COMPARATIVE BREEDING STRATEGIES OF TWO COEXISTING

PASSERINES:

BELL'S VIREO (VIREO BELLII) AND

BEWICK'S WREN (THRYOMANES BEWICKII)

by

Greg Hunt Farley

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INTRODUCTION

Investigations of habitat preference by birds typically involve one-time censuses of particular habitat types, with analysis of the proximate structural variables which can be used to either separate species in a community (e.g. James 1971, Rottenberry and Wiens 1980, Collins 1983) or describe species-specific habitat selection in terms of potential competitors (e.g. MacArthur 1958, Cody 1985). The distribution of species in habitat space is assumed to be the result of active selection of specific structural components by individuals in an attempt to maximize benefits and reduce costs (Hilden 1965, Hutto 1985, Sherry and Holmes 1985). This model is thought to act in selection for foraging sites (James 1976, Holmes and Robinson 1981), wintering habitat (Hutto 1985, Lynch et al. 1985) and breeding habitat (e.g. James 1971, Rottenberry and Wiens 1980, Collins 1983). Once the set of proximate cues has been identified for a given species it is appropriate to consider the ultimate selective advantage to individuals expressing that choice. The evolutionary cause is more difficult to determine, especially in selection of breeding sites. Abundance of prey for both adults and offspring (e.g. Wittenberger 1980), nest concealment from predators (e.g Best 1978, Zimmerman 1984) and social parasites (e.g. Zimmerman 1983) and protection of nests from abiotic factors (e.g. Pleszczynska 1978) are factors which affect breeding habitat selection in birds. Consequently these are the selective agents which determine the suite of proximate habitat cues used by individual species and ultimately the distribution of avifauna observed.

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This investigation addresses the question of how Bell's vireo
(Vireo bellii) and Bewick's wren (Thryomanes bewickii) are distributed
in woody vegetation in the tallgrass prairie and presents hypotheses
concerning the selective factors affecting their habitat choice. I
quantified habitat preference by determining the distribution of each
species in habitat "space" and measuring aspects of the physical
structure of the vegetation (sensu James 1971, Collins 1983). This
approach is experimentally sound because the two species (treatments)
can presumably select from the same range of habitats and by comparing
the choices of two ecolgically similar species I can gain insight into
the evolutionary factors affecting each (Thornhill and Alcock 1983,
Wiens 1983).

Study Area and Methods

Study area

Data were collected between March and September, 1986, on Konza
Prairie Research Natural Area, a 3,486 ha native tallgrass prairie
preserve in Riley and Geary counties, northeast Kansas. The majority of
the study area is covered with a mixture of grasses, Andropogon, Panicum
and Sorghastrum, interspersed with woody vegetation. The woody species
are restricted to riparian zones, scattered habitat islands and
extensive limestone outcroppings, for which the Flint Hills region of
Kansas is named. Rough-leaved dogwood (Cornus drummondii) and, to a
lesser extent, aromatic sumac (Rhus aromatica) and wild plum (Prunus
americana), are the more abundant woody species outside of the riparian
zone (Freeman and Hulbert 1985). These three species occur on both the
limestone ledges and as isolated habitat islands because prairie fires,
a natural disturbance which retards woody plant growth in this
ecosystem, are unable to kill these stands because of insufficient
litter (fuel) accumulation (Hulbert 1969). The remaining woody
vegetation is located in riparian gallery forests along the major
drainages. Bur oak (Quercus macrocarpa) and hackberry (Celtis
occidentalis) are the common lowland species, with chinquapin (Q.
muehlenbergii), American elm (Ulmus americana), honey locust (Gleditsia
triancanthos) and redbud (Cercis canadensis) becoming more common
upslope (Freeman and Hulbert 1985). The latter three species
occasionally grade into the limestone outcrop vegetation.

An intensive investigation of all resident BV and BW was conducted
in a 79 ha watershed on a no-burn fire treatment schedule and a 119 ha

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watershed on a two-year burn schedule. These two watersheds were purposefully chosen in order to maximize the number of breeding territories of BV and BW. I refer to these areas as the "focal" watersheds because thrice-weekly observations of marked individuals were made from early March to 15 May and almost daily observations were made from 15 May to 30 July. All BV nests and at least 90% of the BW nests reaching the incubation stage were located in the focal watersheds.

<div align="center">Capture and marking</div>

Birds of both species were captured using mist nets and tape recordings of male song. Two BW were captured at the nest by blocking the cavity entrance and placing a small hand net over the opening. All captured adult birds and nestlings, age 10-12 days, were marked with a U.S.F.W.S. metal band and a unique combination of 1 - 3 plastic color bands, which were sealed closed with acetone. Measurements of culmen, tarsus, wing chord, bill length and width, weight, molt condition and condition of brood patch were taken from each adult, while nestlings were only weighed.

<div align="center">Vegetation sampling - focal watersheds</div>

Vegetation structure was quantified at all nest sites and at point samples within territories of each resident of both species. At each sample station four aspects of vegetation structure were quantified: canopy height (HT), the number of both live (TS) and dead (DS) stems greater than 2mm diameter within a 1 meter diameter circle, 1 meter off the ground and canopy cover (PCOV). Percent cover was measured using a densiometer, a forester's instrument consisting of a convex mirror with a grid superimposed on its surface, which is used to directly measure

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the degree of overstory closure (Lemmon 1957). The number of cell corners contacting vegetation are counted and the resulting number is converted into % canopy closure. Facing a cardinal direction, I took four readings at each sample station and averaged the four counts. The mean values were transformed from percentages using arcsine prior to statistical analysis.

Two composite variables were created in order to model the use of combinations or proportions of variables in assessing habitat. Vegetation density (VEGDEN) was estimated by dividing canopy height by total stem density. The proportion of dead stems in the total stem sample (STMRAT) was calculated by dividing the number of dead stems by the total number of stems at each point sample. In order to quantify the unique habitat features associated with BV nest sites I measured the following variables: nest height (NHT), compass orientation of nest to main stem of the nest shrub (AN), distance from nest to patch edge (DE), distance from nest rim to the main nest-shrub branch (DM) and aspect of the nest in reference to the nearest patch edge. Because all BW nests were located in cavities a different suite of measurements was used to quantify nest microsites. Nest height (NHT), maximum nest cavity depth (CD), length (CL) and width (CW), snag tree diameter at breast height (DBH) and orientation of the opening (OR) was measured at each wren nest.

The physical structure of the territory was sampled by using the nest as a central point and randomly selecting bearings for sample transects. If unsuitable habitat was encountered along a sample transect I either continued on that bearing until a point sample could be

obtained or turned 90 degrees and continued pacing (Appendix 2). Two
transects, containing four point samples each, were sampled from each BV
territory; four transects were run from each BW nest in an attempt to
control for interspecific differences in territory size (Appendix 3).
Four stations along each transect were selected by choosing a random
number of paces from 1 - 9 and a point sample of structure was taken
following the procedure at nest sites. Analyses of nest site and
territory characteristics involved comparing pooled nest sites and
combined territory point samples in order to assess species-level
habitat preferences.

<div align="center">Vegetation sampling - random sites</div>

Fifty five sites were selected at random across all of Konza
Prairie (Appendix 4) in order to validate the habitat preferences
determined from the focal watershed data. The sites were chosen by
using a hierarchical random sampling method and by chance were located
in watersheds under a diverse array of burning treatments. A 1:20,800
scale map with a 250 x 250m superimposed grid was used to randomly
select 55 grid squares containing woody vegetation. Each square was
then located on a 1:25,000 scale aerial photograph, which I overlayed
with an acetate grid of 4 equal-sized sections. If a randomly chosen
grid section contained a discrete patch of appropriate habitat it was
subsequently sampled in the field. If none of the 4 sections contained
suitable habitat the sample square was omitted. If a section too large
to be accurately censused was selected, an increasingly subdivided grid
was used until a manageable area was chosen. The sampling area varied
due to the size and shape of the habitat patch; sections averaged 75 -

100m on a side. This process is intended to mimic the first level of breeding habitat selection by a migratory bird (Reynolds 1983, Hockey 1982, Hutto 1985). Each random site was inspected on foot between 0600 and 0900h in order to determine occupancy by BV, BW or neither species. I stood at a corner of the sample square and noted numbers of both species seen and/or heard for 3 minutes. If an individual of either species was detected I stopped the census and took a bearing on that location, this line then became the sample transect. If neither species was detected a sampling bearing going throught the habitat patch was selected at random. The number of paces between each of 4 sampling stations was also chosen at random, as in the focal territory sample. At each point sampling station I collected habitat measurements using the focal watershed procedure. One transect was sampled in both occupied and unoccupied patches.

Statistical analysis

The data from focal territories were pooled by species and compared with one-way ANOVA using the SAS "GLM" procedure for unequal sample sizes. Within species comparisons were done in the same manner using data pooled from nest site samples and territory transects. This analysis compares the variance within a sample to the variance between samples (Ott 1984). I considered the vegetation structure as an experimental unit and each species' territory and nest as the treatments. The null hypothesis stated that the treatment means were equal; the alternative states that one or more means were not equal. I used both paired t-tests and the Tukey test as means separation techniques on variables with significant F- values, the former being

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more sensitive to unequal sample size (Einot and Gabriel 1975). The mean separation results were equivalent for all variables. Using the Kruskal-Wallis test, additional ANOVA on ranks of the vegetation values were also performed and no differences from the ANOVA calculations using raw data were detected. In addition, ANOVA on raw data without the wren nest sample were calculated to control for possible confounding effects due to small sample size; no deviations from the ANOVA comparing nests and terrritories of both species were found. Therefore the observed results are not an artifact of unequal sample size.

Using SAS data programs Pearson product moment correlations (r) were calculated between all combinations of vegetation variables in order to identify interrelationships between habitat components and describe overall habitat architecture. Correlations between each vegetation variable and estimators of fitness were used to identify possible proximate habitat cues which might affect productivity. Single and multiple regression models (R^2) were created using SAS programs in an attempt to predict productivity of each species. The measurements of vegetation structure of the nest microsite (TS, DS, HT, PCOV, VEGDEN and ŞTMRAT) and species-specific measures of nest-site structure (e.g. nest orientation, cavity width) were used as independent variables.

Principal components analysis (PCA) was used to produce a multivariate model of BV and BW distribution by habitat. The SAS program "PRINCOMP" was used for calculations and the data was plotted using SASGRAPH V. Following the methods of James (1971) and Collins (1983), I used the correlation matrix to calculate component scores for each observation. Correlations between vegetation variables are

restructured to form new patterns which explain maximum variance. This technique produces linear axes which explain decreasing amounts of total variance in the n-1 multidimensional cloud of observations (Johnson and Wichern 1982).

Niche breadth and overlap

Principal component scores were also used as measures of habitat breadth or tolerance of each species and to estimate the degree of use overlap along each of the principal habitat axes (Rottenberry and Wiens 1980). Each axis was divided into 5 equal segments and the frequency of PCA scores was plotted in each section (Johnson 1977, Rottenberry and Wiens 1980). Breadth was calculated using Hill's (1973) diversity formula:

$$B = 1/\Sigma \ Pi^2$$

where Pi is the proportion of the ith section in the overall histogram of PCA scores (Rottenberry and Wiens 1980). Niche overlap was estimated using the following formula:

$$O = \ XiYi/ \sqrt{\Sigma \ Xi^2 \Sigma \ Yi^2}$$

where xi and yi are the frequencies of each species in the ith sample (Pianka 1974, May 1975, Rottenberry and Wiens 1980).

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RESULTS

Interspecific comparison

Average mean values and standard errors from 285 sampling stations within 35 BV territories and 143 stations from 9 BW territories show differences between species for all but one variable measured (Table 1). BV and BW select territories with significantly different stem density (TS), canopy height (HT) and percent cover values, whereas dead stem densities (DS) are statistically indistinguishable. The composite variables VEGDEN and STMRAT are also effective in discriminating habitats occupied by these species. Low VEGDEN values quantify the dense shrub habitat typical of BV territories, with high stem density and low canopy height (<5m), whereas high values represent the woodland aspect of BW territories, which typically have a low stem density and a high canopy (Figure 1). The ratio of dead stems to total stems (STMRAT) is an additional measure which can be used to distinguish between BV and BW territories.

Model building

A combined correlation matrix from territories of both species within the focal watersheds implies that virtually all of the measured vegetation variables are interrelated (Table 2). The significant r values vary from strong (TS x DS) to weak relationships (PCOV x VEGDEN). This latter catagory of comparisons should be interpreted with caution, as r values below .25 are not considered conclusive (Draper and Smith 1981). The correlation matrix overall provides evidence of interrelationships among the variables and suggests a multivariate model may be most effective in describing species' distributions (Wiens 1986).

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An analysis of the correlation matrices of the vegetation variables by species revealed consistency in the magnitude and direction of the relationship for 5 of 6 variables, suggesting similar patterns of habitat architecture in territories of both species (Table 3). The difference between territories but how different structural components of vegetation relate to each other but in the magnitude of individual variables and in the proportion of one variable to another. An exception is the relationship between total stems (TS) and canopy height (HT). In both BV and BW territories the correlation between these variables is significant, suggesting that values of one variable affect values of the other. The type of relationship is opposite in the two species; it is therefore possible that BW may prefer areas which have decreasing numbers of stems as canopy height increases. This relationship is apparent in the high VEGDEN values of BW territories.

The vegetation variables were combined using principal components analysis (PCA) to create models of habitat selection for each species and to ascertain the weight of each variable in characterizing breeding habitat. Analysis of territories of both species from the focal watersheds using TS, DS, HT and PCOV shows an overlap of utilized habitat based on the first two principal components (Figure 2). The group centroids, however, are different between mean values of the two species. Component I contains strong positive values of both live and dead stem density and therefore represents a gradient from low to high stem density (Table 4). The second axis represents a continuum from a high, full canopy to low, open canopy and is composed of high positive values of both HT and PCOV. A combination of these two

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components produces a model which explains 78% of the variance in the data and results in an informative, descriptive picture of the distribution of BV and BW territories.

Test of Model

The interspecific model of habitat preferences at the territory level was tested using vegetation data collected and analyzed in the same manner, however the territory boundaries were determined using one-time censuses of singing males. The predictions produced from the pairwise t-tests on the focal territories can be compared with the results from 92 random sampling stations in 23 occupied territories (Table 5). The results are consistent for all variables; BV and BW inhabit areas with statistically detectable differences in structure (t-test, $p < 0.05$).

Niche separation

Principal components scores were also used to examine the degree of niche overlap by plotting the frequency of PCA scores by category in order to determine the relative niche breadth of both species along each component (Figure 3). Calculations of estimated niche breadths show similarities in utilization between species for both the "stem" and "canopy" axis (component I: BV=2.03, BW=2.31; component II: BV=2.64, BW=2.78). Maximum values of 5 represent complete overlap for each of the five catagories; likewise minimum values of 0 result from no overlap in any of the five catagories. The similarity in niche breadth is manifested in high proportions of niche overlap, values which quantify the degree of redundancy in the distribution of each species along the

same habitat component. Calculations for both principal component I and II reveal an 81% overlap in habitat utilization between species.

Unoccupied sites

A comparison of the habitat structure of randomly selected sites defended by either BV or BW and unoccupied sites shows that the sites selected by at least one species are significantly different from unused areas for all but one variable (Table 6; t-test, $p < 0.05$). BV defended sites have lower VEGDEN values than unoccupied ones, suggesting a preference for sites containing low values of this variable. BW territories contain detectably fewer stems, greater canopy height, canopy cover and dead stem ratio when compared to undefended habitat. The results suggest that BV and BW may be using these variables as proximate cues for selecting breeding habitat. It appears that a gradient of habitat may exist for each variable and each species is using different variables as indecies of habitat quality.

Intraspecific comparison

One-way ANOVA on focal territory data revealed that for some vegetation variables the pairwise comparisons between territories of both species was unable to explain the significant values. Therefore nest sites and territory point samples within a species must vary for some habiat measures. Pairwise t-tests show that the significance for the DS variable is between BV nest sites and sampling points within territories, suggesting preference by BV for nest sites with those particular characteristics (Table 7). BW also shows evidence of this phenomenon as canopy height at nest sites is significantly lower than an average of points within territories (Table 7). Wren nests have lower

average values for each measured variable at nest sites when compared to territory means but no additional differences are significant. There are no differences in the remaining comparisons of vegetation means at vireo nest sites and within territories.

Productivity

The productivity of all residents was determined in the focal watersheds (Table 8) and dramatic differences exist between species. Forty nests of 17 breeding pairs of BV were located from 22 May (earliest egg date) to 15 August (latest fledge date) (Figure 4). At least one member of every pair was color-marked. An average 40% of eggs layed hatched; this percentage reflects losses due to both predation (14.3%) and abandonment as the result of brown-headed cowbird (Molothurus ater) parasitism (48.6%). In the remaining cases the order of predation and parasitism was not clear (37.1%). Only 36% of hatched eggs produced young of fledging age, which resulted in a two-watershed-region success rate of 1.06 young fledged/breeding adult. A total of 35.3% of breeding adults fledged at least one offspring.

BW productivity within the two focal watersheds spanned from 2 April to 25 June at the 7 known active nests (Figure 5). Although all of the individuals within the focal areas were marked, it is not clear if all nests were located. Fledging rates averaged 6.5 young fledged/female and 4.3 young fledged/male. Most females attempted more than one brood (75%) and mate switching occurred in 67% of cases, after both successfully fledging young and predation events. A single event of cowbird parasitism was recorded and the egg was removed within 24 hrs., presumably by one of the wren parents. Nest losses in this species

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were solely due to predation. A black rat snake (Elaphe obsoleta) was observed consuming four 4-day old nestlings. Snakes were probably responsible for a major proportion of nest losses, as suggested by Best (1978) and Zimmerman (1984). Neither species appeared to loose nestlings to starvation or weather.

Correlations between nest success and nest-site vegetation

A product moment correlation matrix of vegetation structure at BV and BW nest sites and various success measures is presented in Table 9. Significant correlations exist between the density of dead stems at BV nests and both the average number of eggs hatched and number of young fledged. The ratio of dead to total stems also is significantly correlated with number fledged. A non-significant, yet noteworthy, relationship exists between number of cowbird eggs and total stem density. Within BW several strong, positive correlations are apparent. The number of eggs laid is significantly correlated with total stem density and the number fledged is strongly correlated with the ratio variable STMRAT.

Correlations between nest success and microsite structure

Measurements from the area immediately surrounding nests and nests themselves were compared with reproductive success variables using Pearson product correlations (Table 10). Within BV a single comparison was significant, nests placed closer to the main shrub stem had greater numbers of eggs. The number of cowbird eggs is not correlated with any structural variable. BW nest sites also appear to have little direct

influence on success, but cavity placement does show a strong but non-significant correlation with number hatched (Table 10). Nests located in short snags and in cavities near the top of snags hatched more eggs; nests in cavities with small cavity lengths were also more successful. The inability of detecting statistical differences in these data may be partly the result of sample size and does not necessarily negate the chance of biological significance.

Predictors of productivity

Forward selection multiple regression models were useful in predicting productivity using both nest-site vegetation and nest structure data. The best estimate of vireo fitness, number fledged, is most effectively predicted using a combination of total stems, dead stem density and % canopy cover ($R^2 = .37$, p<0.002). The final model selected was based on the low mean square error value, the parsimony of the individual p-values and the biological sense of the variables included in the model (Draper and Smith, 1981). Number of hatched eggs is best predicted using the same model as number fledged ($R^2 = .32$, p<0.005). Vireo clutch size can be estimated using a model containing: dead stem density, % canopy cover, distance from nest to edge of patch and the ratio of nest height to canopy height ($R^2 = .36$, p<0.005). An attempt to predict cowbird parasitism was unsuccssful; the single best estimate is total stem density ($R^2 = .09$, p=0.07), which does not sufficiently explain the variance in the observations.

The number of vireo eggs which hatch and number fledged are significantly affected by the number of cowbird eggs. A model of cowbird eggs regressed on number of vireo eggs hatched shows a

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significant, weakly inverse relationship (R^2=.12, p<0.05). Predictions of number fledged follow the same pattern (R^2=.12, p<0.05), further evidence of the negative impact cowbird parasitism has on vireo productivity. BV abandons nests if 1 or more cowbird eggs are deposited prior to the laying of the third vireo egg (consistent with Barlow 1962), therefore additional cowbird eggs may not have a significant negative impact on rates of nest abandonment.

   Due to the small size of the wren nest sample the use of multiple regression is inappropriate because a model containing several coefficients will explain an inordinately large amount of the variance (Draper and Smith 1981). The chance of finding statistically siginificant results is reduced for the same reason, however this does not negate the chance of finding ecologically meaningful relationships. All vegetation and structural variables were individually regressed on the following success measures: # eggs, # hatched and # fledged. BW clutch size is accurately predicted by total stem density (TS) (R^2=.65, p<0.05); nests with more stems around them contain more eggs. The ratio of nest height to snag height (SHRAT) is the best model for estimating the number of eggs which hatch (R^2=.54, p<0.06) but the relationship is not statistically significant. Number fledged is also influenced by nest microsite stem density (TS) (R^2=.50, p=0.07) but no other vegetation or structural variables can be used to predict success.

Food Types

   Despite the differences in occupied habitats between species there is a high degree of diet overlap. Food preferences were sampled by observing items brought to nests by adults. A total of 239 BW prey and

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23 BV prey were identified to arthropod order during feeding (Table 11). The proportion of each order fed did not vary between species and ad hoc observations of foraging behavior supports a hypothesis of high degree of dietary overlap.

DISCUSSION

Interspecific distribution

In agreement with Hutto (1985) and Rosenzweig (1985) I believe the distribution of species in habitat space reflects a choice of habitat by individuals that maximizes reproductive output. Because BV and BW are exposed to some of the same ecological pressures affecting insectivorous Passerines breeding in the tallgrass prairie, I hypothesized that habitat utilization would be the same along some habitat axes, as both species would converge on successful strategies to avoid similar suites of predators and environmental hazards (Thornhill and Alcock 1983). Based on Gausian principles (Hardin 1960) I also predicted a priori that significant separations along habitat, food and/or temporal axes would also have evolved over evolutionary time to minimize possible competition. The differential use of habitat by both BV and BW is quantifiable, as evidenced by both the paired t-tests on raw vegetation data (Table 1) and the principal component analysis comparing use of all habitat variables (Figure 2). More importantly, the distribution of territories of each species is both predictable and repeatable. The test of the interspecifc habitat selection model was conducted during the same breeding season in order to 1) control for stochastic variables such as weather and 2) control for any possible biases as the habitat preferences were not known a priori.

I propose that the pattern of habitat utilization by BV and BW is due to species-specific selection for particular vegetative architecture, which are the proximate cues used by these species in determining breeding habitat quality (e.g. Pleszczynska 1978, Slagsvold

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1986). Distribution of BV territories is restricted to a zone with maximum canopy height of 6 meters, a range of stem densities from 0 - 39/m circle and a maximum canopy cover of 90%. These values are consistent with published accounts of BV habitat use. Kahl et al. (1985) characterize BV habitat in Missouri as grassland with extensive woody invasion, which is analogous to the distribution of dogwood patches on Konza prairie. The authors suggest the density of small woody stems is the best means of describing BV breeding habitat. Specifically, Missouri Bell's vireos are found in areas with large numbers of small, woody stems (1700-2100 stems <2.5 cm dbh/ha) and low canopy height (2-4 m). Nolan (1960), Barlow (1962) and James (1971) provide similar descriptions of BV inhabiting "thickets" and areas with "numerous small trees 0.3-0.5 m tall".

BW distribution is over a greater range of habitats when both raw data and PCA components are considered (Figure 2) but its distribution on Konza prairie is still predictable. This species is a generalist, as it is found in a wide variety of habitat types both across its entire breeding range and within specific regions (Bent 1948, Robbins et al. 1986). BW breeding territories usually contain mixtures of thick woody vegetation and open woodlands; this habitat type varies in form throughout its range and consequently BW are found breeding in riparian zones, fence rows, pastures and thickets (Miller 1941, Bent 1948, Johnston 1964, Kroodsma 1974). The comparison of niche breadths and overlaps using PCA scores reveals a relatively large degree of overlap in habitat use. A closer inspection of the distributions within each component segment however, shows differential use of both the "stem" and

"canopy" axis (Figure 3). The pattern is consistent with comparisons of raw habitat data, which show little overlap between mean values (+, - standard error) of the TS, HT, PCOV, VEGDEN and STMRAT variables. In addition, only 3 cases of territory overlap were documented and no cases of interspecific territoriality were observed.

These data suggest these two breeding insectivores do not currently compete for space. I propose the distributions of BV and BW are based on active choice and that neither species affects distributions of the other. This is especially true for BW, which initiates territorial song at an early date (LTER data set CBP01) for a migratory, insectivorous Passerine and therefore may have the advantage of selecting preferred sites without interference from potential competitors. Resident individuals normally have territorial rights over newcomers (dickcissels ((Spiza americana)) Finck pers. comm.; bobolinks ((Dolichonyx oryzivorus)) and BW pers. obs.), even with individuals of other species, and therefore the distribution of BW as a species is not likely to be affected by BV. The more typical mid-lattitude Passerine breeding season of BV (Figure 4) exposes this species to potential exclusion from preferred habitat; yet this does not occur. I hypothesize that interference competition does not occur based on the lack of interspecific territoriality (sensu Murray 1971), the overlap of breeding chronologies (Figure 4), the lack of suitable BW nest sites in dogwood patches and the large overlap in diet (Table 11). Furthermore, the presence of unused sites in the random sample with statistically indistinguishable values from occupied sites for some variables suggests the presence of unused, yet low quality, habitat. The unused patches in

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the random sample may also reflect levels of population densities of either species (Collins 1983) or may be due to unmeasured factors which affect breeding distribution, such as distance to a conspecific.

Intraspecific comparison

The comparison of mean values of each vegetation variable between territory samples and nest sites in the focal watersheds revealed significant differences ($p < 0.05$) for at least one varible for each species. This pattern of selection for levels and ratios for a portion of habitat components at the territory scale and choice for different levels of the same variable or a different set of variables can be termed hierarchical nest-site selection.

The selection of breeding habitat by both BV and BW appears to proceed in a hierarchical manner, with specific quantities and/or proportions of specific habitat attributes being preferred at the territory scale and possibly different quantities or ratios being preferred at the nest-site scale. This model of the means by which nest-site selection occurs has been considered for other species (Knapton and Falls 1982, Hutto 1985). But unlike these studies, my data set tests the interspecific model of territory-level habitat selection, and measures the costs and benefits of breeding habitat selection for each species (sensu Caccamise 1977). I used individual reproductive success, measured in terms of clutch size, percent hatched and number fledged, as an estimate of lifetime productivity.

Nest-site selection in both BV and BW occurs in hierarchical fashion and demonstrates specific, proximate habitat cues preferred by these two species. I hypothesize that the vegetation variables which

are selected at the nest site scale are those which should be correlated with reproductive success. In addition to considering the effect of dead stems on productivity it is also valuable to determine if variables closely correlated with the microsite cue (DS) affect productivity, however no relationships are significant within the correlation matrix for BV nest sites. The data show that regardless of which measure of success is used, vireo success is best correlated with the density of dead stems (Table 9). Nest sites are chosen which contain significantly fewer dead stems than within territories, presumably as the result of natural selection favoring individuals which express this behavioral choice. The correlation values and regression models are counterintuitive; nests with more dead stems produce more young. Several hypothesis could explain this apparent contradiction. Natural selection is also acting on nest parasites and predators to maximize their frequency of locating BV nests. Traits for search images of the specific microsite variable will increase in frequency in the predator and parasite population, as those individuals should be more successful at locating BV nests. This would result in decrease in the success rate of BV nest with low DS density. This scenario is only feasible if a stronger selective force is maintaining the low DS preference by breeding BV. I propose the disadvantage in selecting nest sites with many dead stems is the unsuitability of this type of vegetation for nest support. BV builds a classic vireo-style suspended nest (Bent 1950, Barlow 1962) which requires relatively strong support. Two live stems were used for support in every nest located in the focal watersheds (n=37), despite the presence of dead stems in 19% of the nest

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microsites. A second hypothesis for increased success at nests with high DS density states that predators and/or parasites are operating independently of structural cues and locate nests by chance (Zimmerman 1984) or some other cue besides structural. This suggests an experiment to determine if density does indeed affect BV nest success; by artificially increasing the density of dead stems in the nest microsite region the effect of this variable can be ascertained. The procedure would have to include nests with average values for the remaining variables and activity patterns would have to be mimicked at control nests in order to control for the potential effect of human disturbance on predation rate (Westmoreland and Best 1985).

An inspection of the BW nesting success and vegetation correlations reveals a significant relationship between total stem density (TS) and clutch size, and STMRAT and number fledged (Table 9). The microsite variable HT is not significantly correlated with any success measure, therefore no additional vegetation variables appear to have a potential effect on success. Likewise, no nest site structural measures have impact on nest success (Table 10). This result was not expected because factors such as nest height (Stauffer and Best 1982), orientation (Conner 1975) and distance to patch edge (Barlow 1962) could potentially influence success. The lack of significant impact of microsites on success may be due to predators not cueing in on nest microsites per se or as discussed, selective pressure for DS at nest sites may be for reasons of structural support and not an anti-predator strategy.

If BW uses hierarchical nest selection method I suspect that the variable HT should have the greatest affect on productivity and

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therefore should have the strongest R^2 value when regressed on fitness estimators. The most robust model however is one containing TS for number of eggs, the ratio of nest height to snag height (SHRAT) for hatching rate and TS for number fledged. The density of stems, both live and dead, in the 2m diameter cylinder around the nest cavity are the best estimators of productivity. Nests with high surrounding stem densities tend to be more successful. Canopy height, which was determined to be important in nest microsite selection, is a partial predictor of number hatched. The height of snags appears to affect hatching rate, with nests closer to the top of snags being more successful. Probably, this is due to the lower accessibiltiy of these sites to predators.

   These data provide evidence for hierarchical nest-site selection (HNSS) and correlations with several measures of productivity appear to support this hypothesis. The mechanism by which HNSS occurs, however, is not clear. I suggest that natural selection has acted differentially on the sexes of many Passerines and that sex-specific nest-site selection may be a common phenomenon in migratory Passerines. The staggered arrival times of many species has been reported (e.g. Orians 1961, Wittenberger 1978, Finck 1984) and the existing dogma states that territorial males return to breeding sites first and at this time intrasexual sexual selection occurs. Following competition for territories by males, females arrive and mate choice occurs, presumably based on a combination of epigamic and territorial features (e.g. Nagata 1986, Slagsvold 1986, Eckert and Weatherhead 1987). At this time macroselection has already occurred, as males have used proximate cues

to choose territories which will maximize their reproductive output (see Section I). Following mate choice, or possibly as a part of the selection process, females inspect territories for possible nest sites, possibly using a different set of criteria than males. Intersexual differences in habitat selection capabilities have been documented in hooded warblers (_Wilsonia citrina_) during the nonbreeding season (Lynch et al. 1985). Since the scale of nest-site selection is different for each sex, natural selection should 1) act on males to either directly assess microsites when choosing territories or 2) select variables which closely correlate with nest microsite variables e.g. DS in BV. The force of natural selection on females should be stabilizing selection towards that variable which minimizes detection by predators and social parasites and/or the variable which provides the best protection from abiotic factors.

An alternative hypothesis is that HNSS may occur but that both sexes are under the same selective pressures and have converged on the same strategy to maximize productivity. Therefore, the same proximate variables would be used by each sex. The sex-specific hypothesis also does not provide for the influence of the territory on success. Both species maintain type A territories (Mayr 1935) and the effect of territory structure on productivity (the "territory hypothesis") must also be considered. Analysis of feeding rate data from 6 BW nests revealed that the best predictor of the amount of food brought to a nestling was not a territory structure or size componant, but the combined weight of the feeding pair (unpub. data). Both BV and BW, and possibly numerous other Passerine species, show evidence of hierarchical

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nest-site selection. The suite of proximate cues differs from the territory or macroselection scale to the nest or microsite scale. These data do not support a specific hypothesis for the selective advantage of this phenomenon but correlation and regression data provide evidence that nest parasitism by brown-headed cowbirds and rates of nest predation may be affected by the same microsite variables. I propose that selective pressure to minimize these negative affects on productivity have resulted in the evolution of a behavior whereby species, or different sexes of the same species, use different proximate structural cues to select breeding territories and nest sites.

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    habitats and at different nest densities. Wilson Bull. 95: 7-22.

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    density in dickcissels. Condor 86: 68-72.

Table 1. Interspecific comparison of vegetation means (± standard error) in focal watershed territories using t-tests.

| VARIABLE | TERRITORIES | | | | |
	BELL'S VIREO			BEWICK'S WREN	
TS[1]	11.4 ±	.39	***	4.0 ±	.40
DS	2.3 ±	.22	*	1.7 ±	.25
HT	1.9 ±	.04	***	4.4 ±	.25
PCOV	58.4 ±	1.40	*	67.9 ±	1.90
VEGDEN	0.2 ±	.01	***	1.4 ±	.21
STMRAT	0.2 ±	.01	***	0.4 ±	.04
n	285			143	

* = $p < 0.01$

** = $p < 0.0001$

[1]See appendix 1 for variable definitions

Table 2. Pearson product moment correlations of vegetation variables within BV and BW territories in the focal watersheds.

	TS¹	DS	HT	PCOV	VEGDEN	STMRAT
TS		.59 ***	-.29 ***	.12 **	X	X
DS			-.03	.14	-.13 **	X
HT				.43 ***	X	.29 ***
PCOV					.19 ***	.25 ***
VEGDEN						.10 *

* = p < 0.05   ** = p < 0.01   *** = p < 0.0001

¹ See appendix 1 for variable definitions

x = correlations between composite variables and their components are not listed

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Table 3. Pearson product moment correlations between vegetation variables in territories of Bell's vireo and Bewick's wren in the focal watersheds.

	DS[1]	HT	PCOV	VEGDEN	STMRAT
		Bell's vireo (n=285)			
TS	.58***	.23***	.31***	X	X
DS		.30***	.23***	-.25	X
HT			.64***	X	.31***
PCOV				.04	.24***
VEGDEN					-.08
		Bewick's wren (n=143)			
TS	.81***	-.19*	.06	X	X
DS		-.13	-.02	-.26**	X
HT			.44***	X	.10
PCOV				.26***	.16
VEGDEN					-.05

* = $p < 0.05$

** = $p < 0.01$

*** = $p < 0.001$

[1]See appendix 1 for variable definitions

X = correlations between composite variables and their components are not listed

Table 4. Summary of principal components analysis on
mean values of each of the four original vegetation
variables for territories in the focal watersheds.

	COMPONENT	
	I	II
Percentage of total variance accounted for	41.8	36.0
Cumulative percentage of total variance accounted for	41.8	77.8
Correlations to original variable		
TS[1]	.70	.01
DS	.65	.20
HT	-.29	.67
PCOV	.08	.72

[1]See appendix 1 for variable definitons

Table 5. Model predictions based on t-tests on focal territory data and test data (± standard error) from randomly selected territories, also using t-tests.

Vegetation variable	Species with significantly mean using model	RANDOM TERRITORIES		Consistent with model?
		Bell's vireo (n=56)	Bewick's wren (n=36)	
T S[1]	vireo	9.8 ± .75 *	3.4 ± .60	yes
D S	=	1.5 ± .42 ns	1.1 ± .23	yes
H T	wren	2.4 ± .17 *	4.6 ± .57	yes
PCOV	wren	61.0 ± 2.20 ns	68.3 ± 2.80	trend only
VEGDEN	wren	0.3 ± .03 *	1.7 ± .53	yes
STMRAT	wren	0.1 ± .02 *	0.4 ± .08	yes

* = $p < 0.05$

[1] See appendix 1 for variable definitions

Table 6. Comparison of means ($\pm$ standard error) between unoccupied sites and territories of Bell's vireo and Bewick's wren using t-tests.

Vegetation variable	Bell's vireo (n=56)		Unoccupied (n=96)		Bewick's wren (n=36)
T S[1]	9.8 ± .75	ns	8.6 ± .62	*	3.4 ± .60
D S	1.5 ± .42	ns	2.0 ± .37	ns	1.1 ± .23
H T	2.4 ± .17	ns	3.0 ± .28	*	4.6 ± .57
PCOV	61.0 ± 2.24	ns	56.2 ±1.87	*	68.3 ± 2.85
VEGDEN	0.3 ± .03	*	1.0 ± .25	ns	1.7 ± .53
STMRAT	0.1 ± .02	ns	0.2 ± .03	*	0.4 ± .08

* $p < 0.05$

[1] See appendix 1 for variable definitions

Table 7. Within species comparison of vegetation variable
means ($\pm$ standard error) using t-tests.

BELL'S VIREO

Variable	Territory (n=285)		Nest (n=37)		
TS[1]	11.4 ± .39	ns	11.0	±	.94
DS	2.3 ± .22	*	0.5	±	.24
HT	1.9 ± .04	ns	1.8	±	.07
PCOV	58.4 ± 1.40	ns	60.2	±	3.40
VEGDEN	0.2 ± .01	ns	0.3	±	.05
STMRAT	0.2 ± .01	*	0.04	±	.02

BEWICK'S WREN

Variable	Territory (n=143)		Nest (n=7)		
TS	4.0 ± .40	ns	2.9	±	1.64
DS	1.7 ± .25	ns	1.1	±	.51
HT	4.4 ± .25	*	2.6	±	.95
PCOV	67.9 ± 1.90	ns	58.2	±	12.20
VEGDEN	1.4 ± .21	ns	1.7	±	1.12
STMRAT	0.4 ± .04	ns	0.6	±	.18

* = $p < 0.05$

[1]See appendix 1 for variable definitions

Table 8. Reproductive success data from nests in focal watersheds.

BELL'S VIREO	FITNESS ESTIMATE	BEWICK'S WREN
2.3	nests/female	1.7
3.7	mean complete clutch	6.0
40.0	% hatch	88.1
36.0	% fledge	61.9
1.1	fledglings/female	6.5
1.1	fledglings/male	4.3
35.3	% females successful	75.0
35.3	% males successful	66.7
40	nests	7

Table 9. Pearson product moment correlations between nest
 success variables and nest-site vegetation.

	TS	DS	HT	PCOV	VEGDEN	STMRAT
	Bell's vireo (n=37)					
# eggs	−.03	.22	−.21	−.21	−.04	.16
# hatch	−.24	.32*	−.08	−.23	.13	.27
# fledge	−.24	.37*	−.07	−.21	.15	.32*
	Brown-headed cowbird eggs in vireo nests (n=37)					
# eggs	.30@	−.06	.08	.07	−.24	−.13
	Bewick's wren (n=7)					
# eggs	.81*	.62	−.19	.12	−.30	−.31
# hatch	.22	.12	−.11	.16	.32	.33
# fledge	−.71	−.41	−.42	−.50	.51	.98**

* = p < 0.05
** = p < 0.02
@ = p < 0.07
[1]See appendix 1 for variable definitions

Table 10. Pearson product moment correlations between nest success variables and nest-site structure.

	NHT[1]	DE	OR	DM	AN	HTRAT
			BELL'S VIREO (n=37)			
# eggs	.12	.15	−.16	−.36*	−.27	.30@
# hatch	.20	−.11	−.23	−.14	−.19	.12
# fledge	.14	−.08	−.21	−.16	−.17	.07
		BROWN-HEADED COWBIRD EGGS IN VIREO NESTS (n=37)				
# eggs	−.09	.04	−.06	−.07	−.16	−.16

	NHT[1]	SHT	DBH	DCB	CW	CL	CD	OR	HTRAT	SHRAT
				BEWICK'S WREN (n=7)						
# eggs	−.51	−.42	−.56	−.11	−.02	−.40	−.39	.01	−.74	−.64
# hatch	−.56	−.74@	−.19	−.01	−.14	−.72@	−.17	.42	−.92@	−.19
# fledge	.09	−.22	−.03	.37	.33	−.29	.31	.65	−.27	.52

* = p < 0.05

@ = p < 0.07

[1] See appendix 1 for variable definitions

Table 11. Types of arthropod prey delivered to Bell's vireo and Bewick's wren nests in focal watersheds, by order.

	Lepid.	Aran.	Orthop.	Coleop.	Pupae[1]	Dipt.	Neurop.	Unidentified	Total
					BELL'S VIREO				
N	11	2	4	2	2	0	0	4	25
%	.44	.08	.16	.08	.08	.00	.00	.16	1.00
					BEWICK'S WREN				
N	121	31	14	10	15	1	1	46	239
%	.51	.13	.06	.04	.06	.004	.004	.19	1.00

Lepid. = Lepidoptera

Aran. = Araneae

Orthop. = Orthoptera

Coleop. = Coleoptera

Dipt. = Diptera

Neurop. = Neuroptera

[1]This category contains prey from an unidentified holometabolous insect order

Figure legends

Figure 1. Schematic diagram depicting range of values
          for composite variable "VEGDEN", the ratio of
          canopy height to total stem density.

Figure 2. Scatterplot of pricipal components scores for
          territory point samples in the focal watersheds.

Figure 3. Histograms of niche breadth using principal
          components scores and five categories along each
          component or habitat axis.

Figure 4. Nesting chronology of Bell's vireo and Bewick's
          wren from nests in the focal watersheds.

`VEGDEN´

LOW   HIGH
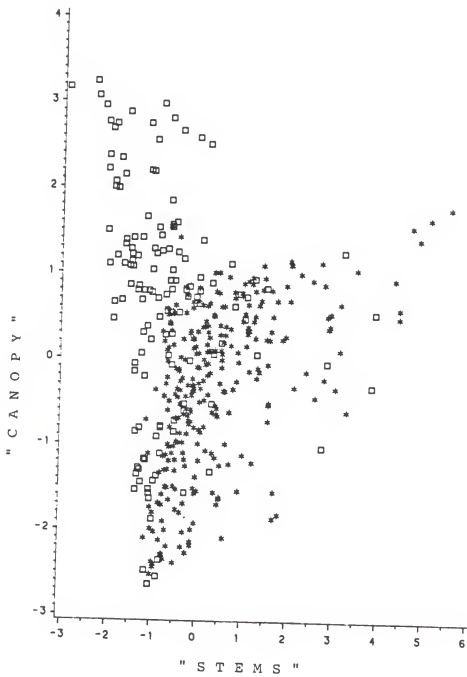
SPECIES: * Bell's vireo

□ Bewick's wren

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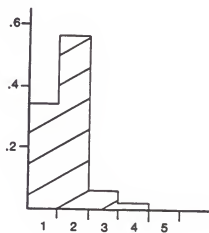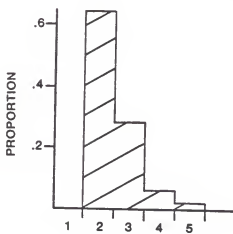Bell's vireo   Bewick's wren

"CANOPY" AXIS
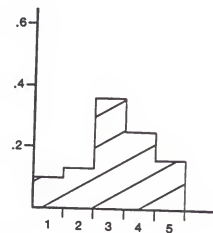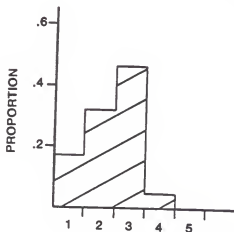
"STEM" AXIS

Bell's vireo   Bewick's wren

Bewick's wren
Nesting cycle

EGG LAYING

HATCHING

FLEDGING

EGG LAYING

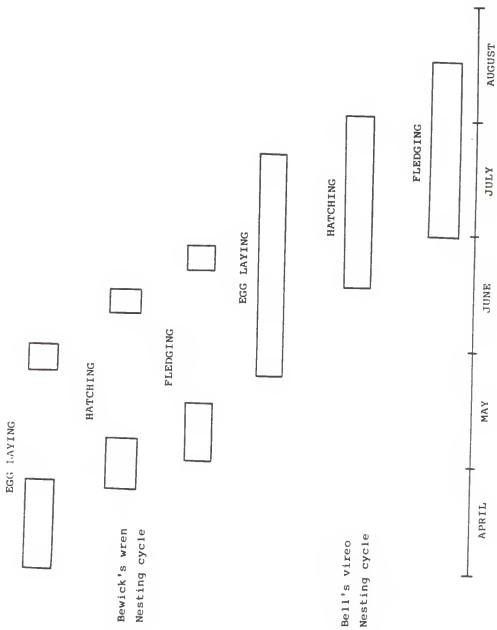Bell's vireo
Nesting cycle

HATCHING

FLEDGING

APRIL   MAY   JUNE   JULY   AUGUST

Appendix 1. Definitions of variable abbreviations.

AN: Compass orientation of BV nest to main stem
         of nest shrub

BV: Bell's vireo

BW: Bewick's wren

CD: Depth in mm of BW nest cavity

CL: Maximum length in mm of BW nest cavity opening

CW: Maximum width in mm of BW nest cavity opening

DBH: Diameter of stem at breast height

DE: Distance in m from BV nest to edge of shrub patch

DM: Distance in cm from BV nest to main shrub branch

DS: Number of dead stems greater than 2 mm in diameter
         within a 1 m diameter circle, 1 m off the ground

HT: Canopy height in m

HTRAT: Ratio of nest height (NHT) to canopy height (HT)

NHT: Nest height in m

OR: Compass bearing of BW nest opening or compass
         aspect of BV nest in reference to nearest patch
         edge

PCOV: Percent canopy cover

SHRAT: Ratio of BW nest height to snag height (SHT)

SHT: Snag height, for BW nests

STMRAT: Ratio of dead stem density (DS) to total stem
         density (TS)

TS: Total number of woody stems greater than 2 mm in
         diameter within a 1 m diameter circle, 1 m off
         the ground

VEGDEN: Ratio of canopy height (HT) to total stem density
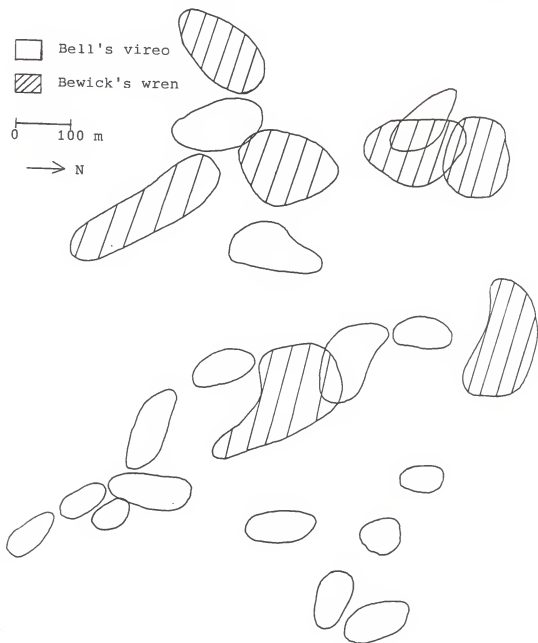   (TS)

Appendix 2. Bell's vireo territory sampling procedure
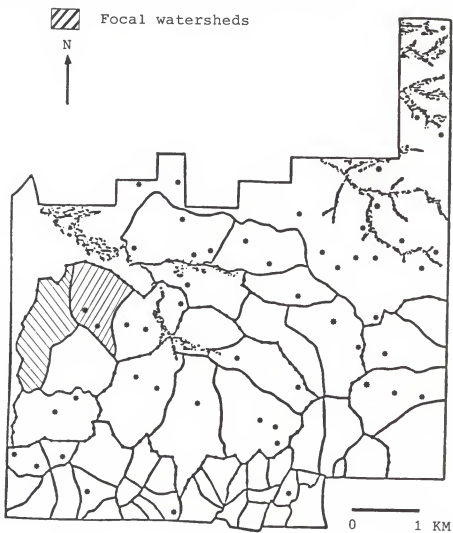
in the focal watersheds.

O   Bell's vireo nest

X   point sample
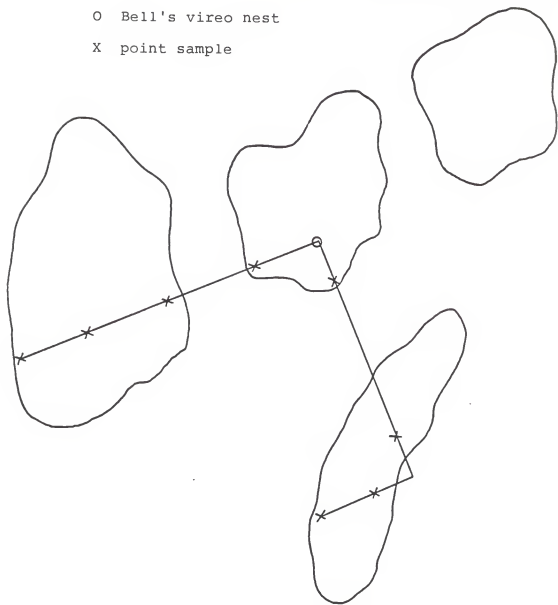
Appendix 3. Territory maps of Bell's vireo and Bewick's
wren in the focal watersheds.

Appendix 4. Distribution of random sampling stations
(*) across Konza Prairie Research Natural Area.

COMPARATIVE BREEDING STRATEGIES OF TWO COEXISTING

PASSERINES:

BELL'S VIREO (VIREO BELLII) AND

BEWICK'S WREN (THRYOMANES BEWICKII)

by

Greg Hunt Farley

B. S. Cornell University, 1982

AN ABSTRACT OF A THESIS

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Manhattan, Kansas

1987

ABSTRACT

Bell's vireo (BV) (*Vireo bellii*) and Bewick's wren (BW) (*Thryomanes bewickii*) were studied on the Konza Prairie Research Natural Area during 1986 to investigate their reproductive patterns and habitat partitioning. Selection of breeding habitat was quantified using structural measurements at both the territory and nest site scale. ANOVA revealed significant differences for each of 5 variables; pairwise t-tests showed BV selects territories with high stem density and low canopy height, whereas BW selects areas with low stem density and a high, full canopy. Within species comparisons showed hierarchical nest-site selection by both species. The territory scale data were used to create a model of habitat selection, which was tested by collecting the same habitat data from randomly selected stations. Analysis of occupied patches in the random sample revealed complete consistency with predictions for both species. A comparison of habitat structure measurements with reproductive success data revealed significant relationships between the proximate habitat cues used by BV and BW and productivity.