habitat discrimination, either as separate cues or together, interacting to provide the bird with a composite or gestalt picture (James 1971) of the habitat.

A variety of multivariate statistical techniques can be used to quantify and integrate the array of vegetational variables which can characterize complex habitats. The advantage of these methods is their ability to reduce a large number of intercorrelated variables to a few uncorrelated axes which explain a large percentage of the variance in the original variates. One such technique is discriminant function analysis (Morrison 1968). This procedure has been directly applied to determine the influence of a number of habitat variables on the distributions and microhabitat selection of both individual species (Martinka 1972, Conner and Adkisson 1976, Smith et al. (in press)) and entire avian communities (Cody 1968, James 1971, Shugart and Patten 1972, Anderson and Shugart 1974, Whitmore 1975).

Discriminant function analysis is a statistical procedure for defining the linear combination of the original response variables (variables describing the habitat structure of the sample plots) resulting in the largest difference among population mean vectors (i.e. maximize the ratio of among-group to within-group sums of squares and cross products). The linear combination is a new, transformed variable composed of the original variables, each weighted according to their power to discriminate. By this process, the relationship of territory sites and unoccupied areas along several

independently measured univariate gradients is reduced to a single position along a multidimensional gradient of habitat structure.

The valid use of discriminant function analysis assumes that the two distributions (i.e. territory sites and unoccupied areas) are multivariate normally distributed with equal variance-covariance matrices. These assumptions are direct extensions of the assumptions on which univariate analysis of variance are based (Snedecor and Cochran 1967).

A direct way to test the discriminating ability of the function is to determine its accuracy in predicting group membership. By calculating the Bayes, or minimum loss, classification function (Morrison 1968) from the resulting discriminant function, each observation (i.e. plot) can be classified as to its probability of group membership on the basis of its position along the discriminant function.

Data on the vegetational structure of both areas selected as territory sites as well as for unoccupied areas were compared using both univariate and multivariate statistics. The two groups of sample plots were compared separately for each variable in Table 1 (p. 17) using both parametric (t-test) and nonparametric (Kruskal-Wallis) (Conover 1971) analyses (Table 2). The comparison of both parametric and nonparametric statistics allows for the determination of problems associated with failures to meet the underlying assumption of normal distributions for the use of parametric multivariate analysis (Deusser and Shugart 1979).

Table 2. Parametric (t-test) and Nonparametric (Kruskal-Wallis-H) Univariate Analysis of Habitat Variables for Territory and Unoccupied Vegetation Plots

Habitat Variable	t-Test	Kruskal-Wallis-H χ^2 (approximate)
GRCV	-2.36 **	4.61 *
SHL5	-2.18 *	4.25 *
SHG5	-3.08 **	6.35 **
CNPY	3.47 ***	9.70 ***
TR1	-1.57	.35
TR2	1.95 *	2.92
TR3	1.19	2.22
TR4	.94	4.89 *
RCBA	-2.22 *	2.01

(* = $p \leq .05$, ** = $p \leq .01$, *** = $p \leq .001$)

Univariate comparisons of occupied and unoccupied areas detected significant differences ($p \leq .05$) in 6 of the 9 habitat variables. Variables on which significant differences between groups were found are: GRCV (ground cover), SHL5 (shrubs ≤ 5 ft.), SHG5 (shrubs ≥ 5 ft.), CNPY (canopy cover), TR2 (trees 3-6 in. dbh) and RCBA (relative conifer basal area). Plots within territories were found to have significantly lower mean values of ground cover (GRCV), shrubs (SHL5, SHG5), mid canopy trees (TR2) and conifer basal area (BCBA), while having significantly greater mean values for canopy cover (CNPY). The failure to show a significant difference between the two groups for the larger tree variables (TR3 and TR4) apparently was a result of the presence of large conifers on the mixed conifer-deciduous stands in the unoccupied areas. With the conifer plots removed from the analysis, territory plots have a significantly higher mean number of larger trees per sample plot.

Kruskal-Wallis test results were qualitatively similar to those of the t-test in the level of significance at which the null hypothesis was rejected and also in the variables for which significant differences were found (Table 2). These results indicate that any non-normality in the distribution of the habitat variables did not greatly effect the outcome of the parametric analysis. For continuity with subsequent multivariate analysis, all remaining analyses of habitat structure will be parametric.

To understand the patterns of covariation among the habitat variables and their ability to discriminate between suitable breeding

habitat and unoccupied areas on the watershed, a discriminant function analysis of the two groups was performed (Table 3).

The derived function was significant ($F = 3.01$, $p \leq .01$) in differentiating between territory sites and unoccupied areas of the watershed. Territory plots show higher values for canopy cover (CNPY), and the larger tree size classes (TR2, TR3, and TR4) while having lower values for ground cover (GRCV), shrubs (SHL5, SHG5) and conifer basal area (RCBA) than unoccupied areas (Figure 3). In a Bayesian classification of plots based on the resulting discriminant function, 94 percent of the territory plots were correctly classified as compared to only 63 percent of the unoccupied plots. This discrepancy is not unexpected, because unoccupied plots may be suitable habitat, but factors other than structural suitability such as patch size, population density of ovenbirds on the study area or proximity to disturbed areas (roads, rain gauge plots, openings, etc.) may influence their probability of use.

A comparison of arthropod biomass showed a significant difference ($t = 27.78$, $p \leq .001$) in prey abundance between territory and unoccupied plots with territory plots having a mean prey abundance of $.1928 \text{ g}/.1 \text{ m}^2$ as compared to $.1181$ for unoccupied areas.

Results of both the univariate and multivariate analyses show the uniqueness of the habitat selection pattern of the ovenbird on the study area. Territory sites were found in areas of the watershed in which the understory and shrub layer was sparse. Ovenbirds were found to select stands dominated by large mature trees in which the canopy was closed, and although birds were found in mixed conifer-deciduous

Table 3. Summary of the Discriminant Function Analysis
of Territory and Unoccupied Sample Vegetation Plots

Eigen value	.2684	
F	3.01	Wilk's Lambda .7884
Significance	$p \leq .01$	
Variable	Standardized discriminant function coefficients	
GRCV	-.0256	
SHL5	-.0108	
SHG5	-.0219	
CNPY	-.0021	
TR1	-.0228	
TR2	.0903	
TR3	.0063	
TR4	.0749	
RCBA	-.0208	
CONSTANT	1.8490	

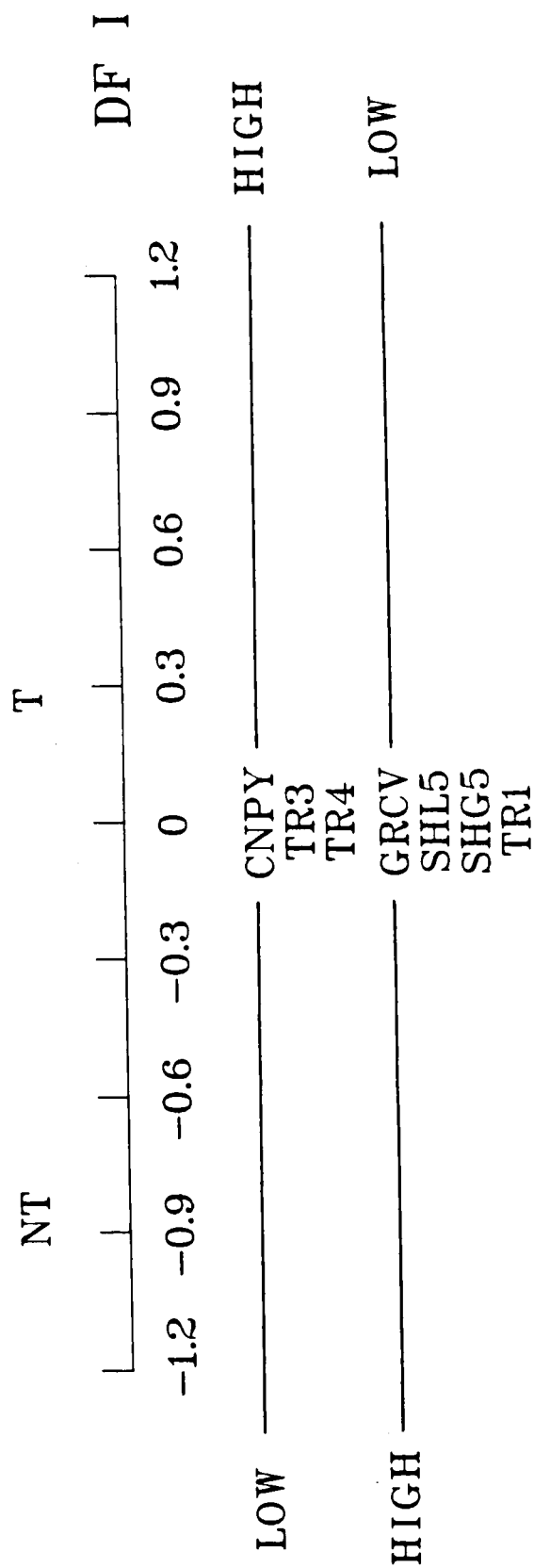


Figure 3. Values for group means along discriminant axis (NT—unoccupied plots; T—territory plots). Axis is labeled to express the variation of the original habitat variables with the discriminant function.

stands, the average conifer basal area of territory sites was less than that found for unoccupied areas of the study site. This pattern results in a significantly greater prey density in territories as compared to unoccupied areas of the watershed, suggesting that the habitat selection pattern of the ovenbird is related to prey abundance.

Interterritory Variation

Variation among the 115 sample vegetation plots located within the 23 breeding territories was also examined. To clarify the patterns of variation in the habitat selection process, the territory sample plots were subjected to a principal components analysis. In this way, both the variance and covariation of the habitat variables could be analyzed as to their importance in accounting for the variation among territories.

Principal components analysis is a method of obtaining those linear combinations of the response variables which explain progressively smaller portions of the total sample variance under the constraints of orthogonality (Morrison 1968). Through this procedure, the 9 inter-correlated habitat variables can be reduced to a few uncorrelated axes which maximize the variation among territory plots. By analyzing the correlation of the original habitat variables to these new axes or factors, the relative input of each habitat feature to the principal components can be assessed.

Results of the analysis show that the first or major component accounts for 38 percent of the total variance with the first three axes accounting for a total of 84 percent (Table 4). The first component is significantly correlated with 6 of the 9 habitat variables:

Table 4. Summary of the Principal Components Analysis
of 115 Territory Vegetation Plots

	Component		
	I	II	III
Eigen value	653.91	522.72	237.80
% σ	38.14	30.49	13.87
$\sum$ % σ	38.14	68.63	83.50
Coefficients			
GRCV	.1913	.0836	-.9453
SHL5	.1194	.7605	.0693
SHG5	.1878	.5255	.1527
CNPY	-.4483	-.1452	.0546
TR1	.0828	.0768	.1942
TR2	-.0062	-.0387	.0068
TR3	-.0039	-.0222	.0004
TR4	-.0090	-.0180	-.0052
RCBA	.8398	-.3350	.1838

GRCV, SHL5, SHG5, CNPY, TR1, TR4 and RCBA (Table 5). The highest correlations are with canopy cover (CNPY) and relative conifer basal area (RCBA). The second component is correlated with 7 of the 9 habitat variables, the highest correlations being with the shrub variables (SHL5, SHG5) and the large size categories of trees (TR2, TR3 and TR4). The third component is correlated with ground cover (GRCV) and the smallest size class of trees (TR1).

The relationship between the structural variation in habitat among the territories with productivity of prey was investigated by examining the correlation between the principal axes and both average biomass and prey size. The first two principal components show a significant correlation with both prey biomass (PC I - $r = -.62$, $p \leq .01$; PC II - $r = -.36$, $p \leq .01$) and prey size (PC I - $r = -.42$, $p \leq .01$; PC II - $r = -.36$, $p \leq .01$). The remaining axes, however, were not correlated ($p < .1$) with either prey variable.

Results show that the combination of conifer basal area and canopy cover account for the greatest variability among territory sites, both important variables in the discrimination of suitable habitat. As the percentage of conifer basal area on the plot increases, the canopy cover decreases. This pattern is a result of structure of conifer-deciduous sites chosen by ovenbirds on the study area. The majority of mixed conifer-deciduous stands chosen as territory sites are stands dominated by a few large conifers with either co-dominant tulip poplar and maples or an understory dominated by hardwood regeneration. Many stands have standing conifer snags and represent a transition between

Table 5. Correlations of Habitat Variables with
First 3 Principal Components

	Component		
	I	II	III
Correlation to original habitat variables			
GRCV	.3137 **		-.9280 ***
SHL5		.8994 ***	
SHG5	.2990 **	.7481 ***	
CNPY	-.7803 ***	.2260 *	
TR1	.2492 *		.3524 **
TR2		-.4520 ***	
TR3		-.4241 ***	
TR4	-.2484 *	-.4432 ***	
RCBA	.9233 ***	-.3249 **	

(* = $p \leq .05$, ** = $p \leq .01$, *** = $p \leq .001$)

conifer and intollerant hardwood stages. Therefore, these stands are characterized by canopy gaps and canopy cover is typically more open than the pure deciduous stands. In comparison, the second principal axis represents a gradient from dense shrub cover and few trees to a plot dominated by large trees with a sparse shrub layer. Both axes appear to be a continuation of the structural gradient defined by the discriminant function. As was the case for the discriminant function, this gradient is correlated with prey abundance.

Habitat Structure and Prey Abundance

The difference in prey abundance between territories and unoccupied areas of the watershed as well as the correlation between prey abundance and the first two principal axes suggests a relationship between productivity and habitat structure which plays an important role in the habitat selection process of the ovenbird on the Walker Branch Watershed. Correlation analysis between prey abundance (i.e. biomass) and the 9 habitat variables measured for each vegetation plot (Table 6) show that 7 of the 9 habitat variables have a significant correlation with prey abundance for the 115 vegetation plots sampled. Prey abundance was negatively correlated with SHL5, SHG5, TR1 and RCBA, while rising as the values of CNPY, TR3 and TR4 increase.

To determine the role of habitat structure on the variation in abundance of litter arthropods, a multiple linear regression (Draper and Smith 1966) for prey abundance including all 9 habitat variables was performed. The 9 variable model (Table 7) was found to be significant ($F = 23.64$, $p < .001$), accounting for 74 percent of the variation in

Table 6. Correlation between Prey Abundance
(Biomass) and Habitat Variables

Habitat variables	Prey biomass (g/m ²) BIOM
GRCV	-.1240
SHL5	-.4327 ***
SHG5	-.4906 ***
CNPY	.4680 ***
TR1	-.4872 ***
TR2	.1016
TR3	.4809 ***
TR4	.5657 ***
RCBA	-.4369 ***

(* = $p \leq .05$, ** = $p \leq .01$, *** = $p \leq .001$)

Table 7. Results of Multiple Regression Analysis of
Prey Abundance with all 9 Habitat Variables

	b	STD b	t for H_0 : $b_i = 0$	p > t
Intercept	.154358		2.53	.0137
GRCV	.000032	.0049	.08	.9380
SHL5	-.001503	-.2836	-3.61	.0006
SHG5	.000629	.0987	1.01	.3170
CNPY	.000234	.0336	.41	.6901
TR1	-.002206	-.1831	-2.17	.0030
TR2	-.000030	-.0006	-.01	.9936
TR3	.028506	.3321	4.61	.0001
TR4	.036006	.3286	4.38	.0001
RCBA	-.002022	-.4594	-5.77	.0001

Model F = 23.64 $p \leq .001$

$R^2 = .75$

prey density. A test of the hypothesis that $b_i = 0$ revealed only 5 of the 9 habitat variables to differ significantly from zero, those being SHL5, TR1, TR3, TR4 and RCBA. As a result of this finding, the maximum R^2 stepwise regression procedure (Draper and Smith 1966) was used to determine a reduced model. Results of this procedure revealed (Table 8) that the 4 variable model including the habitat variables SHL5, TR3, TR4 and RCBA accounted for 73 percent of the variation in prey biomass. Examination of the standardized beta (b_i) coefficients indicates that arthropod biomass decreases as the density of shrubs (SHL5) and conifer basal area (RCBA) increase. In comparison, prey abundance increases with increasing density of large trees (TR3 and TR4).

Both Stenger (1958) and Zach and Falls (1976) found prey size to be an important factor in the foraging behavior of ovenbirds. Although ovenbirds were found to select prey species in proportion to their abundance, both studies found that ovenbirds select proportionately more larger than average prey items. To incorporate the pattern of prey size into the habitat structure-prey abundance relationship, it is necessary to define prey abundance as both prey density (BIOM) and prey size (SIZE). To analyze the relationship between habitat structure and prey abundance, it now becomes necessary to determine the correlation between two sets of variables. Hotelling (1936) has developed a technique, canonical correlation analysis, appropriate for this problem.

The method was developed for studying the relationship between two sets of variables describing the same individuals and is basically an

Table 8. Results of Stepwise Regression Model of Prey
Abundance with Habitat Variables

	b	STD b	t for H_0 : $b_i = 0$	p > t
Intercept	.144175		6.36	.0001
SHL5	-.001212	-.2287	-3.38	.001
TR3	.032640	.3803	6.11	.0001
TR4	.040273	.3675	5.64	.0001
RCBA	-.002219	-.5041	-8.39	.0001

Model F = 51.73 p $\leq$.001

$R^2 = .73$

extension of the principal components analysis. The canonical correlation procedure is a form of generalized regression utilized to extract sets of factors that are uncorrelated within each system (i.e., set of variables), but have maximum correlation for pairs of factors between systems. The first set of factors extracted are those linear combinations of the two sets of original variables which maximize the product-moment correlation between factors (Cooley and Lohnes 1971). Through interpretation of the factor coefficients, the relative contribution of each variable to the correlation can be assessed.

Results (Table 9) show that only the first canonical correlation is significant ($F = 10.34$, $p \leq .001$) with a value of .88 and a canonical R^2 of .79. Examination of the standardized canonical coefficients reveal similar results to those of the multiple regression analysis with SHL5, TR3, TR4 and RCBA having the highest loadings for the habitat axis. However, 7 of the 9 habitat variables were found to have a significant correlation with the first canonical habitat axis (Table 9). Only GRCV and TR2 failed to show a significant correlation. Prey abundance (BIOM and SIZE) was found to increase with increasing canopy cover (CNPY) and the presence of large trees on the plot (TR3 and TR4) while decreasing with increased shrub (SHL5 and SHG5) and understory density (TR1) as well as increasing conifer basal area (RCBA). Both prey variables (BIOM and SIZE) have highly significant negative correlations with the prey canonical function, decreasing in value with increasing scores along the canonical axis (Figure 4). By

Table 9. Summary of Cannonical Correlation Analysis
between Habitat and Prey Variables for Territory
Vegetation Plots

Cannonical Correlation	.88	
Cannonical R ²	.79	
Wilk's Lambda	.19023	
F	10.34	
Significance	p ≤ .001	
	Standardized cannonical coefficients	Correlation with original variable
Habitat		
GRCV	-.00785	.1659
SHL5	.30950	.5407 ***
SHG5	-.09180	.5711 ***
CNPY	-.02037	-.5542 ***
TR1	.14650	.5359 ***
TR2	-.06724	-.2038
TR3	-.41830	-.5628 ***
TR4	-.40152	-.63712***
RCBA	.53789	.5421 ***
Prey		
BIOM	-.81395	-.9659 ***
SIZE	-.30034	-.7120 ***

(* = p ≤ .05, ** = p ≤ .01, *** = p ≤ .001)

Figure 4. Position of 115 vegetation plots along first canonical axes. Ground cover (GRCV), shrub layer (SHL5, SHG5), the smallest size class of trees (TR1) and conifer basal area (RCBA) show increasing values along the habitat axis. Canopy cover (CNPY) and the three larger tree size classes (TR2, TR3 and TR4) decrease with increasing values of the habitat axis. Both prey biomass (BIOM) and average prey size (SIZE) decrease with increasing values along the prey axis.

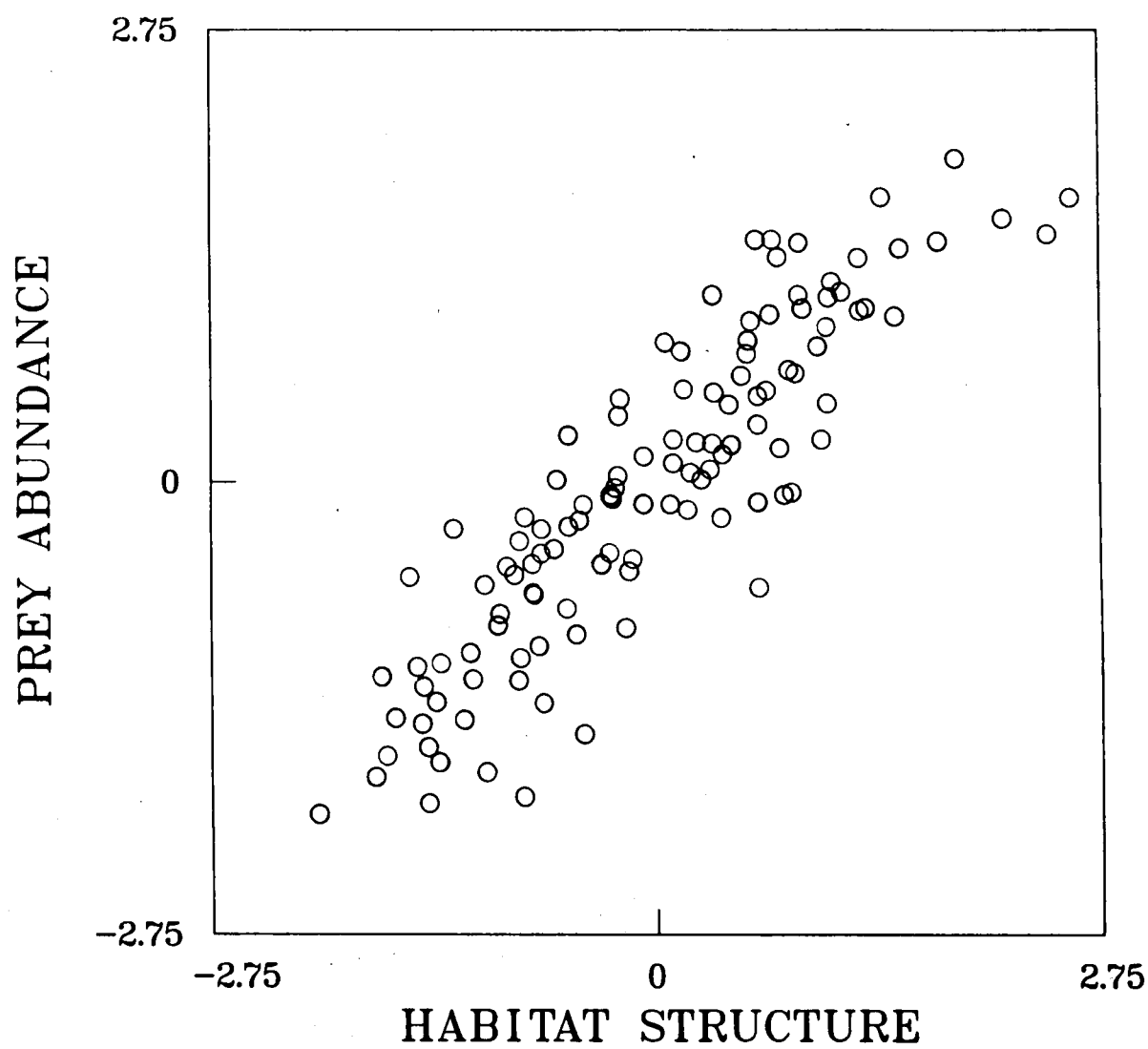


Figure 4

calculating the mean vectors associated with the two sets of variables for each of the 23 ovenbird territories, it is possible to graphically represent the variation of prey abundance with habitat structure for the ovenbird territories (Figure 5).

The role of habitat structure on prey abundance has been suggested by various authors, but few studies have sampled prey abundance in various habitats to substantiate this relationship or define its role in the habitat selection process of the species under study (Riechert 1978, Riechert 1981). Seastedt and MacLean (1979) examined the productivity of three habitat types (wet, mesic and dry) in the Alaskan tundra and the role of habitat productivity on territory size. Stenger (1958) in her study of the role of prey abundance on territory size in the ovenbird, found that the various forest types in her study area had varying levels of prey productivity which resulted in a correlation between habitat type and territory size. Results from the present study suggest a strong correlation between habitat structure and arthropod abundance in the forest litter layer. Results from both the regression analysis and the canonical correlation analysis suggest a pattern of increasing prey abundance as the structure of vegetation goes from an open canopy and dense shrub-understory layer to a stand dominated by larger trees having a closed canopy and sparse understory. Likewise, prey abundance increases dramatically from a pure conifer or mixed conifer-deciduous to a pure deciduous stand. This pattern is most likely due to the corresponding microclimate patterns and chemistry of the forest floor. Those stands which are dominated by large trees with

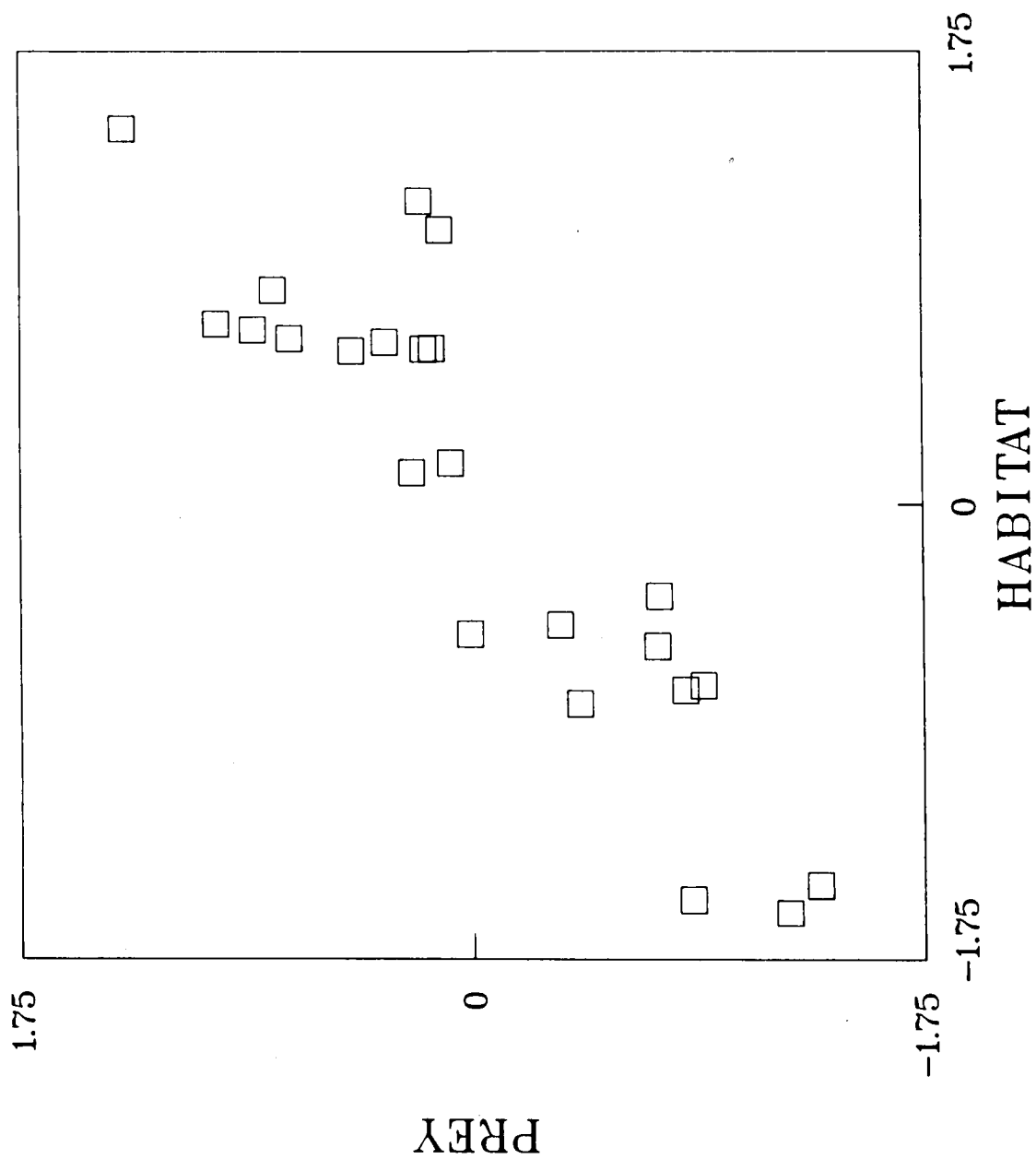


Figure 5. Position of 23 ovenbird territories along first canonical axes. (Axes same as described in Figure 4.)

a closed canopy and sparse understory would be expected to have lower temperatures with less drastic diurnal fluctuations, increased relative humidity and moisture at the forest floor, as well as an increased litter depth compared to those stands with an open canopy and a dense shrub and understory layer (Geiger 1966), thus providing a more favorable environment for litter arthropods (Wallwork 1976). Although leaf area is relatively constant after a stand reaches 20 years of age (Switzer et al. 1968), the accumulation of litter and appearance of tree species with slower litter decomposition rates (e.g., Quercus spp.) continues to increase with stand age. Since leaf litter has a higher moisture holding capacity (Swift et al. 1979), the increased litter layer would aid in moisture retention, reducing temperature fluctuations at the litter layer. All of these factors would increase both diversity and density of arthropods inhabiting the forest floor litter layer (Wallwork 1976). As a stand opens and light and wind penetrate the canopy, the temperature and moisture regime become less favorable and density of litter arthropods decreases.

In the conifer and mixed conifer-deciduous stands, the litter is lower in pH with higher lignin and tannin contents. Conifer litter provides a poorer carbon source for microorganisms and this less favorable environment results in both lower microbial populations and decreased macroarthropod density (Swift et al. 1979).

The relationship between habitat structure and prey abundance appears to be a major factor in the habitat selection pattern of the ovenbird on the study area. Results of the comparison between vegetation

plots sampled within the boundaries of the 23 ovenbird territories and those areas not occupied revealed a significant difference in prey abundance between the two groups. Secondly, the general pattern of variation in the habitat variables responsible for discriminating between occupied and unoccupied areas was the same as the pattern exhibited in the analysis of the relationship between habitat structure and productivity of prey. The pattern of habitat selection by the ovenbirds on the Walker Branch Watershed appears to be directly related to the potential productivity of the litter layer in providing a suitable food resource base. In comparison, analysis of the variation among plots within territory sites revealed that the sources of variation among and within territories was not as directly related to those variables highly correlated with prey abundance as was the variation between territory and unoccupied sites. However, the patterns of variation expressed by the first two principal components were significantly correlated with variation in prey abundance.

An interesting question arises from these findings. If the habitat selection patterns of the ovenbird are linked to quality of habitat with respect to prey abundance, what influence would this relationship have on the evolution of habitat selection in this species? Many studies have dealt with identifying the factors which influence the process of habitat selection and many explanations exist for an array of species. Various works (Cody 1974, Rosensweig 1981, Cody 1981) have addressed the role of interspecific competition on the habitat selection process, whereas other authors have chosen the direction of identifying

environmental factors which influence habitat suitability. Calder (1973) studied the importance of nest sites on two species of hummingbird, while Zimmerman (1971) and Martin (1971) identified habitat quality with respect to nesting sites as a factor influencing the reproductive success of two grassland bird species. Prince and Parsons (1977) showed temperature and humidity preferences in three species of *Drosophila* under laboratory conditions, but were unable to correlate these patterns with species distribution in their natural environments.

Partridge (1976) found a correlation between foraging efficiency and substrate type which correspond to the habitat preferences of two species of Tit (genus Parus) inhabiting broad leaf and conifer forests. Her findings suggest a relationship between habitat selection patterns and habitat structure with respect to foraging efficiency in these species. However, given a fixed foraging behavior (i.e., gleaning prey from the forest litter layer), to what degree do patterns of prey productivity influence the evolution of habitat selection patterns? The ovenbird is a migratory species whose breeding range extends over a wide variety of habitats (see p. 8). If the habitat selection pattern is related to patterns of food productivity, then the preferred habitat type of the ovenbird over its range should reflect the productivity of the spectra of habitats available.

Stenger (1958), in her study of territoriality in the ovenbird in southern Ontario, found a relationship between territory size and habitat type which was correlated to the food value (prey density) of the various vegetation types. Stenger found that prey abundance was

highest in Aspen (Populus spp.) stands, followed by Conifer-birch (Betula papyrifera and Pinus strobus), mixed (Acer spp., Betula lutea and Tsuga canadensis) and maple (predominantly Acer spp.) respectively. This pattern results in a structural sequence of productivity which is the direct opposite of the pattern found in the present study. Stenger and Falls (1959) described the structural pattern that territory size increased (i.e., prey abundance decreased) as canopy height and density increased, as brush and ground cover decreased, and as the forest changed from an early seral stage with many intolerant trees, to a late stage in development characterized by fewer, but more tolerant trees. The difference in these patterns is most likely due to the resulting changes in the litter layer directed by the species present in the various habitat types, rather than their structural configuration per se.

The two habitat types associated with the smallest average territory size in both Tennessee and Ontario represent the preferred habitat types in these regions. The wide differences in the structural configuration of these two habitat types suggest that habitat selection patterns in the ovenbird may well have evolved to the patterns of productivity associated with various habitat types over its geographic range. A multitude of studies on migratory bird species (Drost 1951) have shown the tendency of individuals to return to the same region or in many cases the same location to breed from year to year. This behavior may well be due to an increased information base or pattern recognition by individuals within a geographic region. This poses the

question of selection for different search images (Tinberg 1951) or structural niche gestalts (James 1971) for different geographic clines or populations of the same species. Likewise, many migratory species often select different habitats in their winter ranges than those occupied in their summer breeding range (Lack 1971). These differences in habitat selection patterns may reflect different structural-productivity patterns over different geographic regions such as those seen between Ontario and Tennessee. The winter habitat preferences for these species may be for habitat types of maximum prey productivity with respect to the foraging behavior of the species in the particular region in which they winter. These are questions which are in need of further study involving the determination of habitat selection patterns and habitat productivity for species over a wide geographic range.

Temporal Components of Habitat Structure- Prey Abundance Relationship

Having identified the spatial relationship between habitat structure and prey abundance in the habitat selection process of the ovenbird on the Walker Branch Watershed, it is important to analyze the temporal component of this relationship. Twenty-five vegetation plots, representing a spectra of habitats occupied by the ovenbird on the watershed, were sampled for arthropod abundance on both a yearly basis (Table 10) as well as within a single breeding season (Table 11) to understand the temporal-structural dynamics of prey abundance. Results of a pairwise t-test (Table 12) between years shows a significant increase in prey abundance during 1980 as compared to both 1979 and 1981.

Table 10. Yearly Variation in Prey Abundance for 25 Permanent Census Plots on the Walker Branch Watershed

Plot	1979	1980	1981
1	.4436	.4689	.3698
2	.4330	.4505	.3382
3	.3655	.4457	.3523
4	.3174	.3642	.3316
5	.2717	.3714	.2285
6	.2636	.2115	.2520
7	.2491	.2610	.2286
8	.2360	.2793	.1960
9	.2346	.3150	.2107
10	.2045	.2335	.1683
11	.1948	.2135	.1679
12	.1775	.1888	.1737
13	.1669	.2012	.2113
14	.1658	.1838	.2211
15	.1496	.1725	.1605
16	.1331	.1214	.1317
17	.1330	.1838	.0760
18	.1249	.1602	.1067
19	.1026	.1521	.1432
20	.0927	.1045	.0793
21	.0645	.0411	.0784
22	.0568	.1128	.0518
23	.0559	.0778	.0870
24	.0433	.0685	.0524
25	.0397	.0211	.0726

Prey abundance expressed as g/.1m². Plots are listed from highest to lowest prey abundance for 1979.

Table 11. Monthly Variation in Prey Abundance for 25 Permanent Census Plots on the Walker Branch Watershed

Plot	April	1980 May	June
1	.3423	.4689	.5895
2	.3607	.4505	.6214
3	.3655	.4457	.5002
4	.2045	.3714	.5996
5	.3382	.3642	.4417
6	.3525	.3105	.4136
7	.3321	.2793	.2982
8	.2135	.2610	.3665
9	.2286	.2335	.3525
10	.2047	.2135	.2914
11	.1067	.2115	.2600
12	.1527	.2012	.2773
13	.1375	.1888	.1835
14	.1128	.1838	.2014
15	.1214	.1838	.1911
16	.1669	.1725	.2610
17	.1026	.1602	.2111
18	.0559	.1521	.2286
19	.0927	.1214	.2135
20	.0726	.1128	.1679
21	.0778	.1045	.0995
22	.0175	.0778	.0358
23	.0518	.0685	.0694
24	.0287	.0411	.0473
25	.0553	.0211	.0411

Prey abundance is expressed in $\text{g}/.1\text{m}^2$. Plots are listed from highest to lowest prey abundance for May.

Table 12. Summary of Comparison of Yearly Variation in Prey Abundance and Habitat Structure-Prey Abundance Relationship

		1980	1981
Paired t Scores	1979	-3.97 ***	.92
	1980		3.36 ***
Kendall's Tau (τ)	1979	.8849 ***	.8067 ***
	1980		.7312 ***

Differences in prey abundance between years is tested using paired t-test. Kendall's Tau is used to determine if the habitat structure-prey abundance relationship is maintained from year to year.

(* = $p \leq .05$, ** = $p \leq .01$, *** = $p \leq .001$)

This increase was caused primarily by an outbreak of lepidoptera larvea (Erannis tiliaria) on the watershed in the late spring of 1980.

Kendall's Tau, a nonparametric rank correlation coefficient (Conover 1970), was used to determine if the habitat structure-prey abundance relationship was maintained from year to year. Results (Table 12) show that there is a significant correlation between prey abundance and habitat structure of the plots over the three year period. Although the average prey abundance varied over the three year period of the study, the relationship between habitat structure and prey abundance remained relatively constant. A comparison of the same 25 census plots over the three month period of April-June 1980 (Table 13) shows an increase in prey abundance during the months sampled, however, as was the case for the results of the annual dynamics, the relationship among plots remained relatively constant over the sample period.

Predicted Prey Abundance and Territory
Size: The "Structural Cues Hypothesis"

From the previous results, it is apparent that a relationship exists between the structure of the habitat chosen as territory sites by ovenbirds on the study area and the productivity of those sites with respect to prey abundance. If the birds are using habitat structure as a proximate cue to prey abundance as stated by the "structural cues hypothesis," then it is possible that habitat structure will have a higher correlation with territory size than actual (i.e., sampled) prey abundance. This hypothesis was tested by comparing territory size with predicted prey abundance from the regression of prey abundance with

Table 13. Summary of Comparison of Monthly Variation in Prey Abundance and Habitat Structure-Prey Abundance Relationship

		May	June
Paired t Scores	April	-4.43 ***	-6.24 ***
	May		-1.48
Kendall's Tau (τ)	April	.7980 ***	.7400 ***
	May		.8247 ***

Differences in prey abundance between months is tested using paired t-test. Kendall's Tau is used to determine if the habitat structure-prey abundance relationship is maintained from month to month.

(* = $p \leq .05$, ** = $p \leq .01$, *** = $p \leq .001$)

habitat structure (Table 8, p. 39). The comparison shows an inverse relationship between territory size and predicted prey abundance (Figure 6) with a Pearson product moment correlation of $-.80$ ($p \leq .001$) as compared to $-.66$ ($p \leq .001$) for actual prey abundance. Thus, the results suggest that territory size is more strongly correlated with predicted prey abundance as defined by habitat structure than the actual prey density of the territory. This result would support the "structural cues hypothesis." However, since actual prey abundance and predicted prey abundance are significantly correlated ($r = .88$, $p \leq .001$) and both variables provide an adequate model for explaining the relationship between territory size and prey abundance, it is difficult to determine whether habitat structure is the actual cue used to determine prey abundance, or whether the correlation between predicted prey abundance and territory size is merely a result of the correlation between habitat structure and actual prey abundance.

An experimental test of the "structural cues hypothesis" would be to somehow alter the habitat structure-prey abundance relationship prior to the arrival of ovenbirds onto the study site and thus manipulate prey abundance such that areas which, based on their habitat structure, should provide high prey densities would have lower than predicted prey abundance and those areas which should be low in prey abundance could be supplemented to provide high prey densities. Upon establishment of territories by ovenbirds, territory size could be compared to both actual prey abundance and predicted prey abundance on the basis of habitat structure as a test of the "direct monitoring" and "structural

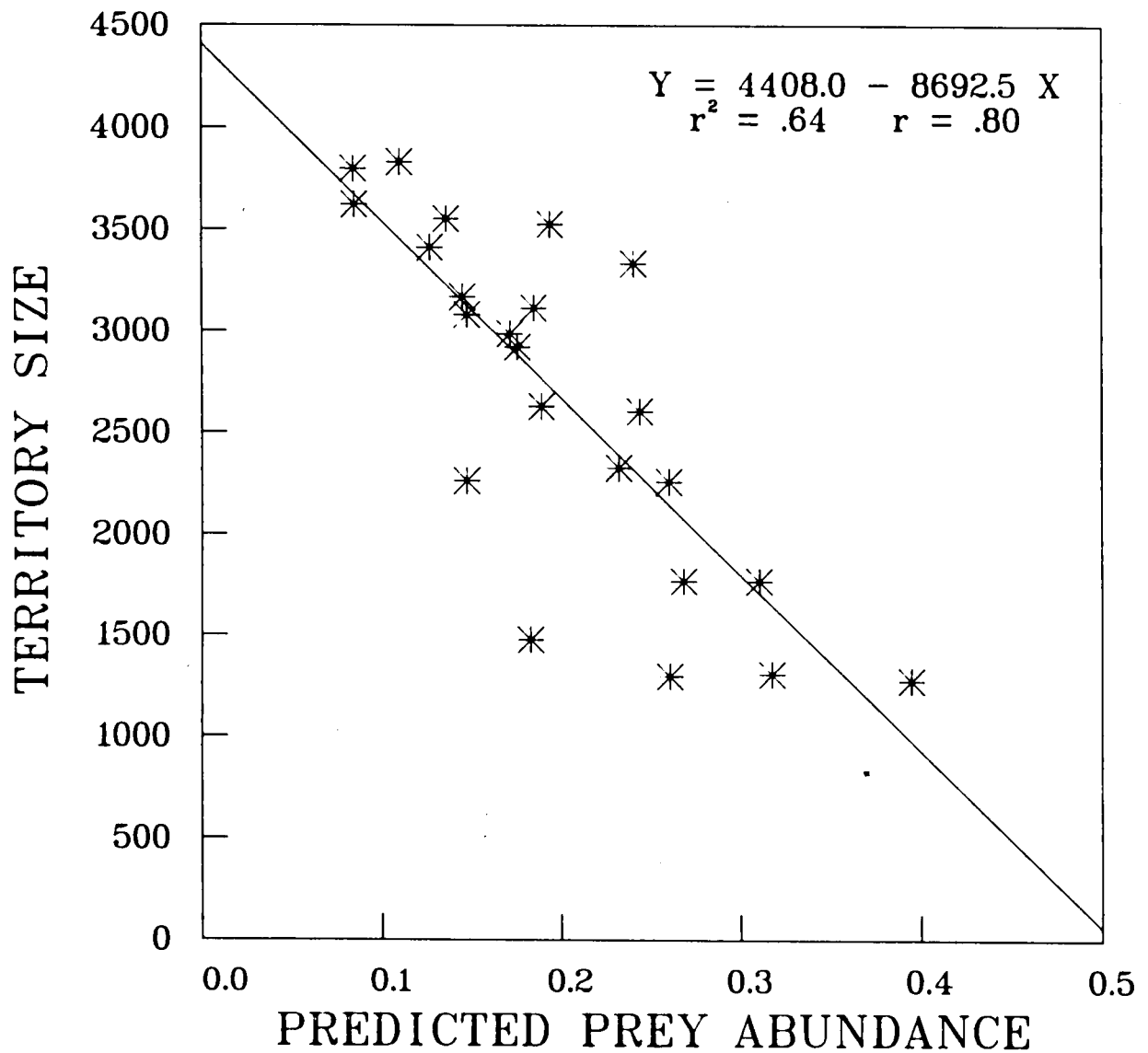


Figure 6. Regression of territory size with predicted prey abundance for the 23 ovenbird territories studied. Territory size is expressed in m^2 and predicted prey abundance in $g/.1m^2$. Predicted prey abundance scores are from the regression of prey abundance with variables describing habitat structure for the territories.

cues" hypotheses. It is possible, however, to develop this same analysis without manipulative experimental data. From the previous regression analysis, predicted prey abundance has been defined as the linear combination of the variables describing the habitat structure of the territories which is most highly correlated with actual prey abundance. Therefore, the difference between actual and predicted prey abundance for a territory represents a deviation of the territory from the habitat structure-prey abundance relationship, the same type of deviation that would ideally be induced under experimental conditions. By analyzing those territories with the greatest deviation between predicted and actual prey abundance for their goodness of fit to the "direct monitoring" (i.e., actual prey abundance) and "structural cues" (i.e., predicted prey abundance) models (Figures 2, p. 22 and 6, p. 57 respectively), the two hypotheses can be tested.

Comparing predicted prey abundance for each of the 23 territories with the actual or sampled prey abundance, 10 territories show a difference of 20 percent or greater. By regressing territory size with both predicted prey abundance and actual prey abundance, the resulting models can be tested for significance as well as their fit to the models previously determined for both predicted and actual prey abundance for all territories sampled.

In the regression of territory size with actual prey abundance for the 10 test territories (Figure 7), actual prey abundance was found to account for only 7 percent of the variation ($r^2 = .07$) in territory size with a correlation (i.e., Pearson product moment) of .22 ($p \leq .44$).

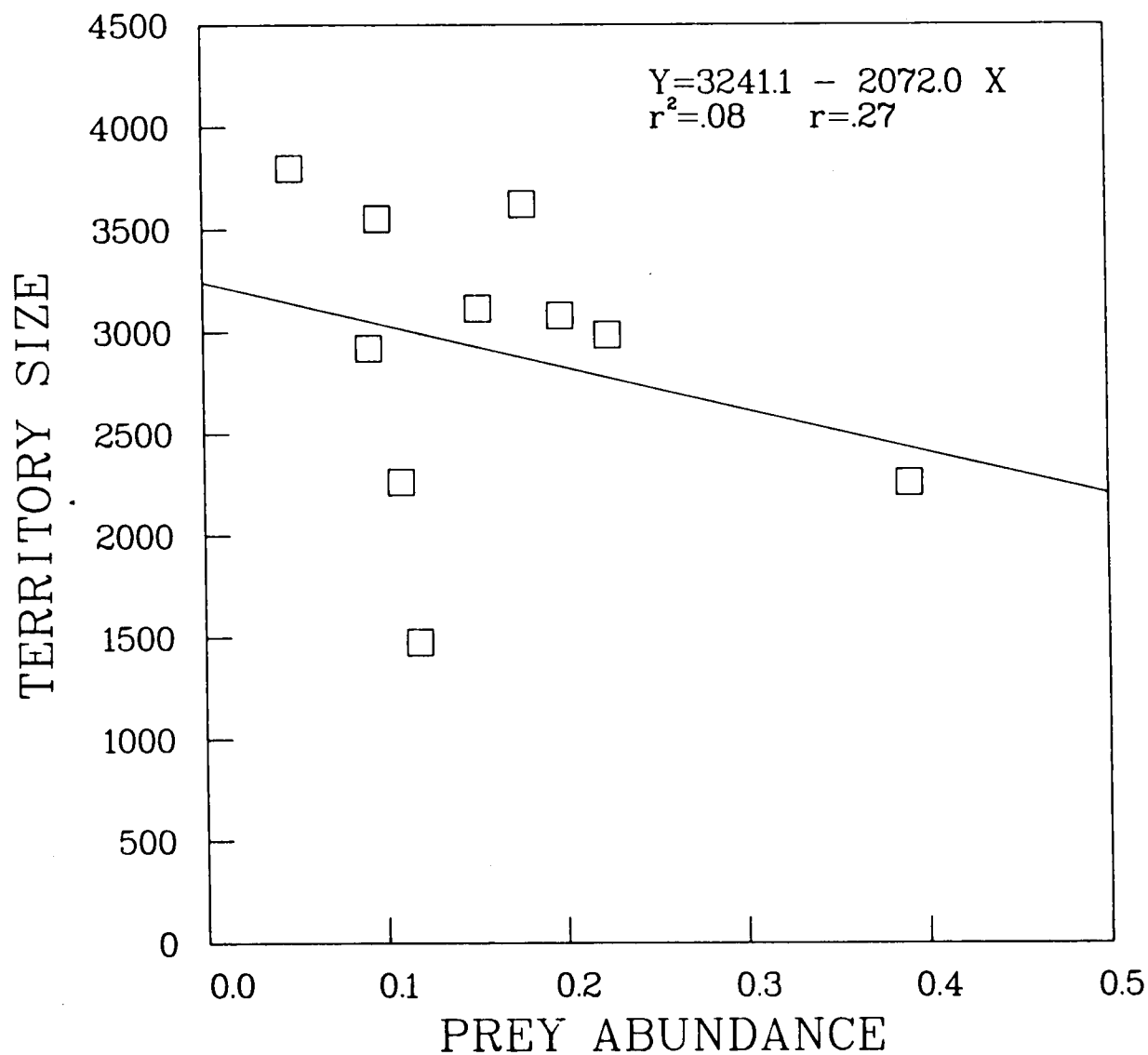


Figure 7. Regression of territory size with prey abundance for 10 test territories. Territory size is expressed in m^2 and prey abundance in $g/.1m^2$.

In comparison, the regression of territory size with predicted prey abundance (Figure 8), a function of habitat structure, shows that predicted prey abundance accounts for 45 percent of the variation ($r^2 = .45$) interterritory size with a correlation of .67 ($p \leq .03$). To determine the significance of the regression models for the test territories, the hypothesis $Y = \bar{Y}$ (i.e., H_0 : the slope of the regression is equal to zero) was tested for both actual and predicted prey abundance models. Likewise, the regression models were tested to determine if they differed significantly from the models based on all 23 territories (i.e., H_0 : slopes of the regressions are equal). Results (Figure 9) show that the slope of the regression of territory size as a function of actual prey abundance does not significantly differ from zero ($t = .67$, $p \leq .44$) and that the regression of the test territories differs significantly ($t = 1.76$, $p \leq .05$) from the full model of the "direct monitoring hypothesis" based on all 23 territories. In comparison, the predicted prey abundance model for the test territories was found to be significant ($t = 6.37$, $p \leq .03$) and the model did not differ significantly ($t = .31$, $p \leq .35$) from the "structural cues model" of territory size as a function of habitat structure. These results show that for those territories in which prey abundance differed from that expected on the basis of habitat structure, territory size was not significantly correlated to actual prey abundance. However, for those same territories, territory size showed a significant inverse relationship with predicted prey abundance, a function of habitat structure.

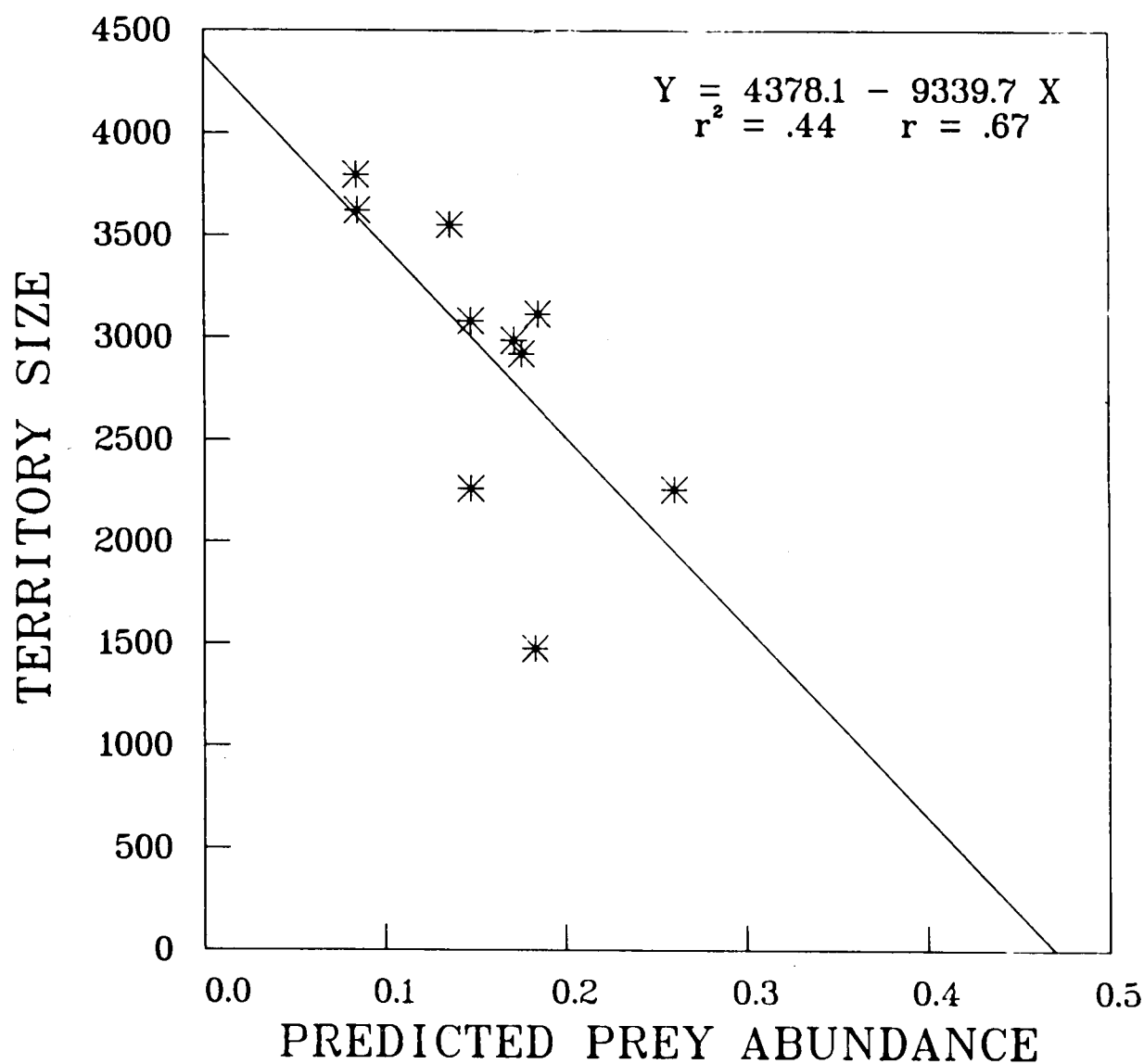


Figure 8. Regression of territory size with predicted prey abundance for 10 test territories. Territory size is expressed in m^2 and prey abundance in $g/.1m^2$.

Figure 9. Comparison of regressions for "direct monitoring" (i.e., territory size = f (prey abundance)) and "structural cues" (i.e., territory size = f (habitat structure)) hypotheses.

- a. Regression of territory size with prey abundance for all 23 territories sampled.
- b. Regression of territory size with prey abundance for the 10 test territories.
- c. Regression of territory size with predicted prey abundance for all 23 territories sampled.
- d. Regression of territory size with predicted prey abundance for the 10 test territories.

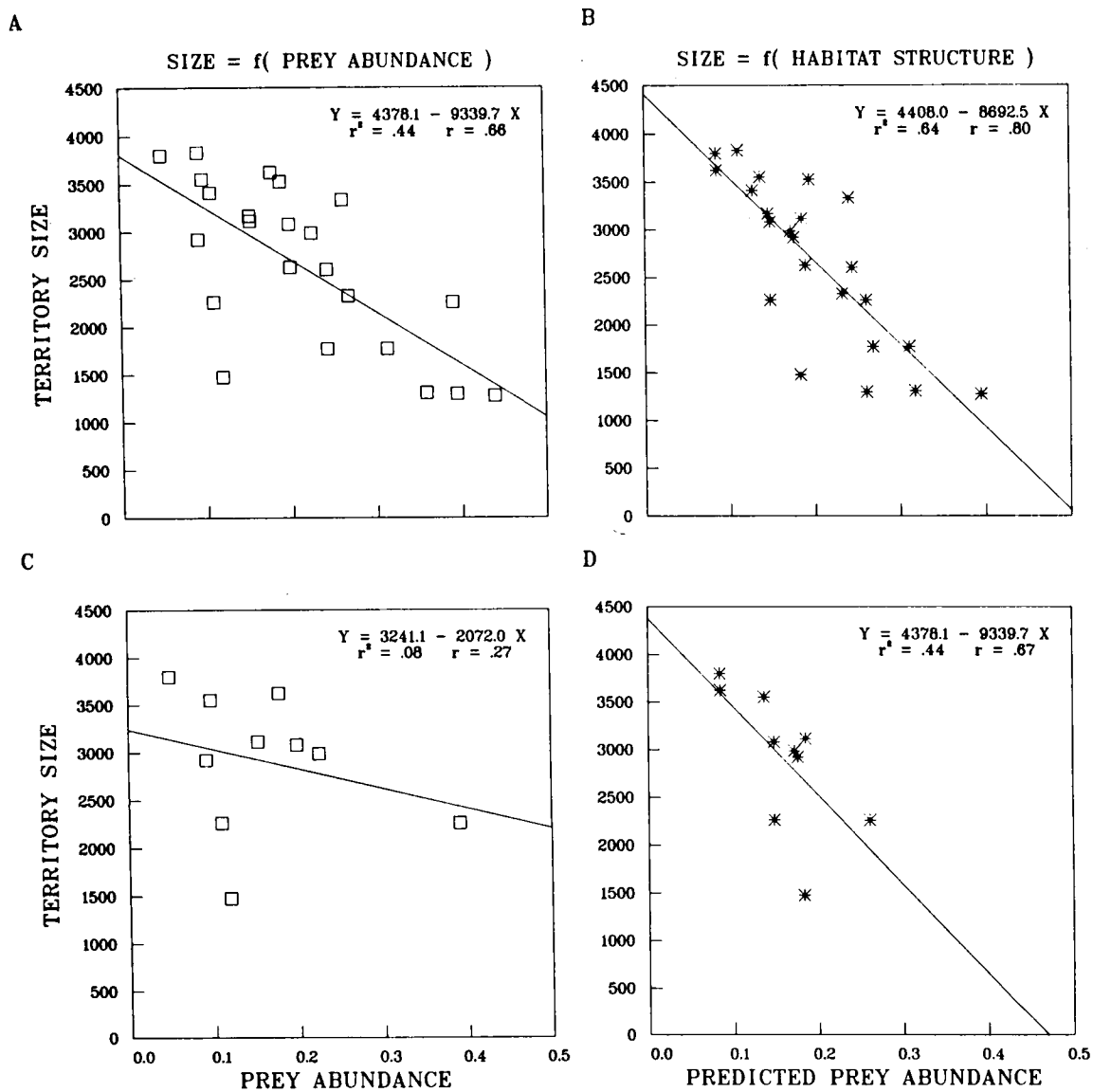


Figure 9

Another way of comparing the ability of the two hypotheses to account for the variation in territory size among those territories which deviate from the habitat structure-prey abundance relationship is through the use of partial correlation analysis (Snedecor and Cochran 1966).

Results of the partial correlation analysis between predicted prey abundance and territory size show a significant correlation ($r = -.61$, $p \leq .01$) after the removal of the effect of actual prey abundance on territory size variation. However, the correlation between actual prey abundance and territory size was no longer significant ($r = .15$, $p \ll .1$) when the influence of habitat structure was statistically removed. These results support the previous findings that a significant correlation exists between predicted prey abundance and that portion of the variation in territory size not explained by variation in actual prey abundance among territories.

Hilden (1965) suggested that birds may respond to proximate cues of food abundance rather than directly assessing the food value of the habitat. If this is the case, then territory size should be related to expected food abundance and not necessarily with actual prey abundance in any one year. This hypothesis necessitates a relationship between habitat cues (e.g., temperature, light regime, vegetation structure, etc.) and the food value or productivity of that habitat type. This relationship is what I have termed the "structural cues hypothesis." The findings of Seastedt and MacLean (1979) (see p. 7) support this hypothesis with territory size of lapland longspurs on their study area

being most strongly correlated with the expected habitat types comprising the territory. The findings of the present study suggest a similar relationship with ovenbird territory size being more strongly correlated with predicted arthropod biomass on the basis of vegetation type and habitat structure than actual (i.e., sampled) prey abundance. There are two possible explanations for this finding. First, the difference between the correlation coefficients could be due to random chance or variability in the sampling procedure. The index of prey abundance used represents an estimate of prey availability and not necessarily the absolute food value of the territory. However, the increase in the correlation between predicted prey abundance and territory size would be expected if the birds were using structural cues to assess habitat quality with respect to food value. Theoretically, the variation in prey biomass unexplained by the regression could be partitioned into three components: (1) sampling error, (2) variation resulting from factors meaningful to the ovenbird, but not included in the analysis, or (3) unpredictable variation of the sample plot from the average productivity of that habitat or structural configuration. This third source of variation could be a result of various biotic and abiotic factors acting at a variety of spatial and temporal scales which may be unpredictable or outside the realm or temporal and spatial scales of perception of the ovenbird. This variability would represent a loss of information when prey abundance is being assessed on the basis of habitat cues. In this case, territory size would be more strongly correlated to the average productivity of the habitat types and structures rather than prey abundance at any one time.

The analysis of territories which deviate from the habitat structure-prey abundance relationship provide a unique opportunity to test the two hypotheses of "direct monitoring" and "structural cues" without actual observer manipulations. This approach provides a "natural" experiment by taking advantage of natural variation in the habitat structure-prey abundance relationship. The results are in general agreement with the "structural cues hypothesis." For those territories which the prey abundance was either greater or less than predicted on the basis of habitat structure, territory size was not correlated to actual prey abundance. However, territory was inversely related to those aspects of habitat structure which are most highly correlated to prey abundance (i.e., predicted prey abundance). Likewise, partial correlation analysis revealed that predicted prey abundance and territory size were significantly correlated after the removal of the effect of actual prey abundance on territory size. However, the correlation between actual prey abundance and territory size was no longer significant when the influence of habitat structure was statistically removed. Therefore, the results suggest a strategy of habitat selection and territorial defense which has adapted to habitat cues as a proximal factor for prey abundance.

Findings on the dynamics of the structural-temporal relationship of prey abundance suggest that this strategy of habitat selection and territory size determination may in fact prove to be a favorable means of quality assurance. Although the actual prey abundance of the various plots representing differing habitat types and structural configurations

varied on both a yearly and within season temporal scale, the relationship between structure and productivity appeared to be relatively constant. This is a necessary prerequisite for the evolution of habitat selection and/or territory size selection on the basis of structural cues. If the relationship were random, the habitat would be a mosaic of patches of varying food quality, changing through time in an unpredictable manner. Under this set of circumstances, it is questionable if territorial behavior for the defense of food resources would exist. Territories selected to provide adequate resources upon arrival to the breeding grounds could well prove to be inadequate for supplying sufficient resources for breeding later in the season.

Upon arrival to the breeding grounds, male ovenbirds almost immediately select sites and defend territory boundaries. The migration onto the breeding grounds is fairly quick with the last males arriving only a few days to a week after the initial arrival of males onto the area. Thus it is important to select a site as soon as possible upon arrival. As the birds begin to establish territories which adjoin each other, the cost of territory expanse becomes higher. Therefore, it is selectively advantageous to select as soon as possible a territory as large as will potentially be needed to meet the energetic needs of the territory holder. Since habitat structure is a predictable cue of food value, the initial size selection based on expected habitat quality would, on the average, result in sufficient resources being contained within the boundary of the territory.

The "Intraspecific Competition Hypothesis"

Although the results suggest that the correlation between territory size and prey abundance is an indirect response to the habitat structure-prey abundance relationship, the question as to the role of intraspecific competition on the territory size-prey abundance relationship must still be addressed. Even though birds are cueing to habitat correlates of prey abundance, differential competitive pressures for areas of varying quality may be the ultimate mechanism for territory size. The "intraspecific competition hypothesis" states that the mechanism for the inverse relationship between prey abundance and territory size is increased competition for areas of higher quality (i.e., prey abundance). Tests of this hypothesis have generally used indices of intraspecific competition, such as intrusion rate and population density, as correlates to territory size. Intrusion rate or indices of "direct" competition may provide the most meaningful approach to testing this hypothesis, but in the present study, such an index was not measured. In fact, very few actual observations of direct conflict between males were recorded over the period of the study. Defense of territories is accomplished primarily by song display and direct conflict among birds (i.e., physical confrontation) seems limited to the period soon after arrival of males to the breeding grounds. As a result, an index reflecting population density or distribution of territories provides the only means of testing this hypothesis without the actual removal of individuals.

To test the "intraspecific competition hypothesis" the shortest distance to the boundary of the nearest neighboring territory was used

as an index of competitive pressure on territory holders. Territories which are bordered by other ovenbird territories will have small values for the index and reflect high competitive pressure for those territory sites during their establishment and defense. In contrast, those territories with high values for distance to nearest neighbor reflect less preference for that habitat or territory site and less resistance to further territory expansion.

Results of a linear regression of territory size with distance to nearest neighbor shows that only 13 percent ($r^2 = .13$, $p \leq .09$) of the variation in territory size can be explained by the variation in the distribution of neighboring territories ($r = .36$). In a comparison of distance to nearest neighbor with both actual and predicted prey abundance, results show a correlation of $-.28$ ($p \leq .18$) between actual prey abundance and proximity of neighboring territories as compared to $-.30$ ($p \leq .17$) for predicted prey abundance. The results therefore suggest that, although the distribution of territories is related ($p \leq .09$) to territory size, "intraspecific competition" as defined by the proximity of neighboring territories does not provide a model which adequately accounts for the inverse relationship between prey abundance and territory size of ovenbirds on the study area.

Despite these results, it is possible that competitive pressures could influence territory size through their interaction with habitat structure or prey abundance. To analyze the influence of competitive pressures on the relationship between prey abundance, either actual or predicted, and territory size, it is necessary to hold the effect of

competition on territory size constant over all observations, therefore, removing the influence of differential competitive pressures on the relationship. This can be accomplished analytically through the use of partial correlation analysis.

Results of the partial correlation analysis between territory size and predicted prey abundance (i.e., habitat structure) after the removal of the influence of competition (i.e., proximity of neighboring territories) shows a significant correlation between the two variables ($r = .75$, $p \leq .001$). The results therefore suggest that the relationship between predicted prey abundance and territory size is not merely a result of greater competition for areas of higher quality (i.e., prey abundance) as measured by the proximity of neighboring territories. On the contrary, it appears as though only a small portion of the variability of territory size among birds is due to differential competitive pressures.

However, there are a number of potential causes for the lack of correlation between habitat structure and/or prey abundance (both measures of habitat quality) and the proximity of territories. The study area can be visualized as a mosaic of habitat patches of various quality as ovenbird habitat. For any patch, the potential competition within that patch will be a function of patch size, patch quality and population of ovenbirds on the study area. Therefore, the potential pressures of competition will vary as the quality and population density of any patch change. As a result, such measures of competitive pressure as proximity to neighboring territories will be greatly

influenced by the population density of ovenbirds on the study area. In years of low ovenbird population, the effects of intraspecific competition on habitat selection and territory size may be small to nonexistent. However, in years of high ovenbird density, territory size may be strongly influenced by intraspecific competition for habitat (Fretwell and Lucas 1969). In such a dynamic system, long term observations over a series of years with varying population densities of ovenbirds on the study area are necessary to completely understand the role of competition for territory sites on territory size variation.

CHAPTER V

CONCLUSION

The analysis of 23 ovenbird territories on the study area revealed that territory size is inversely related to prey abundance. However, the results of this study show that the inverse relationship is an indirect function of the relationship between prey abundance and habitat structure. Analysis of the habitat selection pattern of ovenbirds on the study area show that those habitat variables which best differentiate between territory sites and unoccupied areas are the same variables which correlate with the variation in prey productivity defined as prey density and prey size. Territory sites show a great deal of structural variation, but on the average have lower shrub and understory density with a higher canopy cover and density of large trees. This structural pattern was found to result in territory sites having a higher average prey density per unit area than unoccupied sites. However, the resulting pattern of increasing prey productivity with habitat structure was opposite that found by Stenger (1958) for a similar study in Ontario. This variation in the habitat structure-prey abundance relationship over the ovenbirds' range presents a number of questions concerning the evolution of species' habitat selection patterns and the management of species over a wide geographic area.

Current ecological theory has emphasized the role of interspecific competition on the variation in habitat selection patterns of species

over their geographic range (Yeaton and Cody 1974, Cody 1974, Noon 1981). However, in light of the findings of this study, it is possible that these variations may be a result of differences in habitat structure-prey abundance patterns. The difference in habitat selection pattern of the ovenbird in Ontario (Stenger 1958) compared to that found in Tennessee correspond to the differences in the habitat structure-prey abundance relationship observed between the two areas. Such examples stress the importance of understanding the mechanisms involved in habitat selection rather than merely identifying structural correlates to species presence. A need exists to study the habitat selection patterns of species with wide geographic ranges and identify the influence of food productivity on the habitats chosen. It is only through a complete understanding of the mechanisms of habitat selection that proper tests can be made on current ecological theories concerning the distribution of species and sound programs for habitat management be provided.

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