1968

A Comparative Study Of Habitat Utilization By The Cardinal In Peripheral And Central Breeding Populations

Douglas David Dow

Recommended Citation

Dow, Douglas David, "A Comparative Study Of Habitat Utilization By The Cardinal In Peripheral And Central Breeding Populations" (1968). *Digitized Theses*. 385.
https://ir.lib.uwo.ca/digitizedtheses/385

A COMPARATIVE STUDY OF HABITAT UTILIZATION BY THE CARDINAL IN PERIPHERAL AND CENTRAL BREEDING POPULATIONS

by

Douglas David Dow

Department of Zoology

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Canada
March 1968

ABSTRACT

A bird's habitat is defined as the vegetational and other life-forms present in the area that it occupies. Cardinals (Richmondena cardinalis) were examined in four large study areas (intensively in two) during breeding seasons to determine important aspects of their habitat and to compare utilization of habitat in regions of greatly different population density.

A roadside method, utilizing responses to tape-recorded song, was developed for indexing densities. Censusing showed the central area, in Tennessee, to have a density of 30 males per 100 acres (0.74 per ha.) and the most peripheral area in Ontario to have 0.48 per 100 acres (0.012 per ha.).

In Tennessee, cardinals occupied every available type of vegetational cover; in Ontario, they were found most commonly in the most abundant cover, suggesting little or no selection.

Home-ranges differed in size between central and peripheral populations, 2.91 versus 46.48 acres (1.18 vs 18.81 ha.). Both contained the same proportion of woody cover, but woody "edge" was proportionately greater in the home-ranges of the central population. Most life-forms and substrates in home-ranges occurred with equal frequencies; differences could be reasonably explained in terms of geographic dissimilarity rather than by differential preferences. Peripheral home-ranges contained significantly more coniferous foliage, so birds were not selecting all-broadleaved areas. Although male cardinals discriminated strongly in use of various elements of their habitats, differences in degree of discrimination by foraging but not by singing males occurred between central and peripheral populations. Foraging differences were probably due to seasonal availability of food rather than to population differences. Conifers in peripheral home-ranges were not selected as sites for foraging or singing. They were, however, intensively utilized as nest-sites by peripheral birds. Great variability among habitats was evident, particularly in Tennessee. The only requirements appeared to be adequate low cover for nesting and conspicuous, preferably high, song-perches.

An examination of three areas in Ontario showed type of vegetation to be of little consequence in limiting the species' range. The factor most highly correlated with population density was distance from the nearest river. Further work supported this and suggested that wooded bottomland is of greatest importance in limiting movements and distribution of the Cardinal on the periphery of its range. A peripheral population studied in Ontario showed at least 64 per cent of its breeding males to be first-year birds. The central population showed 11 per cent. It is concluded that great plasticity of response to habitat enables the Cardinal to settle successfully in many regions. It is suggested that peripheral populations are comprised largely of young birds "pioneering" new areas via their river systems, and that the ultimate limiting factor on the edge of the range may be winter snow cover and concomitant food shortage or simply a height of land devoid of wooded stream valleys.

ACKNOWLEDGEMENTS

I am grateful to many people for assistance in the course of this study. S. Pluzak of this department assisted in design and construction of the portable apparatus used for broadcasting recorded songs. H.S. Horn, University of Washington, supplied the circuit design for the interval timer used in sampling tape-recorded observations. C.S. Robbins of the Migratory Birds Populations Station, Patuxent, Maryland, provided unpublished data on population densities of the Cardinal. Climatological data were supplied by the Weather Office at Waterloo-Wellington Airport, Breslau, Ontario. The Ontario Department of Lands and Forests at Toronto and Aylmer West permitted lengthy examination of aerial photographs. Particular thanks is due to L. Stock of the Aylmer West office for his hospitality and assistance. It was encouraging never to be refused permission to tramp over the private preserves of nearly 100 land-owners in Tennessee and Ontario. P.C. Smith provided excellent field assistance in 1965 and 1966 as did P. Spruce, for a short time, in 1967. My wife Anne has provided constant encouragement and has assisted greatly in all aspects including field work, tedious checking of computer print-out, and translation of literature.

The following people provided information on the Cardinal or on various techniques that I used or considered: J.P. Hailman, P.H. Klopfer, R.E. Lemon, R.H. MacArthur, R.A. Norris, and C.S. Robbins. I appreciate the many discussions with some of my fellow graduate students, the time and advice given by members of my advisory committee, M.H.A. Keenleyside and C.D. MacInnes, and the many hours spent with R.K. Misra. I am especially grateful for suggestions from my chief advisor D.M. Scott throughout the course of my work and for many stimulating discussions on many topics.

This work was supported primarily through grants from the National Research Council of Canada to D.M. Scott. In addition, some financial support was given by The Society of the Sigma Xi and The Wilson Ornithological Society. During my studies, I was supported by an Ontario Graduate Fellowship and an N.R.C. Studentship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

An evolutionary specialization in an animal's structure or behaviour can only be considered to have adaptive significance when viewed in the context of environment. Thus, it seems reasonable to assume that the evolution of potentially adaptive changes proceeded simultaneously with the evolution of mechanisms ensuring selection, or at least occupancy, of the appropriate environment.

The selection of a particular type of habitat by an animal is an example of such a mechanism, and recent work strongly suggests that some animals, at least, are capable of making this selection (Goertz, 1964; Hildén, 1965; Klopfer and Hailman, 1965; Naylor and Haahtela, 1966; Wecker, 1964; Wilson and Hunt, 1966; Zimmerman, 1960).

By habitat I refer not to the classic definition of Clements and Shelford (1939: 26), which restricts the term to "physical and chemical factors that operate on a community", but to a definition that includes vegetational cover and the general physiognomy (largely a result of physical factors) of the region being considered. I believe that the definition of Clements and Shelford arose mainly in a botanical context. Concepts of habitat have been much influenced by the organism under study (Young, 1958). The term has been used in many ways, but most researchers working with birds or mammals (e.g., Bendell and Elliot, 1966; Emlen, 1956; Elton and Miller, 1954; Harris, 1952; Stebler and Schemnitz, 1955; Yapp, 1955, 1957) have restricted its use to the structural aspects or physiognomy of an area, while others have considered only vegetation (e.g., MacArthur, Recher, and Cody, 1966). Some zoologists (Udvardy, 1959; see also Davis, 1960) have advocated adherence to the definition suggested by Clements and Shelford (op. cit.). Unfortunately, to comply leaves no descriptive term in English for the "living space" of an organism, a currently used meaning of habitat. My use of the term habitat in this account refers, then, to the vegetational and other life-forms present in the area inhabited by a bird. It should be noted, therefore, that habitat is considered as an attribute of an individual bird or a species. The term is not used in reference to the physical aspects of a region without regard to an animal. The term cover seems adequate for this latter meaning.

The various concepts and problems of habitat selection by birds have been reviewed by Klopfer and Hailman (1965) and by Hilden (1965). Several studies have been made, some dealing with isolated examples of birds in an artificial, i.e., man-produced, habitat that apparently satisfies the species' requirements (e.g., in Miller, 1942; Yapp, 1960) and others describing fairly discrete types of cover or plant communities with attempted quantitative or qualitative studies of species occurring within them (Lack, 1933, 1934; Lack and Venables, 1939; Southern and Venables, 1939; Kendeigh, 1945; Maher, 1959; Yeager, 1960; Kluyver, 1961; Finzel, 1964; Hore-Lacy, 1964).

Most observational studies have been rather vaguely interpreted, and most suffer from the flaw of purporting to show selection of habitat or other requirement of a species without any detailed analysis of the amounts or proportions actually available for selection by the individual or population.

MacArthur's studies (MacArthur and MacArthur, 1961; MacArthur,

MacArthur, and Preer, 1962; MacArthur and Levins, 1964) are more objective attempts at description of habitat and its utilization, and have shown that the presence of certain species, at least those occupying fairly discrete habitats, can be predicted from the "foliage-height profile" of a given area. Experimental work has been done by Klopfer (1963, 1965; 1967) in an attempt to elucidate the innate and learned qualities of habitat selection by tropical and temperate species.

In field studies of habitat selection, two major stumbling blocks seem to have been the difficulty of defining and describing habitat and the virtual absence of sufficiently large tracts of homogeneous cover in which to study utilization.

Habitat can be considered in terms of life-forms rather than plant species comprising it. The justification for this view has developed from early observations that birds, and other animals, were frequently found in association with broad, general types of vegetation to form biomes (Pitelka, 1941; Peterson, 1942). This and further work (Brecher, 1943; Kendeigh, 1954; Shelford, 1945) suggested that the species of plants comprising a habitat had little importance for the bird. The important aspect seemed to be the shape and structure of the plant and thus the individual and, together with other vegetation of the habitat, the collective contribution to shade, concealing cover, provision of nest-sites, song-perches, etc.

It follows that the description of habitat should emphasize these features. Yet most ornithologists eschew direct description of avian habitats and use a system of comprehensive categories such as "forest", "brushland", "barren rocky areas", "thickets", "hemlock-beech forest", or "dry sclerophyll forest". As Emlen (1956) has pointed out, one of the dangers of such classification lies in the fact that it tends to compart thinking of phenomena that are in fact distributed along a continuum.

However, some recent systems of avian habitat classification have stressed individual life-forms and their structural detail or, collectively, their physiognomy (Elton and Miller, 1954; Emlen, 1956; Yapp, 1955, 1957). Botanists, too, have been interested in life-form description (e.g., Küchler, 1949; Dansereau, 1951), but the system of Du Rietz (1931) has proved the most readily adaptable to research in avian ecology. This system, with modification, has been used profitably in studies of habitat (Stebler and Schemnitz, 1955; Jones, 1960, 1964).

The approach of some workers (Southern and Venables, 1939; Kendeigh, 1945; Wasilewski, 1961; Ficken and Ficken, 1967) of locating tracts of "homogeneous" cover (habitat) within a fairly restricted geographic area and studying birds within them, e.g., comparing degree of utilization in terms of numbers of birds per unit area, seems to offer little in the case of a species in which the same individual characteristically utilizes several types of habitat. The Cardinal (Richmondena cardinalis) is typical of woodland edge (Kendeigh, 1944: 96) and, thus, probably not a species that could be profitably studied in samples of homogeneous or even reasonably discrete types of cover.

Instead of examining birds in this way, I decided to select individual birds at random in the same restricted geographic area and examine the types of habitat that they utilized. The problem of a bird's utilizing more than one discrete habitat type is eliminated as such differential utilization is actually the basis for measurement of utilization, this being a main advantage of the approach. In other words, habitat, as previously defined, is considered as a characteristic of an individual bird and is subject to individual variation. Thus, observations of a bird's behaviour serve to determine what elements of the habitat are actually being utilized.

The question of habitat selection is particularly interesting in species that are undergoing rapid changes in their geographic range. The Cardinal is such a species. The Cardinal has demonstrated considerable success in colonizing areas that it has recently invaded (Beddall, 1963). Does this success result from great plasticity in response to potential habitat, i.e., the capacity to immediately occupy novel habitats, or are historic and parochial limiting factors gradually lessening in effect and permitting the Cardinal to live successfully in new areas containing cover similar to ancestral habitat.

This research was undertaken to elucidate aspects of habitat that may by necessary for inducing the Cardinal to settle, and to compare the utilization of habitat by the Cardinal in regions of different population density, one being in a high density population near the centre of the species' range in Tennessee and the other in a sparsely populated area on the periphery of the species' range in Ontario.

STUDY AREAS AND METHODS

Populations of cardinals were studied in four main areas, three in Ontario and one in Tennessee (Figure 1). These areas are referred to by the name of an associated town or village. Their locations are more precisely described by the following method. The position of one corner of a study area is given by its latitude and longitude. The direction of one side is given in degrees from the corner. All study areas were square and lay to the left of the line when viewed from the corner. Locations were as follows: Melbourne, Ontario, 42° 33' 19" N., 81° 36' 28" W., 47°; Simcoe, Ontario, 42° 40' 02" N., 81° 24' 07" W., 47°; Elmira, Ontario, 43° 31' 14" N., 80° 20' 21" W., 0°; and Dresden, Tennessee, 36° 16' 58" N., 88° 30' 00" W., 0°.

Birds in the Melbourne and Simcoe areas were studied in 1965, and those in Tennessee and Elmira in 1966 and 1967 respectively. However, data collected in 1965 have been virtually eliminated from the analyses because of incompatability of methods used in the two more recently studied areas. In 1966, the method of collecting behavioural data was modified. Prior to this time birds studied had not been banded, an insufficient amount of time had been spent on each, and my definition of an"area of maximum utilization" (analagous to the "100 ft square most used by the bird" utilized by MacArthur, MacArthur, and Preer (1962: 170) to define their sample area) in which to sample vegetation was later deemed unrepresentative and unsatisfactory because of the heterogeneity of a Cardinal's habitat.

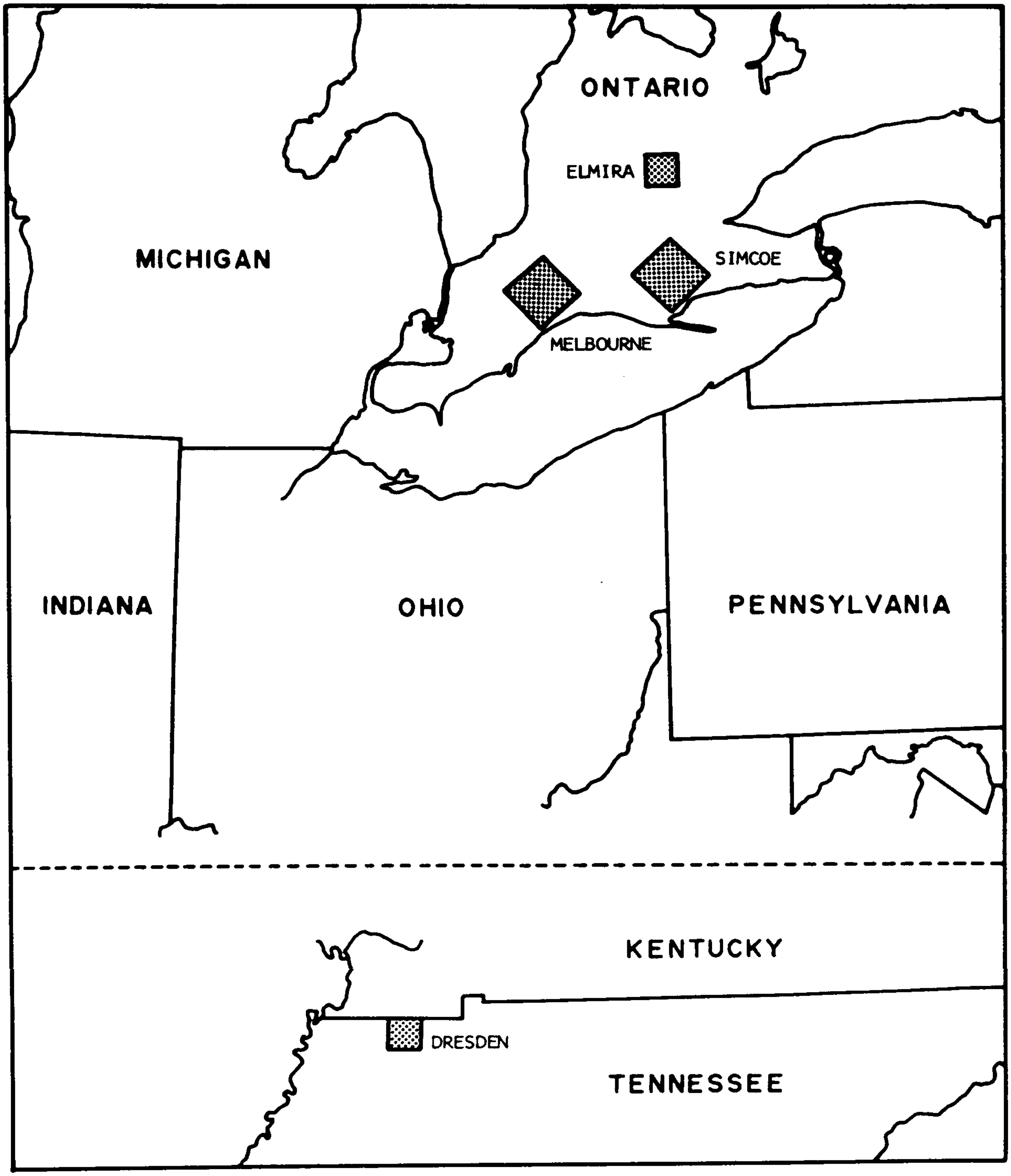


Figure 1. Location of study areas. These are called by names of associated towns. They were sampled as follows: Melbourne, 1965; Simcoe, 1965; Dresden, 1966; and Elmira, 1967.

Because of this, further details are presented only for the Elmira, Ontario, and Dresden, Tennessee, study areas. The centre of the Tennessee study area was located 45 miles east of the Mississippi River and 33 miles west of the Tennessee River, in the heart of the deciduous forest biome. The land was rolling and irregular with a gentle slope southwestward. Elevation ranged from 330 to 570 feet above sea level. The area was drained by the North and Middle Forks of the Obion River and its tributary creeks. Sand was prevalent in uplands, and often stream beds, roadsides, and abandoned farms were severely eroded. Many such areas had recently been planted with pine (Pinus taeda). Most of the land area was under agriculture. Forest and woodland covered 24 per cent of the land area of Weakley County, which contained most of the study area.(Tennessee Conservation Needs Committee, p. 28). If "other land" is included as likely containing cover of importance to cardinals, i.e., only urban areas, cropland, and pasture are excluded, the total is increased to 32 per cent. Upland forests consisted mainly of oak-hickory associations (Quercus-Carya), while bottomland consisted typically of oak-cypress (Quercus-Taxodium). Prominent species of trees included sassafras (Sassafras albidum), tulip (Liriodendron tulipifera), locusts (Gleditsia triacanthos and Robinia pseudo-acacia), sycamore (Platanus occidentalis), hackberry (Celtis sp.), and persimmon (Diospyros virginiana). Hedgerows were a characteristic feature of the landscape, both as roadside borders and field edges. An important aspect of the vegetation was the dense growth of many species of vines. The most abundant was honeysuckle (Lonicera spp.), some being evergreen. Others included grape (Vitis spp.), poison-ivy (Rhus radicans), greenbriar (Smilax spp.), Virginia creeper (Parthenocissus quinquefolia), and trumpet creeper (Campsis radicans). Climatological data were available from Dresden, a town located within the study area. The average daily temperatures followed by the average daily maximum and minimum, in °F, in April, May, June, and July 1966 were as follows: 57.0, 68.2, 45.7; 65.1, 77.3, 52.8; 73.9, 87.8, 60.0; 80.8, 93.6, 68.0. The total precipitation, in inches, for the same periods was 6.60, 6.80, 1.24, and 5.02. Incidentally, in the western half of Tennessee, 1966 had the driest June in 13 years and, at a few locations, the driest in 30 to 35 years (U.S. Dept. of Commerce, 1966).

The Elmira study area's centre was situated 43 miles northwest of Lake Ontario and 61 miles east of Lake Huron. The topography was less irregular than that of the Tennessee area. Drumlins were characteristic of the region. Elevation ranged from 1025 to 1575 feet above sea level with a gradual slope from east to west and from north to south. The area lay in the watersheds of the Grand, the Conestogo, and, to some extent in the east, the Speed River. Extensive forests were absent, most wooded areas being in the form of neat woodlots or being confined to bottomland. The study area lay in the southern part of the ecotone between deciduous and boreal forests. Woodlots consisted largely of beech-maple (Fagus-Acer) giving way to the dominant white cedar (Thuja occidentalis), alder (Alnus sp.), willow (Salix spp.), and much dead American elm (Ulmus americana) in the lowlands. It was my impression that the maximum height of trees in southern Ontario was less than that in Tennessee, presumably as a result of intensive lumbering and subsequent second-growth of vegetation in Ontario. Extensive vines, as were found in Tennessee, were absent, although grape was common in some places. Hedgerows were fewer in number and smaller, presumably a result of "clean"farming. Climatological data are summarized from those collected at the Waterloo-Wellington Airport, 2.4 miles south of the study area. The average daily temperatures followed by the average daily maximum and minimum, in °F, in April, May, June, and July 1967 were as follows: 43.2, 53.4, 33.0; 48.2, 58.3, 38.1; 68.6, 79.2, 58.0; 65.1, 74.7, 55.5. The total precipitation, in inches, for the same periods was 3.73, 1.76, 9.13, and 1.80.

The Tennessee area was selected because it supported a high density of cardinals near the geographic centre of the species' range (Mexico and Central America excluded). This was determined partly by my own observations of cardinals in eastern North America. These observations were unsystematic and qualitative in nature, but I was familiar with the species in almost every state in which it occurred north of the Mexican border. I paid close attention to the relative abundance of the species particularly in southern Ohio, Kentucky, southern Indiana, northern Florida and southern Georgia, and eastern Texas (Santa Ana National Wildlife Refuge near Brownsville and the Welder Wildlife Refuge near Sinton). I found the Cardinal to be most abundant in the basin of the Mississippi River. Examination of Christmas Bird Counts for the years 1961 to 1964 published in Audubon Field Notes supported these observations. Despite the shortcomings of these reports, when counts were standardized by using the number of birds per party-foot-mile, the species was seen to have its greatest abundance in a wide strip along the Mississippi from Louisiana to Kentucky. A second, high concentration appeared in eastern Kentucky. (The southeastern states are poorly represented in these counts.) A similar trend of population density was described for the Cardinal by Young (1946).

The Elmira region was selected as an area of low population density situated on the edge of the species' range at a point where mainly broad-leaved started to give way to largely coniferous vegetation.

I obtained an index of the population density of each area by a song-sampling method. A standard procedure of four tape-recorded songs amplified from roadside positions was used, and the number of males responding in two minutes of listening was scored. Each study area was divided into a grid of one-mile cells, and a random sample of 140 (160 in the two large areas) points, one per cell, were measured. This method and the factors that influence it are more fully discussed in an appendix. To obtain further information on population density and general impressions of utilization of gross vegetational types, 14 one-mile strip censuses were made on the two most recently studied areas. See Hayne (1949) for the field and computational methods.

Further song-sampling was conducted in southern Ontario late in the summers of 1965, 1966, and 1967. This was done to delineate the edge of the species' range in this region and to obtain information about the presence of birds relative to other factors.

Between 16 May and 5 July 1965, 12 birds were studied at Melbourne and 8 at Simcoe. In 1966, in Tennessee, and in 1967, at Elmira, 10 birds were studied, being a more manageable number. The periods of observation were between 25 April and 23 July, and 24 April and 15 June respectively. In Tennessee, the male nearest each of ten random points on a map of the study area was selected. In the other study areas, birds were selected at random from those located during song-sampling.

All males studied in 1966 and 1967 were individually marked with combinations of coloured plastic leg-bands. In addition, most were marked with a one-inch wide black band of commercial marking ink across the breast. Although this mark usually faded rapidly, for four to six weeks it provided identification of birds at long range and in situations where leg-bands were invisible. All netting and marking of birds was done at least one week in advance of initial systematic observations.

Each male was observed for three to six hours on three to seven mornings. Observation was started at the onset of local civil twilight. Experience had shown that attempted observation was very unproductive late in the day as birds were inactive. An effort was made to observe the bird as continuously as possible with binoculars from a distance sufficiently great to prevent disturbing or alarming it. Behaviour and vocalizations were noted as well as the visual or vocal presence of other cardinals. The type of life-form being utilized was noted along with its height, height of canopy bottom, type of foliage, and height and position of the bird. All of these were recorded continuously on a small portable tape-recorder while the location of the bird was marked on a map. Afterwards, the tape was sampled systematically using an electronic timing device that produced an audible "beep" every 15 seconds. The behaviour and related observations occurring at that instant were transcribed to a coded sheet and subsequently punched on an IBM data card.

Stress was placed on the definition of home-range rather than territory. The concept of territory as a defended area (Nice, 1941) is not a particularly useful one owing to the great amount of time required to delimit an area on the basis of observations of territorial strife. Also, in peripheral areas of very low population density, the concept may be almost meaningless because of the low probability of intraspecific encounters.

Home-ranges were defined by the method of Odum and Kuenzler (1955). This method entails plotting the bird's location at five-minute intervals and forming a polygon by joining the peripheral points after each ten consecutive observations. An arbitrary stopping point is defined as the point where an additional observation yields less than one per cent increase in the area of the polygon. This polygon is defined as the "maximum home range".

This method has been criticized by Weeden (1965) on the grounds that the asymptotic [sic] portion of the observation-area curve can not always be differentiated from a plateau or step on the curve. This, of course, is a valid criticism, which can only be circumvented by a sufficiently large number of observations. Nevertheless, the method provides a fast, objective technique for defining the home-range of a particular bird, which in my case was also defining the area for vegetational sampling.

In Tennessee, large-scale maps of home-ranges were constructed using aerial photographs in conjunction with field maps with plotted compass bearings and pacing or chain measurements. At Elmira, aerial photographs were enlarged photographically and used as field maps. Maps of home-ranges were drawn directly from these using a pantograph. Areas of home-ranges were obtained with a planimeter.

In order to make valid statements about the preference of particular life-forms, it is necessary to have some measurement of their availability. The measurement of frequency (Greig-Smith, 1964: 9) seems appropriate. Frequency is the chance of finding a particular life-form (in some predetermined quadrat size) in an area in one trial. Thus, it is a straightforward probability measure suitable for obtaining various expected distributions under different hypotheses. Postulating no discrimination, we might consider a bird, over a sufficient period of time, moving about its home-range and utilizing at random the life-forms within it. Thus, a measure of the relative frequency of occurrence of particular life-forms at such random points is most desirable.

The measurement of frequency is basically simple. A number of sampling units (circle of area one square metre) were laid out at random in the area to be sampled. If a particular life-form occurred within the sampling unit, it was scored; this was a simple yes or no proposition. The proportion of sampling units containing that life-form represented its frequency of occurrence. In addition to the type of life-form, its height and the height of its lowest branches (perches) were noted, along with type of foliage, density of foliage (in three classes: sparse, moderate, dense), and presence of lianas. With practice it was possible to estimate life-form heights consistently within 10 per cent. A Toko Range-Height Finder, Model K (Tokyo Optical Co.), was used regularly to check estimations for precision. At each sample point, the type of substrate was also recorded.

Relatively homogeneous patches or strata of cover within each home-range were determined visually by inspection of aerial photographs. All parts of the home-range were sampled, the intensity of vegetational sampling in each stratum being determined by the proportion of time the bird had spent there. Each home-range was divided into a grid of ten-foot squares and the appropriate number of samples were selected randomly within each stratum. Thus, the frequency of occurrence of any life-form within a home-range could be readily ascertained. The physical aspects of home-ranges at Elmira and Tennessee could then be compared statistically to determine, for example, if differences existed between frequencies of various life-forms.

The degree of utilization of life-forms for any type of behaviour could be determined. The basic method of MacArthur and MacArthur (1961) yields a figure representative of the diversity of life-forms used for any behaviour. This figure is computed from the formula $-\Sigma p_i \log_e p_i$ where p_i represents the proportion of observed behaviour in the i^{th} life-form category. To obtain a measure of discrimination or diversity of choice between two experimental situations, Klopfer (1965) used a modified version of this formula:

$$\text{Discrimination index (H)} = 1 - \frac{p_1 \log_e p_1 + p_2 \log_e p_2}{0.693}$$

Thus, a non-stereotyped individual should select each discriminandum 50 per cent of the time, and H will approach zero as this situation is reached. A stereotyped individual's choices will deviate from the 50 per cent level and result in a higher value of H. Of course, an equal probability of random choice is assumed in the two experimental situations.

In my work, it was necessary to obtain a similar method of measuring discrimination among many choices occurring, in quite different proportions, in the home-range of a bird. I decided to use a modification of the methods of MacArthur and Klopfer, and developed the formula

$$H = 1 - \frac{\Sigma p_i \log_e p_i}{-\log_e k}.$$

This formula assumes unrealistically that the k choice situations occur equally. To compensate for this bias, weights were determined for each of the k situations. Multiplication by these weights resulted in $p_1 = p_2 = p_3 = \cdots = p_k$ under the condition of no discrimination. These corrected p_i values were then used to calculate H. Thus, for no diversity, H = 0, and for maximum diversity, H = 1. Weights were obtained by first converting frequency of occurrence for all life-forms under consideration into proportions of the overall frequency and dividing each proportion into the largest proportion, i.e., $W_i = \max f/f_i$ where $f_i = F_i/\Sigma F_i$ and W_i is the weight for the i^{th} life-form and F_i is the frequency of occurrence of the i^{th} life-form.

A simple example should make the method clear. Consider the hypothetical data of Table 1. Three life-forms, A, B, and C, are present in proportions 0.500, 0.375, and 0.125. If a bird is not discriminating among them, we expect it to spend proportionately the same time among them. If we were to apply the data on proportion of time spent by the bird in each life-form directly to the formula, the resulting H value of 0.113 would be obviously incorrect as we know the bird is showing no discrimination. By calculating and applying weights to the p_i values, they are changed from 0.500, 0.375, and 0.125 to 0.333, 0.333, and 0.333. When these are applied to the formula, H = 0.

Most of the analyses were done wholly or in part using the IBM 7040 digital computer on the campus of the University of Western Ontario.

Additional details of methodology are included when required for clarity.

TABLE 1

EXAMPLE OF THE METHOD OF CALCULATING DISCRIMINATION INDEX (H)

USING HYPOTHETICAL DATA FROM A BIRD SHOWING NO DISCRIMINATION

Life-form	Frequency F_i	Proportional frequency f_i	Weight W_i	No. observations of bird n_i	Proportion of total observs. p_i	Weighted proportion $W_i p_i$	Adjusted proportion $P_i = W_i p_i / \Sigma W_i p_i$
A	0.8	0.500	1.000	328	0.500	0.500	0.333
B	0.6	0.375	1.333	246	0.375	0.500	0.333
C	0.2	0.125	4.000	82	0.125	0.500	0.333
Totals	1.6	1.000		656	1.000	1.500	0.999

POPULATION DENSITIES IN STUDY AREAS

The results of indexing populations using the song-sampling method are summarized in Table 2. For a detailed breakdown of these results see Table 3. As data obtained by this method had a Poisson rather than a normal distribution, it was necessary to transform them before making parametric statistical tests. The transformation, $X' = \sqrt{X + \frac{1}{2}}$, suggested by Winer (1962: 220) for such data was used. An analysis of variance was performed on the data of Table 3 after transformation. The summary of the analysis is presented in Table 4; the differences among the four means were found to be significant ($P<0.001$). A Newman-Keuls test (Winer, 1962: 80) showed all means to differ significantly from each other at the 0.01 probability level except those of the Simcoe and Elmira areas, which differed at the 0.05 level.

To take some account of vegetational cover, the data were stratified after sampling according to elevation and amount of cover in each study area. Elevation was that above the nearest river while cover was measured from aerial photographs in a circle of one-quarter mile radius with its centre at the sample point. All sample values were placed in one of two groups: the criterion being whether the elevation was above the median value. Within each group, all values from sample points with no cover were placed in the same stratum. The remaining values were divided approximately equally into five remaining strata based on amount of cover. This resulted in 12 strata. An adjusted or weighted mean was calculated for each study area by the formula:

TABLE 2

COMPARISON OF INDICES OBTAINED IN FOUR STUDY AREAS

USING SONG-SAMPLING TECHNIQUE

	Ontario			Tennessee
	Melbourne	Simcoe	Elmira	Dresden
Area (square miles)	625	625	225	225
Number of points sampled	160	160	140	140
Number of males responding	155	60	31	598
Index value	0.97	0.38	0.22	4.3
Range	0-4	0-2	0-2	1-8
Weighted index value	1.14	0.49	0.36	4.3
Percentage woody cover*	11	14	14	26

* Calculated from amount of cover present in a circle of one-quarter mile radius with centre at sample point.

TABLE 3

DISTRIBUTION OF NUMBERS OF MALE CARDINALS FOUND BY SONG-SAMPLING IN DIFFERENT STUDY AREAS

No. of birds per point	Ontario			Tennessee
	Melbourne	Simcoe	Elmira	Dresden
0	56	108	111	0
1	65	44	27	3
2	28	8	2	5
3	10	0	0	26
4	1	0	0	45
5	0	0	0	43
6	0	0	0	15
7	0	0	0	2
8	0	0	0	1
Total points	160	160	140	140
Total birds	155	60	31	598

TABLE 4

ANALYSIS OF VARIANCE SUMMARY OF TRANSFORMED† DATA OF TABLE 3 FROM SONG-SAMPLING IN FOUR STUDY AREAS

Source	df	SS	MS	F
Among areas	3	164.92	54.97	625.4***
Within areas	596	52.40	0.0879	
Total	599	217.32		

† $X' = \sqrt{X + \frac{1}{2}}$ *** $P<0.001$

$$\overline{X} = \frac{\Sigma(f_i/n_i)\overline{x}_i}{\Sigma f_i/n_i}$$

where $\overline{X}$ = the weighted mean,

$\overline{x}_i$ = the mean of the samples in the i^{th} stratum,

f_i = the number of points in the i^{th} stratum at which birds were found, and

n_i = the number of points sampled in the i^{th} stratum.

The proportion f_i/n_i represents the frequency with which the species was found in a stratum and, therefore, provides a relative measure of the degree of utilization of different strata. Thus, most weight is given to means of strata in which the Cardinal is most frequently found, and the weighted index value reflects the density of cardinals in occupied habitat rather than only the density per unit area. These weighted index values are shown in Table 2.

It is important to recognize that these are indices, not absolute measures of density. An independent measure of density was available from 14 strip censuses in Tennessee and 14 at Elmira. The areas to be censused were selected at random from the grid of square-mile cells in each of the study areas. Each census path was a one-mile, randomly oriented straight line. The results are presented in Table 5. The mean density in Tennessee was 30 males per 100 acres (0.74 per ha.), and at Elmira it was 0.48 per 100 acres (0.012 per ha.). Cardinals, in all areas, were found associated with woody cover. Therefore, differences in song-sampling and census results could reflect differences in distribution or availability of cover. The proportions of woody cover in the four study areas are shown in Table 2. Tennessee appears to have an

TABLE 5

RESULTS OF 14 STRIP CENSUSES† IN TENNESSEE AND ELMIRA

	Tennessee	Elmira
	15.6	0.0
	17.4	0.0
	17.8	0.0
	21.3	0.0
	22.5	0.0
	22.7	0.0
	24.4	0.0
	27.7	0.0
	32.0	0.2
	40.3	0.6
	41.1	0.8
	41.3	1.0
	41.3	1.4
	55.2	2.7
Mean	30.0	0.48

† Densities are expressed in number of male cardinals per 100 acres.

appreciably higher value (26 per cent) than the three areas in Ontario (11, 14, and 14 per cent). However, as this cover was calculated in a circular area with its centre on a roadway, we can expect the measurements to be biassed according to the agricultural and land-clearing practices of the region. In Ontario, more so than in Tennessee, land close to roads is usually cleared; this results in woodlots set back from the road. Therefore, the figures given are probably too low to be representative of the regions. Additional measures of cover were obtained in the two areas where strip censuses were made. These measurements are described in the following section. The amounts of cover estimated by this method were 44 per cent in Tennessee and 29 per cent at Elmira.

Since cardinals are largely confined to woody cover (But a bird's home-range may contain much open area.), density might be meaningfully expressed in terms of cover, remembering, of course, that in this case density was not determined by examining stands of such cover. Average figures of 68 males per 100 acres of woody cover in Tennessee and 1.7 at Elmira were computed from the results previously presented.

GENERAL HABITAT FEATURES

Each male cardinal observed on the 14 strip censuses in Tennessee and Elmira was classified according to the vegetation or cover type with which it appeared associated. This, of course, yielded only a crude measurement as the bird was observed for a very short time. All birds were associated with woody vegetation of some type ranging from narrow hedgerows and deciduous scrub to extensive heavily wooded areas. No effort has been made here to differentiate forests or woodlots on the basis of the amount of coniferous vegetation contributing to the total. Generally, this was low in Tennessee and considerably higher at Elmira. Also, a bird did not have to be well within a cover type to be classified with it. For example, a cardinal observed on the edge of a woodlot was classified the same as one in the centre of it.

Despite the small number of cardinals observed at Elmira, there were apparent superficial differences (Table 6) in association with vegetational categories between the two areas. At Elmira, 69.2 per cent of observed males were confined to a single vegetational category (woodlot>25 acres) while only 2.0 per cent of Tennessee cardinals were confined to the same category, or 23.6 per cent if forested areas are included.

To determine whether preference or discrimination was being shown by these birds, it was necessary to know something of the availability of cover types in the two study areas. The strip censuses, in addition to estimating population density, provided a general measure of the

TABLE 6

ASSOCIATION OF MALE CARDINALS OBSERVED ON STRIP CENSUSES WITH GENERAL TYPES OF VEGETATIONAL COVER

Cover type	Tennessee			Ontario		
	No. birds	% total birds	% total cover	No. birds	% total birds	% total cover
Woodlot (<5 acres)	26	10.6	8.2	0	0.0	1.0
Woodlot (5-25 acres)	33	13.5	16.8	1	7.7	7.2
Woodlot (>25 acres)	5	2.0	5.2	9	69.2	55.9
Forest (extensive)*	53	21.6	36.3	0	0.0	6.6
Hedgerow (<3m wide: road border)	12	4.9	0.5	0	0.0	0.4
Hedgerow (>3m wide: road border)	3	1.2	1.1	0	0.0	0.0
Hedgerow (<3m wide: field edge)	13	5.3	1.5	0	0.0	1.7
Hedgerow (>3m wide: field edge)	8	3.3	2.0	0	0.0	0.3
Narrowly wooded strip: larger than hedgerow - not river or creek border	16	6.5	3.8	0	0.0	0.5
Narrowly wooded river or creek border	49	20.0	3.6	1	7.7	1.8
Deciduous scrub	25	10.2	19.4	1	7.7	20.0
Farmstead	2	0.9	1.6	1	7.7	4.6
Total	245	100.0	100.0	13	100.0	100.0

* Woodlots were in the form of "islands" and rarely larger than 100 acres. Forest was usually larger than 100 acres with less well defined edge.

relative abundance of different types of vegetational cover in the two study areas. The one-mile transect or census path was used as a base, and the proportions of each cover type were obtained by measuring the length of the transect crossing them on an aerial photograph. For a detailed discussion of the statistical properties of this method, see Bauer (1943). The results of this sampling are included in Table 6. The estimates of the total amounts of woody cover differed between the two study areas: 44 per cent in Tennessee and 29 per cent at Elmira.

The distribution of birds in the cover types in Tennessee was tested against the distribution of cover types present using the Kolmogorov-Smirnov goodness-of-fit test (Siegel, 1956: 47). The two distributions were found to be significantly different ($P<0.01$). There was no significant difference ($P<0.20$) between the corresponding distributions at Elmira. Thus, in Tennessee, cardinals appear to be discriminating among the types of vegetation available to them. For example, 20 per cent of the birds were found in narrowly wooded creek edge, which comprised only 3.6 per cent of the total available vegetation. At Elmira, little can be said about discrimination among available cover types. The small sample size undoubtedly reduced the information available from the statistical test, but cardinals were found most frequently in the most abundant vegetation.

If forests and woodlots are combined, their percentage in Tennessee is 66.5 and at Elmira is 70.7 of the total cover. Combining hedgerows and narrowly wooded regions yields 12.5 and 4.7 respectively. These figures, along with the finer division of Table 6, give a reasonably clear reflection of apparent historic and agricultural differences between the two regions. The land in Tennessee is more rolling and irregular than at Elmira. There are still large tracts of forest that have not been cleared, although peripheral inroads may have created more interface or edge (see Figures 2 and 3). Farming in Ontario is"cleaner", hedgerows are removed, woodlots are neatly trimmed.

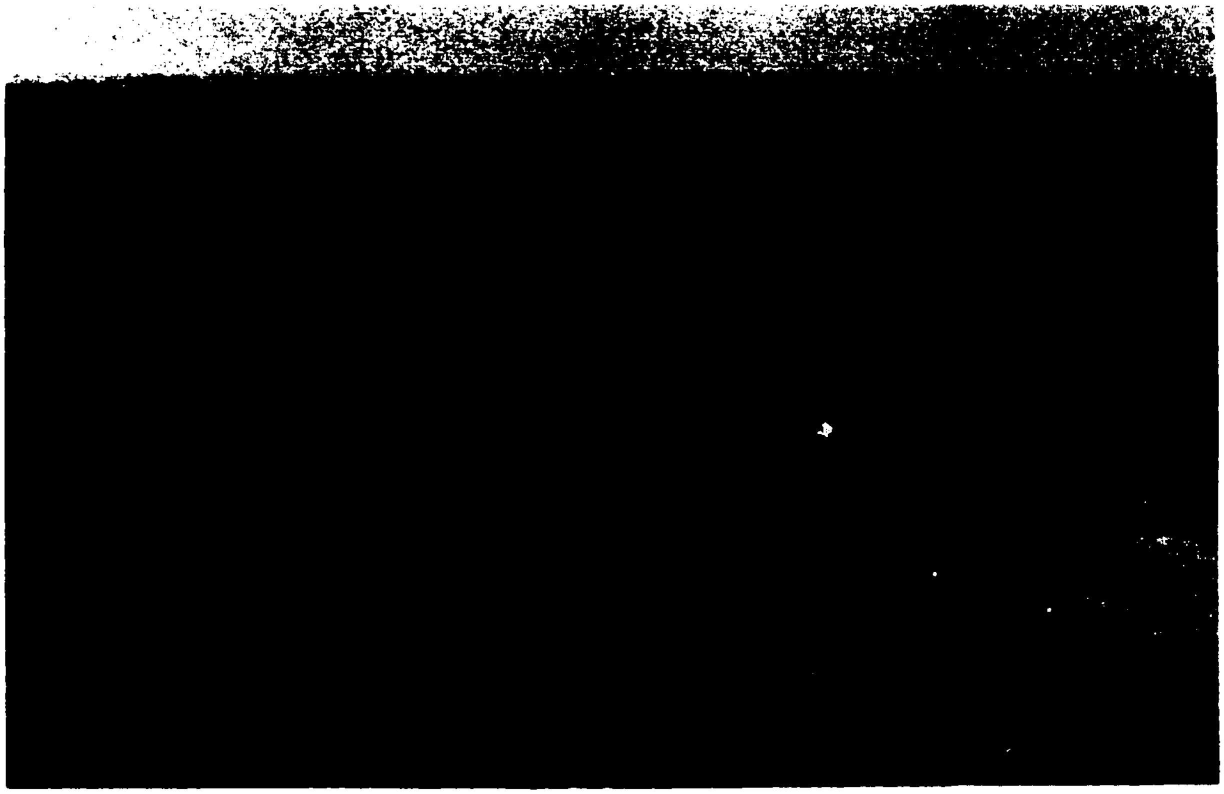


Figure 2. Extensive oak-hickory upland forest in the Tennessee study area.

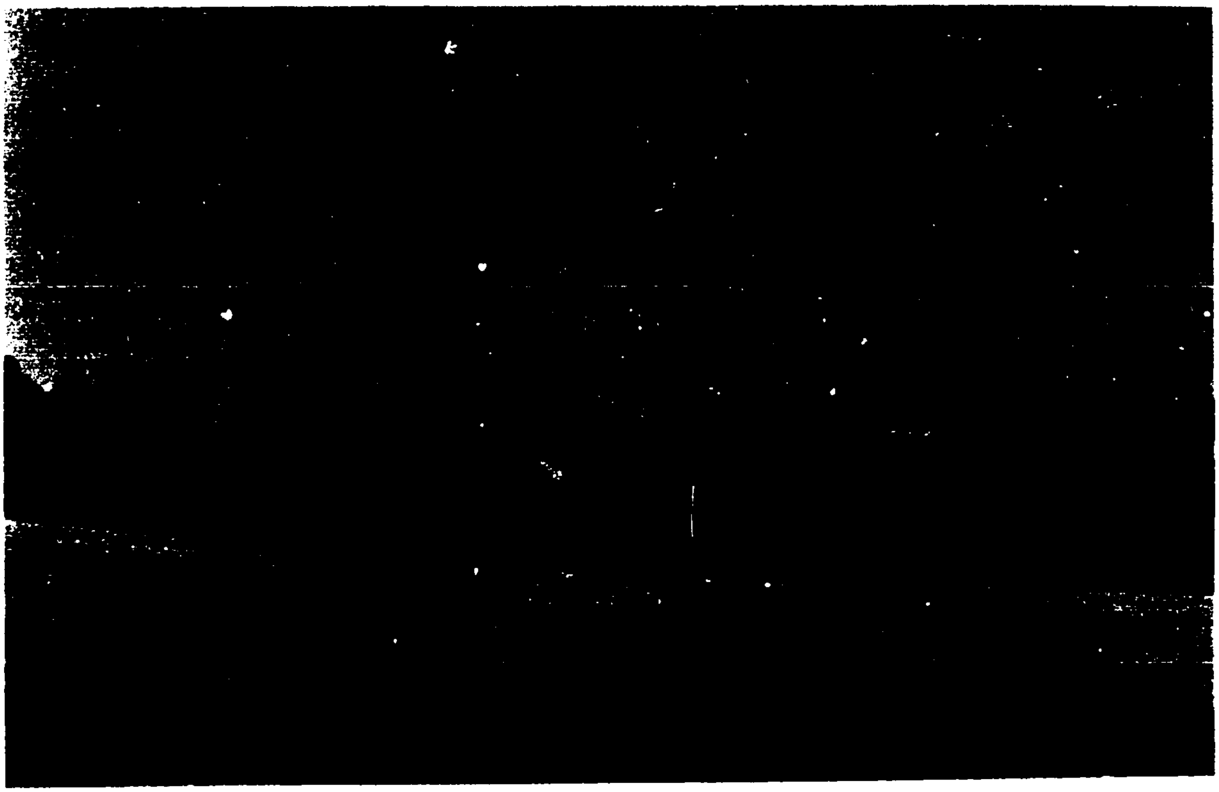


Figure 3. Typical small roadside hedgerow in the Tennessee study area. Arrow indicates approximate location of cardinal's nest. Nearest heavily wooded area was about 200 metres.

Figure 2. Extensive oak-hickory upland forest in the Tennessee study area.

Figure 3. Typical small roadside hedgerow in the Tennessee study area. Arrow indicates approximate location of cardinal's nest. Nearest heavily wooded area was about 200 metres.

AGE STRUCTURE OF POPULATIONS STUDIED

As the birds studied in 1965 were not banded, no estimate of the age structure of these populations could be made. During spring, at least some cardinals can be identified as first-year birds on the basis of plumage (Scott, 1967). The proportion of the population so allocated is conservative because not all first-year birds can be identified.

In the peripheral population studied at Elmira in 1967, 7 of 11 males banded (64 per cent) were in their first year. This proportion is significantly different ($P<0.02$ in binomial test: see Siegel, 1956: 36) from that obtained by Scott (1967) at London, Ontario, some 55 miles west, where 28 per cent of 53 males were in their first year. And it certainly differs from the population studied in Tennessee in 1966 where only 11 per cent of 19 males were obviously immature.

Scott's method of age determination is based on the shape of the rectrices. However, some birds show noticeable traces of an incomplete postjuvenal moult in other feather tracts, particularly in the remiges and their coverts. It is not known if such incomplete moult reflects hatching late in the previous season and should, consequently, be regarded as an indicator of younger age than pointed rectrices alone suggest. In any case, it is notable that of seven males with pointed rectrices examined at Elmira, all but one possessed old, i.e., unmoulted, secondaries. In three cases, the feathers involved were Secondaries 1 through 6, and in the other three were Secondaries 2 through 6, 4 through 6, and 5 and 6 respectively. In the first three cases, the greater primary coverts had also been unmoulted. In Tennessee, where two males showed pointed rectrices, only one showed incomplete moult of secondaries, 3, 5, and 6 being old. Also, the tail contained some new rectrices, contrasting with the unmoulted ones in both shape and length. In all the above cases, the incomplete moult of remiges was symmetric.

Adult and first-year birds were treated similarly in analyses of habitat utilization. The small sample precluded finer analyses based on age. Also, there were no obvious differences in behaviour apparent in the field that could be attributed to the ages of the males.

ASPECTS OF HOME-RANGES IN PERIPHERAL AND CENTRAL POPULATIONS

Home-ranges were compared with regard to several measurements (Table 7). Some very great differences in mean sizes are immediately apparent: 2.91 versus 46.48 acres; 167.1 versus 731.9 metres in length; and 429.1 versus 1,766.8 metres in perimeter. Other large differences such as area of woody cover, length of woody edge, and length of home-range boundary coincident with woody edge are obviously related to difference in size. In view of the great absolute differences, it was of interest to examine relative differences. The relative variability of the measurements is given by their coefficients of variation (Table 7). The significance of the difference between coefficients of variation can be tested by comparing the variances of the same data after logarithmic transformation (Snedecor, 1956: 321). No significant differences were found between any of the pairs (Elmira versus Tennessee) of coefficients of variation given in Table 7. Thus, it was concluded that the great increase in home-range size in the peripheral region had not been accompanied by an increase in variability of measured factors. In fact, a slight, but not statistically significant, decrease in variability was evident.

To determine whether the configuration of the home-ranges differed, the relationship of perimeter and area was used as an indicator of general shape. An analysis of covariance performed on these two variables showed no difference in length of perimeter when areas were adjusted. Similar results were obtained from an analysis of covariance

TABLE 7

COMPARISON OF HOME-RANGES IN TENNESSEE AND ELMIRA

	N	Mean and SE	Range	Variance	Coefficient of variation (%)
Area (acres)					
Tennessee	10	2.91 ± 0.387	1.26 - 5.73	1.498	42.1
Elmira	10	46.48 ± 3.40	27.11 - 57.42	115.5	23.1
Area of woody cover (acres)					
Tennessee	10	1.61 ± 0.216	0.64 - 2.96	0.4676	42.5
Elmira	10	27.63 ± 2.93	18.54 - 49.24	85.93	33.6
Proportion of woody cover (%)					
Tennessee	10	59.5 ± 6.76	17.0 - 100.0	456.4	35.9
Elmira	10	62.4 ± 6.86	37.0 - 96.0	470.0	34.7
Length (metres)					
Tennessee	10	167.1 ± 10.48	108.0 - 217.0	1097.5	19.8
Elmira	10	731.9 ± 39.95	554.0 - 974.0	15,960.	17.3

(continued)

TABLE 7

(CONTINUED)

	N	Mean and SE	Range	Variance	Coefficient of variation (%)
Woody edge (metres)					
Tennessee	10	339.5 ± 61.38	116 - 673	37,675.	57.2
Elmira	10	1,874.5 ± 312.9	427 - 3,144	978,932.	52.8
Perimeter (metres)					
Tennessee	10	429.1 ± 25.31	293 - 567	6,405.9	18.7
Elmira	10	1,766.8 ± 72.94	1,403 - 2,133	53,200.	13.1
Boundary coincident with woody edge (metres)					
Tennessee	10	80.4 ± 25.01	0 - 231	6,256.	98.4
Elmira	10	471.2 ± 63.94	95 - 720	40,879.	42.9

of area and boundary of home-range coincident with edge.

The relative amounts of woody cover in the home-ranges were compared. There was no significant difference between variability or mean values of the two sets of measurements of percentage of woody cover in home-range after transformation (arcsin) of the data.

Finally, the amounts of woody edge in home-ranges were compared by an analysis of covariance using the area of the home-range as the independent variable. The amount of edge per home-range was relatively higher ($P<0.01$) in Tennessee than at Elmira.

The finer detail of each home-range could be determined from the sampling of life-forms and substrates. Substrate was defined as low, ground cover and could consist of soil, rock, water, etc., or vegetation occurring in fairly uniform layers, mats, or patches rather than as prominent or discrete units. The system of identifying life-forms was a modification of the classification of Du Rietz (1931). Eleven life-forms were defined in the following way.

Tree -- A woody plant of any height above 0.25 metres with a distinct main trunk remaining unbranched in its lower part.

Shrub -- Woody plant higher than 0.25 m. without a distinct main trunk, i.e., with stem branching from its basal part or just below the soil surface.

Woody cushion -- A clump of trees or shrubs growing with all branches very tightly packed together so that the collective structure rather than the individual plants appeared to be the main unit. Sumac (*Rhus spp.*) frequently assumes this form.

Vine tangle -- Woody lianas, typically honeysuckle, grape, poison-ivy, etc., often grow in dense mats or globular clumps. Often they will cover a shrub, tree, or other life-form so thickly that the supporting structure can not be seen.

Brush pile -- Most frequently, this was a man-made clump of dead or live branches piled together. Fallen trees were also included here.

Forb -- All herbaceous, broad-leaved plants were included.

Graminoid -- All herbaceous plants with narrow, grass-like leaves were included.

Pole -- Any vertical structure with no extensive branches was included, e.g., fence posts, telephone poles, some dead trees.

Horizontal line -- A wire fence, telephone line, or any similar horizontal man-made structure that could be used as a perch.

Horizontal limb -- A fallen tree after losing its branches was included here, as were rail fences and gates when they occurred.

Building -- A man-made structure, quite different from any natural object, was included here whether chicken-coop or farmhouse.

The frequency of occurrence of each type of life-form was obtained by sampling 145 to 902 points in each home-range depending upon its size. An overall frequency for each type of life-form in a home-range was obtained by calculating the weighted average of the frequency in each stratum, with the area of the stratum being used as its weight. These frequencies are shown in Tables 8 and 9.

The data were transformed (arcsin), and an analysis of variance was performed (Table 10) using the repeated measures design of Winer (1962: 302). Of course, the highly significant difference among life-forms was predictable and is of little relevance here. However, the significant ($P<0.05$) interaction between life-forms and areas, as well

TABLE 8

FREQUENCY OF OCCURRENCE† OF LIFE-FORMS IN TEN TENNESSEE HOME-RANGES

Home-range Life-form	1	2	3	4	5	6	7	8	9	10	Mean
Tree	99.3	56.3	59.2	41.9	9.6	69.5	48.6	63.9	26.7	50.1	52.5
Shrub	35.1	21.3	27.0	34.2	13.4	44.8	35.2	44.6	9.6	14.7	28.0
Woody cushion	8.7	7.7	5.3	7.9	1.3	4.1	2.3	6.6	0.4	0.9	4.5
Vine tangle	1.4	11.6	1.2	19.1	3.2	8.1	0.1	7.8	0.3	10.4	6.3
Brush pile	0.0	0.9	0.3	0.2	0.0	0.0	2.0	0.0	3.8	0.0	0.7
Forb	2.8	0.3	3.1	6.7	1.8	0.6	0.0	0.3	1.8	0.7	1.8
Graminoid	0.0	0.6	0.1	0.4	0.0	0.0	0.0	1.8	0.4	0.0	0.3
Pole	2.2	0.9	0.3	0.3	0.6	0.6	2.7	1.1	0.6	0.8	1.0
Horizontal line	2.4	1.6	0.0	1.6	1.7	0.9	1.9	2.1	1.2	0.8	1.4
Horizontal limb	4.8	1.2	1.1	0.7	0.1	1.1	1.2	2.0	0.3	3.4	1.6
Building	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	3.5	0.0	0.4

† Expressed as a percentage.

TABLE 9

FREQUENCY OF OCCURRENCE† OF LIFE-FORMS IN TEN ELMIRA HOME-RANGES

Home-range Life-form	1	2	3	4	5	6	7	8	9	10	Mean
Tree	72.9	89.2	33.8	78.6	58.1	22.5	53.2	24.6	52.5	37.1	52.2
Shrub	36.3	9.8	8.0	13.6	8.8	25.8	18.0	19.8	35.7	10.3	18.6
Woody cushion	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	T
Vine tangle	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	T
Brush pile	1.0	5.4	1.9	1.8	3.4	0.4	0.3	0.1	4.3	2.8	2.2
Forb	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	T
Graminoid	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	T
Pole	0.0	0.5	0.0	0.0	0.3	0.4	0.0	0.3	0.0	0.0	0.1
Horizontal line	4.0	0.8	0.1	0.0	1.1	2.1	1.9	1.1	1.6	1.2	1.4
Horizontal limb	2.2	5.0	0.8	1.2	3.6	1.4	0.7	1.9	2.3	2.3	2.1
Building	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.1	0.1

† Expressed as a percentage.

T Present in amounts between 0.004 and 0.05 per cent.

TABLE 10

ANALYSIS OF VARIANCE SUMMARY OF DATA†
OF TABLES 8 AND 9

Source	df	SS	MS	F
Areas	1	413.87	413.87	6.38 *
Home-ranges w. areas	18	1,168.11	64.90	
Between home-ranges	19	1,581.98		
Life-forms	10	43,557.38	3,959.76	113.07 ***
Life-forms X areas	10	1,229.55	111.78	3.19 **
LF X HR w. areas	180	6,933.62	35.02	
Within home-ranges	200	51,720.55		

† arcsin transformation

*** $P<0.001$; ** $P<0.01$; * $P<0.05$

as the difference between mean values for areas, clearly shows that the composition of life-forms in the home-ranges of cardinals in Tennessee differed from that of Elmira. An examination of differences between mean values of specific life-forms in the two areas, using the approximate method of Winer (1962: 311), showed that the significant differences were found between shrubs ($P<0.05$), woody cushions ($P<0.01$), and vine tangles ($P<0.001$), these life-forms all being more common in Tennessee.

As the Elmira region was selected partly because of its extensive coniferous vegetation, a similar analysis was made of frequency of occurrence of different foliage types in birds' home-ranges. The frequencies of coniferous and broadleaved foliages are shown in Table 11. The

TABLE 11

FREQUENCY OF OCCURRENCE† OF CONIFEROUS AND BROADLEAVED FOLIAGE ON LIFE-FORMS IN TENNESSEE AND ELMIRA HOME-RANGES

Home-range	Tennessee		Elmira	
	Coniferous	Broadleaved	Coniferous	Broadleaved
1	1	100	2	81
2	18	64	25	88
3	1	63	5	39
4	5	68	28	78
5	0	22	49	42
6	8	81	10	36
7	8	73	28	50
8	5	78	11	33
9	1	32	32	53
10	3	53	3	40
Mean	5.0	63.4	19.3	54.0

† Expressed as percentage.

analysis (Table 12) showed no significant difference between the overall means for Tennessee and Elmira, but the significant interaction ($P<0.05$) showed that the relative proportions of the two types of foliage differed between the two regions.

TABLE 12

ANALYSIS OF VARIANCE SUMMARY OF TRANSFORMED† DATA OF TABLE 11

Source	df	SS	MS	F
Areas	1	104.24	104.24	NS
Home-ranges w. areas	18	3,381.02	187.83	
Among home-ranges	19	3,485.26		
Foliage types	1	11,283.50	11,283.50	80.87 ***
Foliage X areas	1	997.72	997.72	7.15 *
Fol. X HR w. areas	18	2,511.56	139.53	
Within home-ranges	20	14,792.78		

† arcsin transformation

*** $P<0.001$; * $P<0.05$

Table 13 summarizes the mean value for frequency of occurrence of 25 different types of substrates. Again, the analysis (Table 14) showed no significant difference between the overall mean amounts of substrates present in the two regions, but the relative proportions of various substrates differed. Those differing significantly are marked on Table 13.

The vertical distribution of life-forms is shown in Figure 4. These profiles were constructed by superimposing the height of each life-form and the height of its canopy bottom (lowest potential perches) for each stratum and then calculating a weighted average for the home-range in the same manner as was done for frequency. Thus, the area

TABLE 13

FREQUENCY OF OCCURRENCE† OF SUBSTRATES IN TENNESSEE AND ELMIRA HOME-RANGES

Substrate	Tennessee	Elmira	P
Forbs[1] (<0.25 m.)	35.6	30.6	
Forbs[1] (0.25 - 0.8 m.)	18.7	36.2	**
Forbs[1] (0.8 - 2.0 m.)	1.6	0.9	
Graminoids[1] (<0.25 m.)	42.4	30.6	
Graminoids[1] (0.25 - 0.8 m.)	33.9	55.4	***
Graminoids[1] (0.8 - 2.0 m.)	9.8	0.9	*
Woody (<0.25 m.)	57.3	11.2	***
Deciduous leaves	56.1	20.8	***
Coniferous leaves	1.6	8.7	*
Bare soil	26.8	30.1	
Dead wood (<0.25 m.)	9.9	20.8	*
Lichens or moss	4.1	11.2	
Sand	0.8	0.1	
Gravel	0.1	0.4	
Clay	0.0	0.0	
Rock	0.1	5.4	*
Road - gravel surface	0.1	0.7	
Road - paved surface	0.0	0.0	
Standing water	0.4	7.6	**
Dry creek bed	1.8	0.5	

(continued)

TABLE 13

(CONTINUED)

Substrate	Tennessee	Elmira	P
Marshy	0.0	14.2	***
Rotting wood and stumps	0.01	0.5	
Dung (cattle and horses)	1.3	0.7	
Anthills	0.0	0.1	
Rubbish	0.2	0.2	

† Expressed as a percentage.

[1] Forbs and graminoids as substrates differed from those called life-forms in forming mats or extensive patches rather than discrete plants.

*** P<0.001; ** P<0.01; * P<0.05

TABLE 14

ANALYSIS OF VARIANCE SUMMARY OF TRANSFORMED† DATA OF TABLE 13

Source	df	SS	MS	F
Areas	1	144.67	144.67	1.83 NS
Home-ranges w. areas	18	1,420.51	78.92	
Among home-ranges	19	1,565.18		
Substrates	24	106,098.90	4,080.73	62.07 ***
Substrates X areas	24	14,915.54	573.65	8.73 ***
Subs. X HR w. areas	432	30,754.84	65.74	
Within home-ranges	480	151,769.28		

† arcsin transformation

*** P<0.001

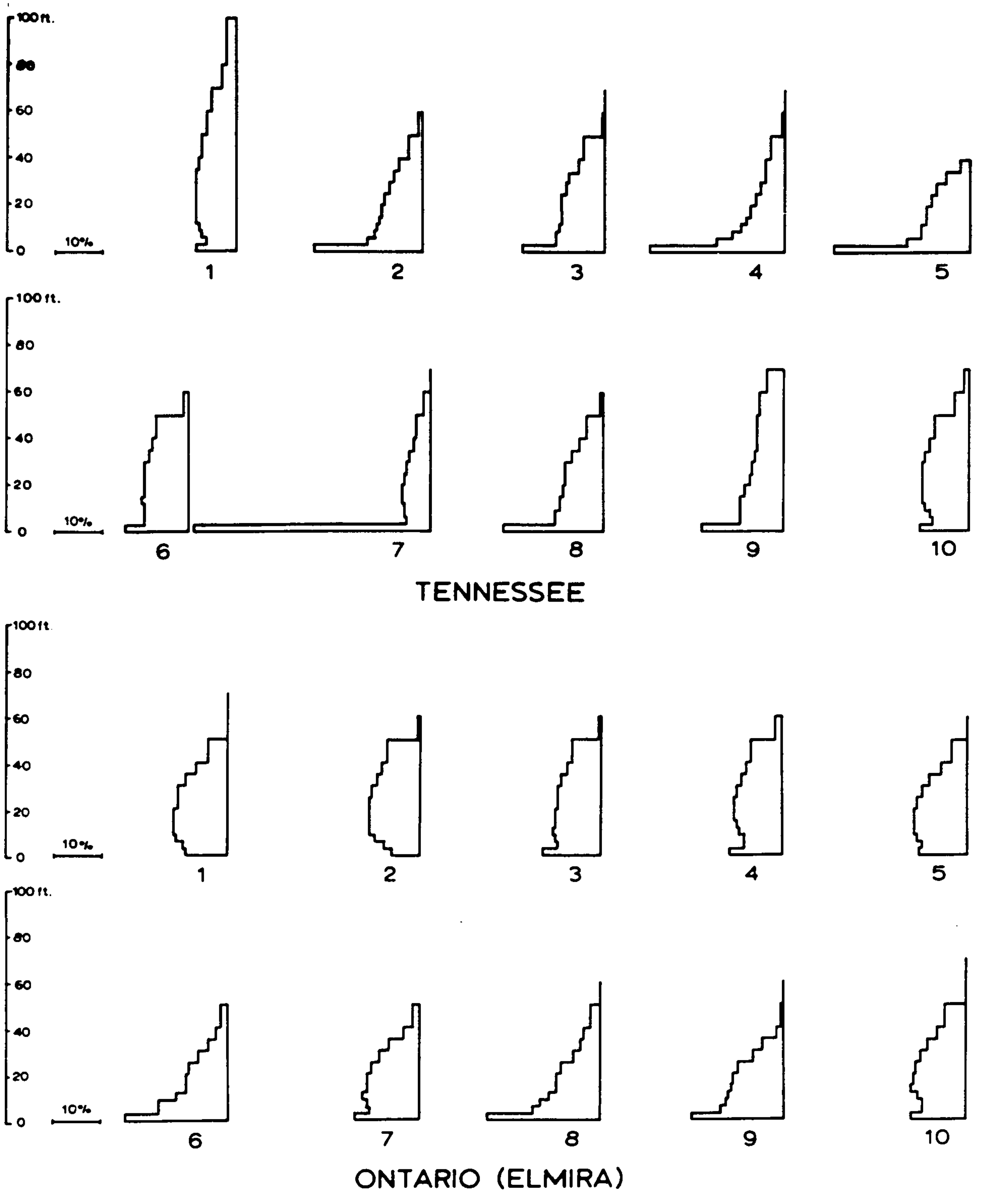


Figure 4. Profiles showing the percentage vertical distribution of life-forms in Tennessee and Elmira. Note, in Tennessee, the greater proportion of low life-forms, the greater incidence of life-forms over 60 feet, and the greater variability among profiles.

enclosed by each profile represents 100 per cent of the life-forms from lowest perches to top. The percentage of usable life-forms at any height can be determined by inspection. The points of main importance from Figure 4 are the following: 6 of 10 Tennessee home-ranges contained life-forms higher than 60 feet, compared with 2 of 10 at Elmira; Tennessee home-ranges show a higher percentage of their total-life-forms at heights between 0 and 10 feet; and the variability among the Tennessee profiles appears greater than that among Elmira profiles -- those of Elmira, with the exception of No. 6, 8, and 9, are basically similar.

The results of this section show that differences in home-ranges between Tennessee and Elmira take the form of differences in size, differences in frequency of occurrence of some life-forms and substrates, and differences in the vertical distribution of life-forms.

CATALOGUE AND FREQUENCY OF OBSERVED BEHAVIOUR

Only gross behavioural patterns were recorded during systematic observations of selected birds. For convenience, these have been divided into (a) activities, i.e., patterns involving overt movement, (b) vocalizations, and (c) social contacts and displays, i.e., relationships actually or potentially involving conspecifics. Only behaviours that were observed are included; they are described below.

(a) Activities

Flying -- Straightforward flight only; "hovering" or "flutter-diving" was excluded.

Hovering -- This was seen rarely during feeding.

Hover-flight -- This locomotory pattern was usually associated with "flight-song". Less forward motion resulted than in normal flying, and the wings were beat at a fast rate suggesting hovering. The flight path was most often a slow descent about 30° below horizontal. However, I observed both horizontal and ascending flight paths. The head was held up and back and the breast forward with the feathers somewhat fluffed.

Flutter-diving -- This, like hovering, was observed only in a feeding context. It was not a dive as such, but a very rapid vertical descent. It was a common locomotory behaviour used when dropped food was recovered.

Hopping -- Hopping was the usual means of locomotion on the ground; it was seen less often in other life-forms.

Foraging -- Hopping could be accompanied by food-seeking movements.

Foraging also occurred among the foliage of trees or in other life-forms. In general, it included any behaviour when the bird appeared to be searching for food (whether food was actually observed).

Feeding -- Feeding was defined as the observation of food held briefly in the bill of a foraging bird prior to and during ingestion.

Food-carrying -- This was defined as the holding of food in the bill without attempting to ingest it.

Nest-building -- Any aspect of manipulation of material or construction at a nest site was included.

Foraging (nest-material) -- Any behaviour similar to foraging, where nest-material rather than food was seen to be the object.

Carrying (nest-material) -- Any behaviour involving the holding or carrying of nest-material, excluding manipulation at the nest-site.

Perching -- Defined as the absence of locomotory or other activity involving definite motion of the bird, this could occur on the ground as well as on the branches of trees or parts of other life-forms.

Preening -- Preening included any general behaviour involving manipulation of parts of the plumage with the bill.

Scratching -- This included any scratching of the head or other parts with the feet. Head-scratching was always indirect, i.e., over the wing.

Pecking at bands -- This was defined as any contact of bands and bill where the bill was moved towards the bands rather than vice versa.

Bill-wiping -- This included the rubbing of facial parts (fairly uncommon) on branches, etc., as well as the more common bill-wiping movement.

Shower-bathing -- Drying or bathing movements of a bird during a rain shower.

Leaf-bathing -- Typical bathing movements performed in foliage.

(b) Vocalizations

Singing -- All typically loud advertising song was included except the following.

Counter-singing -- If two birds could be heard singing the same song-type, they were said to be counter-singing. This did not necessarily imply duetting or regular antiphonal singing. (I have, however, heard both in this species.)

Weak singing -- Like singing but with incomplete songs, usually delivered with less volume.

Weak counter-singing -- The same as weak singing whenever another cardinal could be heard singing the same song type.

Muted singing -- Like singing, with little volume; the songs, although complete, were only audible if the listener were close to the bird.

Muted counter-singing -- Like muted singing when the song type was similar to that of another singing cardinal.

Flight-song -- Any song uttered while the bird was in flight. Usually the song was associated with the hover-flight but, occasionally, a song was given during normal flight. In the latter case, the regular undulating pattern of flight was disrupted when the bird sang.

Silent -- No vocalization of any kind.

Silent between songs -- A brief silent pause between songs within a bout of singing.

Silent between counter-songs -- As above, with a counter-singing bird audible.

Chipping -- Any of several loud call notes, excluding "chattering" and "chatting".

Chattering -- A series of high staccato call notes. This is undoubtedly the vocalization that Shaver and Roberts (1933) described as "rattling notes that resembled the sound made by shaking small metallic balls in a globe."

Chatting -- High call notes, very similar to the elements of chattering but given slowly.

Soft chipping -- Very high pitched chipping notes delivered softly and in very rapid succession. This was usually associated with copulation.

(c) Social contacts and displays

Wing-roll -- The bird, usually presenting a lateral aspect to another, rolled the body on its longitudinal axis and fluttered one wing so that the light-coloured under-wing coverts were alternately covered and exposed, producing a flashing effect. At high intensity, both wings may be fluttered, the lower one not so vigorously, and the tail may be fanned and held in an almost vertical plane.

Sway -- The crest was held erect and the neck somewhat stretched, giving the body an elongated aspect. Rigidity was maintained while the bird swayed from one side to the other.

Sidle -- One bird may approach another by sidling along a branch towards it. This was observed only once.

Flatten -- With crest depressed and plumage sleeked, a bird lowered its body so that it was almost horizontal.

Following -- In flight, one bird may fly close behind another without appearing to chase or overtake it. There was a definite impression that distance was being maintained.

Chasing -- This was quite distinct from following, and it usually involved birds of the same sex.

Courtship-feeding -- Any passage of food to a non-young bird away from the nest.

Soliciting -- Wing fluttering and crouching behaviour typical of young passerines in begging for food, except that the bill may be closed. This behaviour was seen in female and rarely in male cardinals.

Copulating -- Any mounting of female by male was considered copulation.

Fighting -- Physical contact must be involved.

The amount of time spent in the field is shown in Table 15.along with the disposition of different types of observations. Despite bright plumage and loud song, male cardinals are often difficult to find and to observe continuously because of the obscuring foliage that they frequent. In one case in Tennessee, a banded male, although singing sporadically, was glimpsed only twice in three hours of searching the four wooded acres where he was known to be. No further observations were attempted, and the bird was excluded from analysis (also excluded from Table 15). Similarly, one bird at Elmira was excluded because I could not find it in 50 acres of densely forested cedar swamp after four hours' searching.

Unless a bird was singing or calling, it was often impossible to find. This introduced a certain bias into the recorded behaviour as observations of silent birds were usually preceded by vocalizations.

Table 15 shows that in Tennessee the locations of resident males were known 44.0 per cent of the time spent searching for them (162.2 hours). At Elmira, their locations were known 42.9 per cent of the 180.7 hours spent searching. However, the males were actually seen only 21.9 per cent of the total time spent searching in Tennessee and 14.1

TABLE 15

SUMMARY OF FIELD OBSERVATIONS ON 10 HOME-RANGES IN TENNESSEE AND ELMIRA

	Tennessee	Elmira
Total time spent in field (hours)	162.2	180.7
Number of potential observations†	38,928	43,368
Total observations where location of resident male was known and vocalizations recorded	17,128	18,605
Percentage of total field time	44.0	42.9
No. observations when male actually seen	8,526	6,121
Percentage of total observations	49.8	32.9
Percentage of total field time	21.9	14.1
No. of additional observations:		
Resident female	4,128	526
Foreign males and females	3,666	0
Total bird-observations	24,922	19,131

† Since observations were made at 15-second intervals, a total of 240 per hour could be made.

per cent at Elmira. I think that this difference reflects two conditions: the larger areas occupied by cardinals in Ontario, and the greater amount of dense coniferous foliage.

In Tables 16 to 18, the distribution of different activities, vocalizations, and other behavioural relationships of resident males is shown for Tennessee and Elmira. From examination of these tables, it can be seen that most behaviours occurred relatively infrequently, or at

TABLE 16

DISTRIBUTION OF OBSERVED BEHAVIOUR BY RESIDENT MALE CARDINALS IN TENNESSEE AND ELMIRA

Behaviour	Tennessee		Elmira	
	Number of observations	Per cent of total	Number of observations	Per cent of total
Flying	585	6.86	98	1.60
Hovering	7	0.08	0	0.00
Hover-flight	3	0.04	0	0.00
Flutter-diving	8	0.09	0	0.00
Hopping	421	4.94	229	3.74
Foraging	3,383	39.67	2,420	39.54
Feeding	227	2.66	10	0.16
Food-carrying	116	1.36	0	0.00
Nest-building	0	0.00	0	0.00
Foraging (nest-material)	0	0.00	0	0.00
Carrying (nest-material)	8	0.09	0	0.00
Perching	3,295	38.64	3,211	52.46
Preening	299	3.51	110	1.80
Scratching	15	0.18	12	0.20
Pecking at bands	24	0.28	21	0.34
Bill-wiping	28	0.33	0	0.00
Shower-bathing	0	0.00	0	0.00
Leaf-bathing	8	0.09	0	0.00
Wing-roll	9	0.11	0	0.00
Sway	8	0.09	0	0.00
Sidle	1	0.01	0	0.00

(continued)

TABLE 16

(CONTINUED)

Behaviour	Tennessee		Elmira	
	Number of observations	Per cent of total	Number of observations	Per cent of total
Flatten	11	0.13	1	0.02
Feeding young	9	0.11	0	0.00
Courtship-feeding	44	0.52	8	0.13
Soliciting	9	0.11	0	0.00
Copulating	3	0.04	2	0.03
Fighting	5	0.06	0	0.00
Totals	8,526	100.00	6,121	100.00

TABLE 17

DISTRIBUTION OF RECORDED VOCALIZATIONS BY RESIDENT MALE CARDINALS IN TENNESSEE AND ELMIRA

Vocalization	Tennessee		Elmira	
	Number of observations	Per cent of total	Number of observations	Per cent of total
Singing	1,817	10.61	2,154	11.58
Counter-singing	513	3.00	76	0.41
Weak singing	291	1.70	56	0.30
Weak counter-singing	7	0.04	2	0.01
Muted singing	138	0.81	95	0.51
Muted counter-singing	16	0.09	0	0.00
Flight-song	5	0.03	2	0.01
Silent	8,476	49.48	7,384	39.69

(continued)

TABLE 17

(CONTINUED)

Vocalization	Tennessee		Elmira	
	Number of observations	Per cent of total	Number of observations	Per cent of total
Silent between songs	2,434	14.21	7,218	38.80
Silent between countersongs	548	3.20	130	0.70
Chipping	2,722	15.88	1,484	7.97
Chattering	104	0.61	0	0.00
Chatting	54	0.32	4	0.02
Soft chipping	3	0.02	0	0.00
Totals	17,128	100.00	18,605	100.00

TABLE 18

NUMBER OF INTERACTIONS OR POTENTIAL INTERACTIONS INVOLVING RESIDENT MALE CARDINALS IN TENNESSEE AND ELMIRA

Interaction	Tennessee	Elmira
	Number of observations	Number of observations
Following mate	79	15
Followed by mate	5	0
Chasing	108	0
Chased	47	0
Others singing	6,815	294
Others chipping	1,565	1,364
Other males present	388	0
Other females present	147	0
Mate present	4,446	3,730
Young present	9	0
Young calling	226	0

least were recorded infrequently. For example (Table 17), only singing, silent, silent between songs, and chipping occurred more than ten per cent of the time the bird's location was known. (It should be noted that these figures do not represent the percentage of total time -- see Table 15.) The percentage of singing was about the same in Tennessee (10.61) as Elmira (11.58). However, the percentage of silence between songs was different (Tennessee, 14.21; Elmira, 38.80). This suggests that approximately the same number of songs were given in both regions, but that at Elmira they were given more slowly and hence birds spent proportionally more time in singing behaviour.

Among observed behaviours, only perching and foraging occurred in more than ten per cent of the observations (Table 16). Since perching is the most frequent posture associated with singing, it is likely that it is also measuring singing activity as well as "loafing".

Therefore, the utilization of habitat was determined only for the two activities that occurred most frequently, singing and related behaviour, and foraging.

UTILIZATION OF HABITAT

Habitat was measured not only in terms of life-forms but on the basis of the heights of life-forms occurring within the home-range. Field measurements of height, made as accurately as possible, were converted for analysis to one of 18 height classes between 0 and 100 feet. By using a system of height classes for all measured heights of life-forms and birds, it was thought that errors of measurement would be minimized and calculations made easier. The height of the canopy bottom or lowest potential perches of each life-form permitted the mapping of the highest and lowest parts of a life-form that a cardinal could use. Thus, by amalgamating the extremes from 20 home-ranges, 110 categories were obtained, each resulting from a unique combination of life-form and height class (Figure 5).

Analysis of habitat utilization using a modification of the methods of MacArthur and MacArthur (1961) and Klopfer (1965) was restricted to behaviour associated with singing and foraging, for reasons presented in the previous section. For this purpose, the following previously defined vocalizations were considered to comprise singing behaviour: singing, counter-singing, weak singing, weak counter-singing, muted singing, muted counter-singing, silent between songs, and silent between counter-songs. All observations involving any of these vocalizations were used. The discrimination index H was calculated for each stratum in a bird's home-range using the categories of Figure 5 that occurred in the stratum. An average H value for the bird was obtained by taking

HEIGHT CLASS (FT)	TREE	SHRUB	WOODY CUSHION	VINE-TANGLE	BRUSH PILE	OTHER WOODY VEGETATION	FORB	GRAMINOID	POLE	HORIZONTAL LINE	HORIZONTAL LIMB	BUILDING	GROUND
80 - 100		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
70 - 80		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
60 - 70		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
50 - 60		▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨
40 - 50			▨	▨	▨	▨	▨	▨	▨		▨	▨	▨
35 - 40			▨	▨	▨	▨	▨	▨			▨	▨	▨
30 - 35				▨	▨	▨	▨	▨			▨		▨
25 - 30				▨	▨	▨	▨	▨			▨		▨
20 - 25				▨	▨	▨	▨	▨			▨		▨
15 - 20				▨	▨	▨	▨	▨			▨		▨
12 - 15				▨		▨	▨	▨			▨		▨
9 - 12				▨		▨	▨	▨			▨		▨
6 - 9				▨		▨	▨	▨			▨		▨
3 - 6						▨							▨
1.5 - 3						▨							▨
0.8 - 1.5						▨							▨
0 - 0.8			▨										▨
0			▨						▨	▨	▨		

Figure 5. The unshaded portion represents the maximum possible number of categories that could be found in a home-range. Each category results from a unique combination of life-form and height class. The distribution is based on extremes found in 20 home-ranges. Note that the total range of height is not divided equally among height classes.

the weighted average of the stratum H values for the home-range. The number of observations of singing behaviour in a stratum served as the weights for that stratum.

The H values obtained for birds in Tennessee and Elmira are shown in Table 19. The mean value ($\overline{H}$) of the discrimination index for Tennessee was 0.7462 while that for Elmira was 0.7975. The difference between these values is not statistically significant (Mann-Whitney U test). Thus, it was concluded that males showed no difference in degree of diversity of utilization or in discrimination of the various elements of their habitats between Tennessee and Elmira.

However, the high value of $\overline{H}$ suggests that birds discriminated strongly in the use of the various defined portions of their habitats. My general impressions of cardinals in the field supported this interpretation. Singing was influenced by the activities of other birds. For example, a male cardinal that had been foraging silently on the ground for some time, upon hearing a song from a neighbour, occasionally uttered his first few songs from the ground or low vegetation. He then gradually worked his way higher into the trees and eventually continued and concluded his bout of singing from a high perch.

A similar analysis was made of foraging behaviour, which included feeding and foraging as previously defined. The results are presented in Table 20. The mean H value for Tennessee was 0.7838; that for Elmira was 0.9136. These values are significantly different ($P<0.05$). Again, a high discrimination was being shown for various elements of habitat, with birds at Elmira showing greater discrimination than those in Tennessee.

It should be recalled that the Elmira area was selected because of

TABLE 19

DISCRIMINATION INDICES (H) FOR SINGING BEHAVIOUR OF TEN MALE CARDINALS IN TENNESSEE AND ELMIRA

Tennessee		Elmira	
Bird No.	H	Bird No.	H
1	0.5477	1	0.7588
2	0.8273	2	0.7281
3	0.6882	3	0.7936
4	0.8394	4	0.8671
5	0.4759	5	0.7938
6	0.8590	6	0.8002
7	0.8796	7	0.8711
8	0.7631	8	0.7409
9	0.8829	9	0.8236
10	0.6987	10	0.7975
Mean	0.7462		0.7975
Median	0.7952		0.7956

TABLE 20

DISCRIMINATION INDICES (H) FOR FORAGING BEHAVIOUR OF TEN MALE CARDINALS IN TENNESSEE AND ELMIRA

Tennessee		Elmira	
Bird No.	H	Bird No.	H
1	0.8022	1	0.9810
2	0.8604	2	0.7802
3	0.8014	3	0.9785
4	0.6455	4	0.9463
5	0.5656	5	0.9810
6	0.6935	6	0.9135
7	0.8562	7	0.9675
8	0.8267	8	0.8162
9	0.8455	9	0.8580
10	0.9405	10	†
Mean	0.7838		0.9136
Median	0.8238		0.9463

† This value was not computed as it was based on fewer than 120 observations.

its high percentage of coniferous vegetation. Therefore, it was of interest to determine whether differences in behaviour were also related to type of foliage. The proportional amounts of time spent by singing males in life-forms of known foliage types are shown in Table 21. It is apparent that Elmira birds were either avoiding coniferous foliage or showing preference for other foliage types, as only 4.75% of singing time was spent in the coniferous foliage, which comprised 24.33% of the total available. In Tennessee, the difference was not so great relative the small amount of coniferous foliage (2.91% of time spent in 6.47% of foliage). The same is true, even more markedly, of foraging behaviour (Table 22). Elmira cardinals foraged 1.90% of the time in 22.81% of the foliage, and Tennessee cardinals foraged 4.94% of the time in 6.47% of the foliage.

Observations of other behaviour of Elmira birds, although not analyzed quantitatively, suggested no obvious differences in utilization of habitat. In general, where coniferous vegetation occurred, it was used for most behaviour, except foraging and singing as previously shown. It should be pointed out, however, that foraging sites, perhaps more than those used for other behaviour, underwent strong seasonal influence. The Cardinal is an opportunistic feeder, as probably are most fringillids. Early in the season, most foraging occurred on the ground in freshly cultivated fields, old grassy meadows, or among the leaf-litter of the forest floor. As the season progressed, foraging sites presumably followed the availability of food. Buds of trees were nibbled between song phrases. When the canopy was fully developed, cardinals foraged among the leaves for insect larvae. Individuals tended to exploit whatever was growing or available in the region of their territory, and in

TABLE 21

TIME SPENT SINGING IN LIFE-FORMS WITH CONIFEROUS FOLIAGE

Home-range	Tennessee			Elmira		
	Number of observations	Time spent in conifers*	% conifers present†	Number of cbservations	Time spent in conifers*	% conifers present†
1	113	0.0	1.0	221	0.0	2.4
2	276	19.6	22.0	430	6.0	22.1
3	666	3.4	1.6	202	0.0	11.4
4	599	0.0	6.8	181	0.0	26.4
5	480	0.0	0.0	632	6.6	53.8
6	496	0.0	9.0	148	13.5	21.7
7	122	5.5	9.9	376	0.0	35.9
8	132	0.0	6.0	603	21.4	25.0
9	234	0.6	3.0	318	0.0	37.6
10	84	0.0	5.4	64	0.0	7.0
Mean		2.91	6.47		4.75	24.33

* Expressed as a percentage of total time spent singing in life-forms with either coniferous or non-coniferous foliage.

† Figures obtained from Table 11.

TABLE 22

TIME SPENT FORAGING IN LIFE-FORMS WITH CONIFEROUS FOLIAGE

	Tennessee			Elmira		
Home-range	Number of observations	Time spent in conifers*	% conifers present†	Number of observations	Time spent in conifers*	% conifers present†
1	177	0.0	1.0	45	0.0	2.4
2	125	4.0	22.0	38	0.0	22.1
3	217	9.2	1.6	40	5.0	11.4
4	124	0.0	6.8	17	5.9	26.4
5	477	0.0	0.0	0	††	53.8
6	196	0.5	9.0	74	0.0	21.7
7	31	25.8	9.9	46	4.3	35.9
8	35	0.0	6.0	55	0.0	25.0
9	89	0.0	3.0	68	0.0	37.6
10	25	0.0	5.4	0	††	7.0
Mean		4.94	6.47		1.90	22.81

* Expressed as a percentage of total time spent foraging in life-forms with either coniferous or non-coniferous foliage.

† Figures obtained from Table 11.

††Never observed foraging in these life-forms; corresponding value excluded in calculation of mean percentage of conifers present.

Tennessee frequently trespassed silently into a neighbour's territory to feed.

The discrimination shown by a male in almost any behaviour was probably lessened by the presence of his mate. The male generally followed and accompanied the female when she left the nest. The home-range, as determined by observations of the male when the female was not present, was often exceeded by the female, e.g., when she left the nest to forage. At such times, a female may fly well into the territory of a neighbouring male. This led to many violent encounters for males in the dense Tennessee population. A female, on entering another male's territory, was rarely attacked, except by the resident female if present, while her mate was attacked persistently. A male driven out of the territorial region of a neighbour had to then enter it again and again until his female left with him. Likewise, the foraging and other habits of the male as well as his locations tended to be similar to those of the female when she was in his company. This presumably resulted in a greater diversity of habitat utilization by a male than that shown by an unaccompanied bird.

To obtain further information on the utilization of song-perches by male cardinals, an analysis of their heights was made. Table 23 shows the mean height of singing for males on the 20 home-ranges studied. The mean height in Tennessee was 27.05 feet and at Elmira was 32.85 feet. The respective coefficients of variation were 24.9 and 13.8 per cent. The difference between the two means is significant ($P<0.05$). Also shown in Table 23 are the mean ratios of singing height to height of life-form used, a measure of the bird's position relative to the maximum height of potential song-perches. The mean valuesfor Tennessee and

TABLE 23

AVERAGE AND RELATIVE HEIGHTS OF SONG-PERCHES USED BY MALE CARDINALS

Home-range	Tennessee Number of observations	Tennessee Mean height(ft)	Tennessee Song/height ratio*	Elmira Number of observations	Elmira Mean height(ft)	Elmira Song/height ratio*
1	137	31.1	0.77	233	29.0	0.71
2	276	28.4	0.76	386	37.8	0.77
3	564	34.9	0.84	219	34.1	0.79
4	635	27.0	0.80	215	38.2	0.78
5	487	13.2	0.71	601	36.1	0.79
6	499	31.9	0.80	145	22.9	0.84
7	122	18.7	0.69	378	34.2	0.79
8	141	28.5	0.79	593	31.8	0.83
9	236	24.0	0.73	318	33.4	0.77
10	127	32.8	0.76	120	31.0	0.75
Mean		27.05	0.765		32.85	0.782
S.E.		2.13	0.0142		0.157	0.0117
Coeff. of variation		24.9%	6.0%		13.8%	4.7%

* Singing height divided by height of life-form.

Elmira were 0.765 and 0.782; their coefficients of variation were 6.0 and 4.7 per cent. The difference between these means is not significant ($P<0.40$). Thus, singing heights of Tennessee cardinals were more variable and, on the average, were lower than at Elmira. But the similar ratios suggest that life-forms were used in the same manner regardless of height.

Of all locations used for activities by birds, the nest-site is unique in its fixity. However, the numbers of nests (16 in Tennessee; 6 at Elmira) found within home-ranges of birds studied are too small for a quantitative appraisal of selection of nest-site. Only two of the nests found in Tennessee were in coniferous trees (red cedar). The home-ranges containing these nests had a measured frequency of one, and five per cent coniferous vegetation compared with that of broad-leaved vegetation, which was 63 and 68 per cent respectively. All nests (8) at Elmira were found in coniferous trees (white cedar). The average frequency of occurrence of such vegetation in home-ranges where nests were found was 17.5 per cent; broadleaved vegetation comprised 49.5 per cent. The variability of these cover types is shown in Table 11.

The heights of 29 nests were measured in Tennessee. These measurements were divided into two groups: nests found before 15 May and nests found on 15 May or later. The 11 early nests ranged from 1.5 to 13 feet with a mean of 4.21±0.885 feet. The 18 late nests ranged from 2.2 to 28 feet with a mean of 6.65±1.40 feet. Early nests were significantly less variable in height than late ones. The increase in variability was largely due to one very high (28 feet) nest. In view of this high variability, the median values of 3.8 and 5.1 feet were considered to be of more descriptive value than the means. These data suggest a slight rise in nesting height later in the season, but differences between mean or median heights are not statistically significant. At Elmira, eight nests ranged in height from 4.0 to 9.0 feet with a mean of 5.39±0.653 and a median of 4.5 feet.

DISTRIBUTIONAL ASPECTS

As a result of using the song-sampling technique in different parts of southern Ontario in 1965 as well as sampling four 30-mile line transects by the same method in 1966, I was able to map the edge of the species' range with fair accuracy (Figure 6). Using either the number of birds responding or the number per 100 hectares of wooded cover, inspection of Figure 6 shows a gradient of density across southern Ontario from west to east. The unexpected difference between New York state and the adjacent region of Ontario may be due to the heavily industrialized urban area along the Niagara River acting as a buffer to the recent population increase in New York described by Beddall (1963). A similar area was suggested as acting as a barrier to cardinals on Long Island, New York, by McKeever (1941: 111). This work suggested a fairly abrupt edge to the range in southern Ontario, which was not correlated with suitability of vegetation or other factors obvious at the time of sampling.

Attention was then turned to an examination of factors possibly limiting distribution in this region. As mentioned previously, the study area near Elmira was selected because it was near the edge of the range and because it was intermediate between broadleaved forest to the west and much coniferous forest to the east. This difference in vegetation is perhaps the most obvious one in the region. The four study areas were re-examined to determine if correlates existed between the presence of cardinals and other physical features: vegetation, elevation, distance, etc.

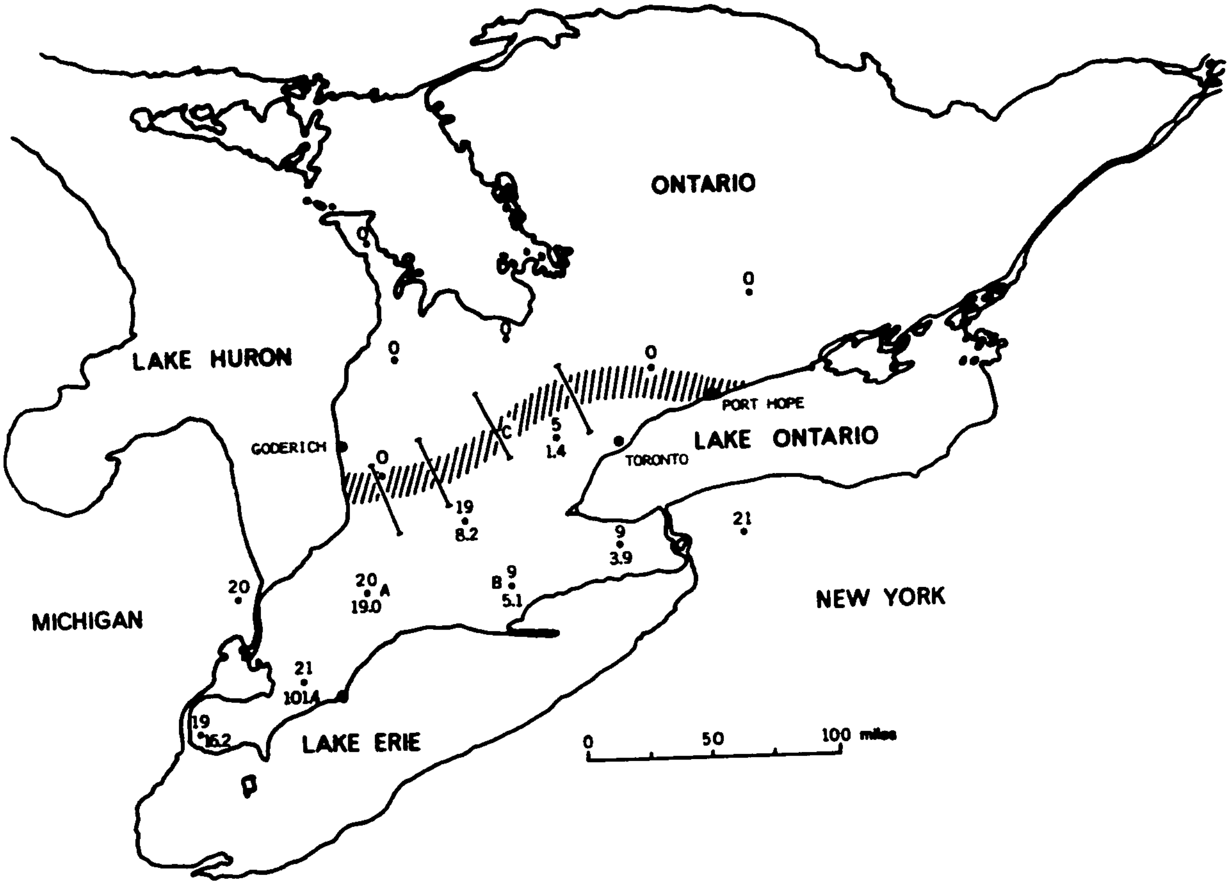


Figure 6. Each solid circle shows the centre of a sample area of 20 points. The total number of birds recorded at each point is shown above its location. The figure below the location is the number of birds per 100 ha. of woody cover, where cover was measured from aerial photographs in a circle of one-quarter mile radius about each sample point. Letters A, B, and C indicate the approximate centre of the study areas, i.e., Melbourne, Simcoe, and Elmira respectively. The cross-hatched zone shows the edge of the Cardinal's range based on four 30-mile transects in August 1966 in addition to the figures shown. Locations of transects are indicated by lines. A few small, extralimital populations are known to the north and east of this area.

The first step was to determine if cardinals tend to be found in clusters, particularly in regions of low overall density, or if they are spread evenly throughout the area. This presented a problem, particularly in the Elmira area, as almost all cells with positive response had only one bird responding, so that direct comparisons tended to be meaningless. To overcome this difficulty, I took into account the responses at adjacent points and calculated a new value for each point sampled. This value I called a cluster-index as it reflected the amount of clustering in the vicinity of the sample point.

The cluster-index (CI) weighted each sample point in the study area according to the number of responses at the point, the number af adjacent points, and the number estimated for adjacent points that were not sampled.

$$CI = X + Y + \frac{Q}{2} \cdot \frac{X}{P}$$

where: X = the total number of birds in adjacent cells,
Y = the number of birds in the main cell,
P = the number of adjacent cells sampled, and
Q = 8 - P.

Each study area was divided into 25 equal-sized cells for analysis. Each cell contained several cluster-indices, and their average values were compared using the Kruskal-Wallis one-way analysis of variance (Siegel, 1956). The averages are shown in Figure 7; these were found to differ significantly ($P<0.001$) in each area. Biologically, this meant that in all study areas, although cardinals could be found in any part, their density differed from one part to another. What then

2.93	5.81	4.63	0.86	6.12
2.80	3.83	4.23	5.50	5.20
5.70	4.88	3.46	5.78	7.46
8.50	15.8	9.40	12.8	9.12
7.96	7.25	4.48	1.75	7.99

ONTARIO (MELBOURNE)

3.62	3.94	2.24	3.70	1.44
0.33	4.44	4.30	1.25	3.41
0.00	1.91	3.47	1.41	3.33
3.22	2.52	3.43	3.00	0.95
0.00	0.33	3.82	0.00	0.17

ONTARIO (SIMCOE)

28.3	29.4	34.2	18.5	24.8
29.9	31.2	28.6	33.7	31.1
37.4	31.0	33.6	28.8	30.4
36.3	30.8	37.1	35.6	31.8
25.7	29.6	29.7	31.6	33.9

TENNESSEE

0.00	1.35	0.51	2.99	1.32
0.00	0.00	2.03	1.70	0.63
0.75	2.33	1.83	0.86	2.40
0.46	1.38	1.08	0.73	2.86
1.18	4.75	3.54	1.73	1.95

ONTARIO (ELMIRA)

Figure 7. The average cluster-index is shown for the points occurring within each cell of four study areas. A significant difference ($P<0.001$) was found among the cells of each area.

caused these local differences in density? Were they due to differences in vegetational cover within the areas or was some other factor involved? But I have shown previously that habitat requirements per se do not seem to limit distribution, or, at least, cardinals can apparently utilize quite different types of vegetation in different regions.

In addition to the distribution of cover as a possible limiting factor, it was thought that other factors might perhaps be mediated through elevation. From aerial photographs I measured the amount of woody cover available at each point sampled in the study areas. As I had noticed that river edges usually contained cardinals, I measured the direct distance from the sample point to the nearest river system and recorded the difference in elevation of the sample point and the elevation of the river.

Spearman rank correlation coefficients were calculated for the variables measured in all four study areas (Table 24). In Ontario, the correlation of cluster-index with distance to nearest river was consistently the highest of those pairs involving the cluster-index (-0.308, -0.308, and -0.504). These values are all significantly different from zero ($P<0.001$). There was no consistent pattern of significant correlations between cluster-index and other variables measured. The correlation coefficients between all pairs of variables are included in Table 24 to provide some indication of the general interactions. In Tennessee, where cardinals were found in all types of wooded cover ranging from immense cypress swamps to straggling hedgerows, no such significant correlation was found between birds and rivers. Thus, there is statistical support for the observed association of high Cardinal density and riparian situations, at least in peripheral

TABLE 24

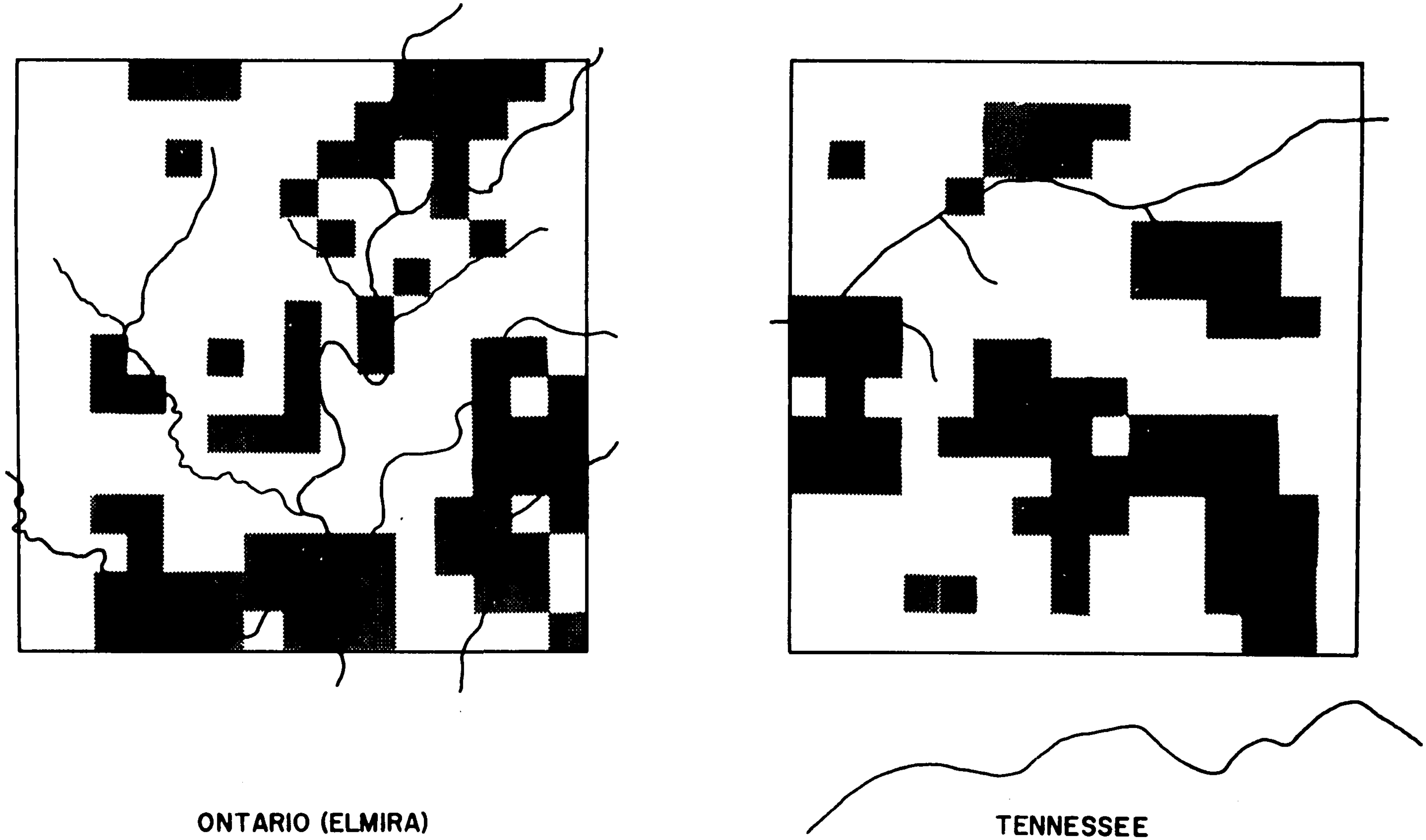
SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN FACTORS
MEASURED IN FOUR STUDY AREAS

	Ontario			Tennessee
	Melbourne	Simcoe	Elmira	
Cluster-index and distance to river	-0.308***	-0.308***	-0.504***	0.065 NS
Cluster-index and elevation above river	-0.120 NS	-0.015 NS	-0.208*	-0.200*
Cluster-index and amount of cover	0.280***	0.016 NS	0.003 NS	0.061 NS
Distance and elevation	0.593***	0.190*	0.224**	0.458***
Distance and cover	-0.159*	-0.123 NS	0.061 NS	0.200*
Elevation and cover	-0.228	-0.091 NS	-0.175*	0.405***

*** $P<0.001$; ** $P<0.01$; * $P<0.05$ in test of whether r_s differs from zero.

populations. The relationship between density and river systems is illustrated in Figure 8 for Tennessee and Elmira, the two extremes of density studied.

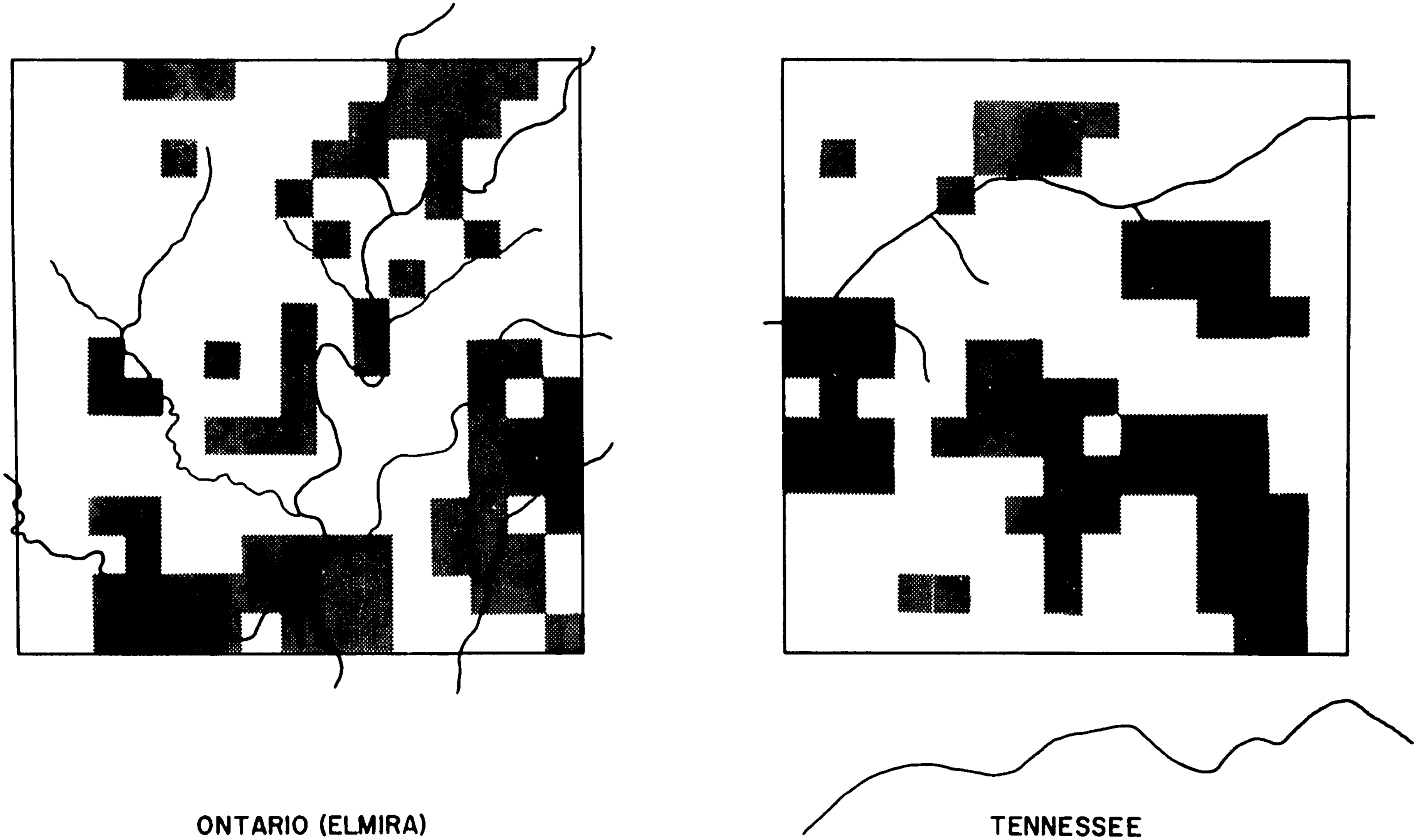
An examination of the edge of the range is southern Ontario in July and August of 1967 was made to obtain more information on possible limiting factors. I examined the distribution of the Cardinal in a zone with boundaries 16 miles south and 16 miles north of a line representing the edge of the range (Figure 6). This zone started at the shore



ONTARIO (ELMIRA)

TENNESSEE

Figure 8. Relationship between cluster-indices and river systems in the study areas of extreme densities. Shaded regions represent cells having cluster-index values equal to or greater than the median value.



ONTARIO (ELMIRA)

TENNESSEE

Figure 8. Relationship between cluster-indices and river systems in the study areas of extreme densities. Shaded regions represent cells having cluster-index values equal to or greater than the median value.

of Lake Huron and extended about 73 miles east. It was divided into a grid by north-south lines every four miles intersecting nine lines that paralleled the edge of the range and were also four miles apart. This resulted in 171 intersections. Sample points were defined as "patches" of vegetational cover nearest the mapped intersections that I deemed sufficiently large to support cardinals. These were determined by inspecting topographic maps. The location of the sample points is shown in Figure 9.

All sample points were visited on foot during the first four hours of daylight. An amplified tape-recording of a cardinal song was played, and if no bird responded within five minutes of intermittent playing and listening, the species was considered to be absent from the area. Visual estimates of the percentage of coniferous vegetation were made, and the following information was recorded: latitude; longitude; elevation, in feet above sea level; elevation, in feet above the nearest river; and distance to the nearest river or lake shore. Since it seemed reasonable to assume that the wooded banks of a river or creek were of more importance to a dispersing or settling cardinal than the river or creek per se, the distance to the nearest bottomland was also measured. Bottomland is defined as low-lying land along stream courses, which is subject to flooding. It is usually wooded in this region. Distances were measured directly from soil maps prepared by The Ontario Soil Survey.

The classification of birds as present or absent is a typical dichotomized variable, and its correlation with the continuous variables can be measured by the point biserial correlation coefficient (McNemar, 1962: 192). The correlations between presence or absence of cardinals

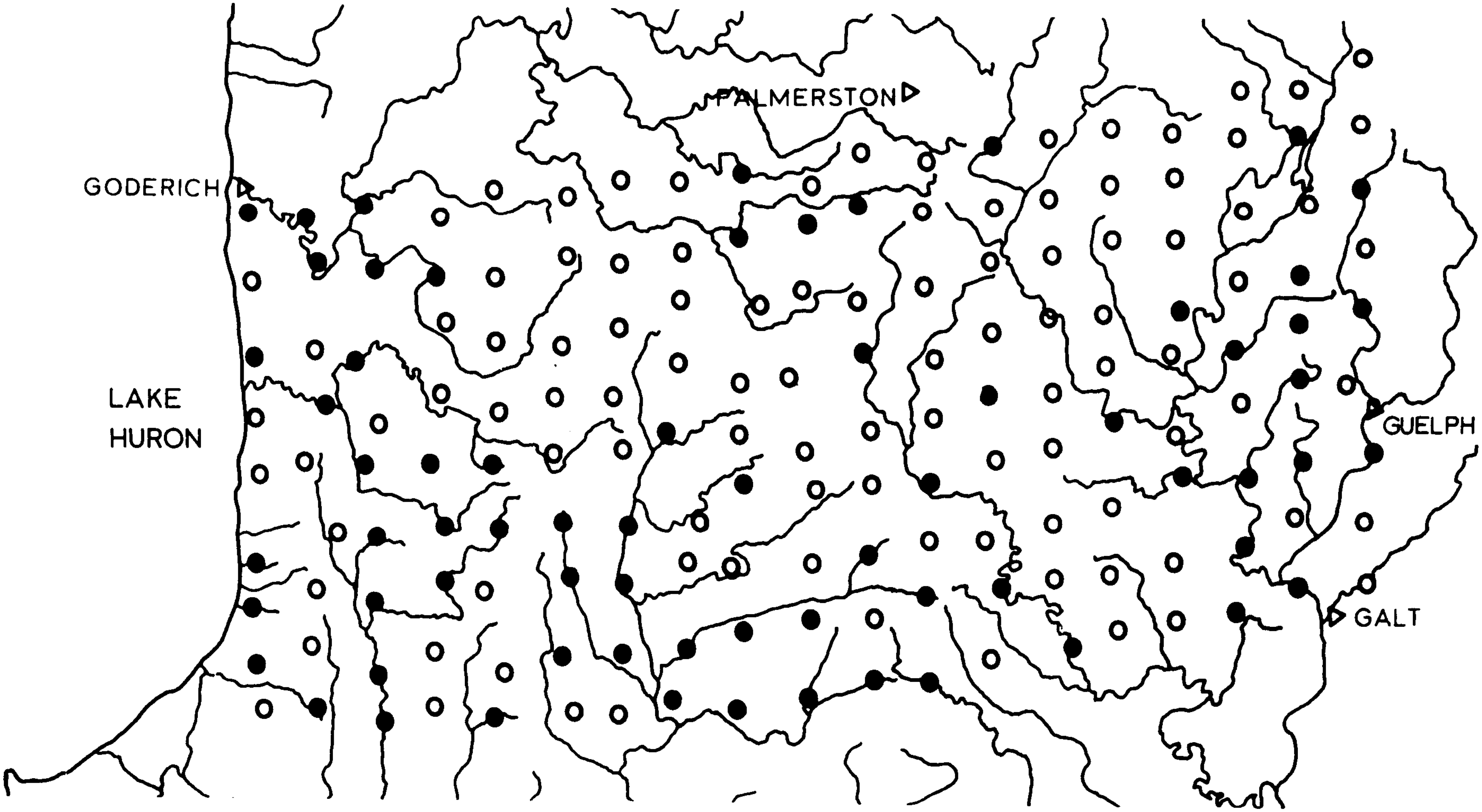


Figure 9. Distribution of sample points checked at edge of range just east of Lake Huron. Solid circles are points where birds were found; open circles points where no birds were found. Note the close association between birds and rivers. Base map: Canada Dept. Mines and Technical Surveys -- Windsor-Toronto N.W. 42/83.

TABLE 25

POINT BISERIAL CORRELATION COEFFICIENTS BETWEEN PRESENCE OR ABSENCE OF CARDINAL AND VARIOUS OTHER MEASURABLE FACTORS AT THE EDGE OF THE SPECIES' RANGE IN ONTARIO

Factor	Correlation coefficient	
Percentage coniferous vegetation	0.0062	NS
Latitude	-0.00008	NS
Standard latitude†	-0.262	**
Longitude	0.00011	NS
Elevation above sea level	-0.100	NS
Elevation above nearest river	-0.039	NS
Distance to nearest river or lake shore	-0.00017	NS
Distance to nearest creek or river	-0.00002	NS
Distance to nearest bottomland	-0.410	***

† Measured as degrees of latitude above or below edge of range.

*** $P<0.001$; ** $P<0.01$

and the other measured variables are shown in Table 25.

The non-significant correlations involving latitude and longitude and the significant one involving latitude above or below the edge of the range support the placement of the range edge in Figure 6. The low correlations with coniferous vegetation (0.0062) and elevations (-0.100, -0.039) suggest that these factors may be of little direct importance. The low correlation with distance to river or creek (-0.00002) and the highly significant one with distance to nearest bottomland (-0.410), at first sight, seems paradoxical. This is largely explained by the fact that of the 171 points examined, 39 of the 69 points at which birds were found were located in bottomland. Only nine bottomland points lacked birds.

Birds were found to be absent in areas that were similar to those in which they were present. This is hardly surprising. Information on preference for a particular type of vegetational cover or other factor by a species with a sparse population can not be obtained indirectly by examining the areas from which it is absent. It is likely, in such situations, that insufficient time has elapsed for the species to exploit much potential habitat; also there may be little dispersal owing to reduced population pressure. Therefore, the most valid information about preferred habitat is to be determined from those areas where individuals are actually established. The close association between cardinals and river systems among birds representing a most peripheral population is clearly shown in Figure 9. The vegetation at these points was varied, and in many cases was largely coniferous.

In conclusion, there seems to be good evidence for a strong association with river systems in peripheral populations that is not displayed by birds in the central part of the range, yet the type of vegetation close to these rivers does not appear of much importance as long as it is sufficient for nesting.

DISCUSSION

It might be asked if the high density of the Cardinal population that I studied in Tennessee was approaching the maximum possible for the species. The figure of 30 males per 100 acres was based on sampling the countryside in a random manner, and did not take into account the suitability of cover as potential habitat.

Densities of the Cardinal in different regions have been measured by various means. Crowell (1962) analyzed breeding bird censuses from 13 years of Audubon Field Notes and reported the Cardinal, in seven habitat types in eastern United States, to have a mean density of 16.5 pairs per 100 acres and a maximum density of 75 pairs per 100 acres. In several habitats in Bermuda, he found the density to vary from 30 to 76 pairs per 100 acres. But even higher densities have been described. Graber and Graber (1963: 493) reported densities of 160 cardinals per 100 acres in "edge shrubs" in southern Illinois, with hedgerows averaging about 240 birds per 100 acres. However, in interpreting these figures, Kendeigh's (1944: 94) criticism should be kept in mind: "In order to arrive at some common denominator for comparing the abundance of forest-edge species, it may be necessary to use length rather than breadth ... it may be desirable for a general standard to base comparisons on the unit length of one kilometer." In a species such as the Cardinal where vegetation characteristic of edge situations may be of great importance, area may be of little consequence as long as sufficient distance can be maintained between birds. For example, a density of

DISCUSSION

It might be asked if the high density of the Cardinal population that I studied in Tennessee was approaching the maximum possible for the species. The figure of 30 males per 100 acres was based on sampling the countryside in a random manner, and did not take into account the suitability of cover as potential habitat.

Densities of the Cardinal in different regions have been measured by various means. Crowell (1962) analyzed breeding bird censuses from 13 years of Audubon Field Notes and reported the Cardinal, in seven habitat types in eastern United States, to have a mean density of 16.5 pairs per 100 acres and a maximum density of 75 pairs per 100 acres. In several habitats in Bermuda, he found the density to vary from 30 to 76 pairs per 100 acres. But even higher densities have been described. Graber and Graber (1963: 493) reported densities of 160 cardinals per 100 acres in "edge shrubs" in southern Illinois, with hedgerows averaging about 240 birds per 100 acres. However, in interpreting these figures, Kendeigh's (1944: 94) criticism should be kept in mind: "In order to arrive at some common denominator for comparing the abundance of forest-edge species, it may be necessary to use length rather than breadth ... it may be desirable for a general standard to base comparisons on the unit length of one kilometer." In a species such as the Cardinal where vegetation characteristic of edge situations may be of great importance, area may be of little consequence as long as sufficient distance can be maintained between birds. For example, a density of

240 birds per 100 acres of hedgerow represents one bird per 300 yards, if the hedgerow is 20 feet wide. This probably represents an average of one pair every 600 yards. In more extensively wooded areas in Tennessee, it was not unusual to find active nests of different pairs within 100 yards of each other.

Norris (1951: 45) reported the density of cardinals in a beech-magnolia hammock in southwestern Georgia as 101.6 pairs per 100 acres. This value was based on sampling an area of 12.8 acres. Crowell's (1962) areas of representative "major habitat types" were considerably smaller, varying from 4.7 to 10.0 acres. Much caution must be exercised in extrapolating density from such tiny fragments; a change in density of one bird on a 5-acre plot is magnified to a change of 20 birds per 100 acres. From the foregoing discussion, it should be obvious that, at best, available measurements of density are crude. It is difficult to make valid comparisons between results obtained by different methods or different workers. Plot censuses probably do give more reliable estimates than strip censuses (Kendeigh, 1944: 78), but only if the plot is sufficiently large. Strip censuses, such as those I conducted, probably give results more representative of wide areas and varied habitats. Therefore, it is difficult to determine if an area of greater population density of the Cardinal could have been found since most published figures are based on sampling of very small areas. My study area contained many regions where, if small (5 to 10 acres) plots of "homogeneous" vegetation such as woodlots or forested river edges had been sampled separately, the resulting density figures would have been upward of 100 birds per 100 acres.

The most recent and extensive comparative index of population densities of the Cardinal in the breeding season is found in the results of the widespread roadside count being developed by the Migratory Bird Populations Station at Patuxent, Maryland (unpublished data). This shows a high density where I worked in Tennessee, as well as several small pockets of higher density at various widespread localities.

Related to population density, the difference in sizes of home-ranges between Elmira and Tennessee was of interest. Home-range was more easily defined than territory for field use. Territory, in the sense of an area defended against conspecifics, had little meaning in the Elmira study area, where only two males out of ten had neighbours close enough for intraspecific encounters to occur. In Tennessee, chasing occurred whenever one male encountered another, and the measurements I have given for home-range size would be only slightly larger than territory size measured in the traditional way. Birds studied near Melbourne and Simcoe, Ontario, had home-ranges larger than those of Tennessee but smaller than those of Elmira. Likewise, territories were larger than those of Tennessee, judging by observation of occasional strife between neighbouring pairs. Although these birds were unbanded, a territory size of ten acres would not be unduly large as an estimate of the average. This is about the same figure estimated by D.M. Scott (pers. comm.) for the population that he has studied on the campus of the University of Western Ontario at London. Casual observations also support the measured decrease in territory size from Elmira to Tennessee. In southern Ontario, a 10-acre woodlot was never found to support more than one pair of cardinals; whereas, in Tennessee, I found up to five pairs utilizing parts of woodlots only three acres in extent.

The average home-range size of 2.91 acres in Tennessee suggests that territory size is smaller than that of cardinals studied in Arizona (Gould, 1961: 254), where territories ranged from 3.5 to 4.1 acres. Crowell (1962: 78) reported that the "minimum" territory size on the North American mainland (based on observations of territorial behaviour presumably near Media, Pennsylvania, and Caldwell, New Jersey, but no number of observations or details of method are given) did not differ from the "maximum" territory size on Bermuda (obtained by dividing area by number of pairs). Estimates from the two areas were in the range of 1.5 to 2.0 acres. It is regrettable that his measurements of territories were not made in a similar manner. But despite this shortcoming, in view of the fact that the average _minimum_ territory size of one area did not differ from the average _maximum_ territory size of the other, his conclusion that "reduction of territory size has not occurred in proportion to increase in density" is most peculiar and seems completely unjustified.

My work suggests a definite reduction in the area occupied or utilized by cardinals under increased population density. In the absence of crowding by neighbours, home-ranges averaged 46.5 acres in the most peripheral population studied. This is very similar to the situation found in the Mockingbird (_Mimus polyglottis_), a species also actively shifting the northern limit of its range, where two pairs in Michigan were found to occupy home-ranges of 45 acres (Adkisson, 1966: 104), compared with 2.5 acres in Tennessee.

In Tennessee, territories of cardinals were adjacent and much chasing and occasional fighting by males was evident throughout May and June. Chases frequently involved four males, occasionally five, and once six. In southern Ontario (Melbourne, London, and Simcoe) territories, although much larger, were also frequently adjacent. At Elmira, in two cases, males that I studied had home-ranges contacting those of neighbouring pairs, but fights or chases were never observed. Two other males had home-ranges within earshot of other cardinals but without overlap. Thus, there was evidence for contiguous distribution even in very sparse populations. This is quite in contradistinction to Crowell's (1962: 78) observation that "territories are usually not adjacent on the mainland [North America], but may be widely separated".

The wide variety of habitats used by Ontario cardinals studied in 1965 followed by observations, in 1966, of Tennessee cardinals occupying an even wider variety (see Figures 2 and 3) suggested that a species-characteristic response to vegetation, if it existed, was not very stereotyped. This conclusion is supported by descriptions of habitats used in areas outside of my own (Gould, 1961; Hamilton, 1962). My observation of cardinals, in both areas, in pine plantations, cypress swamps, or other extensive coniferous vegetation suggested that the southern edge of the boreal forest was, by itself, insufficient to limit the northern range expansion of the species. The location of the 1967 study area at Elmira was chosen to obtain further information on actual utilization of coniferous vegetation.

The more detailed examination of life-forms occurring within the home-ranges at Elmira and Tennessee, while showing no difference between frequency of occurrence of trees, for example, did show differences between frequencies of shrubs, woody cushions, and vine tangles. Also, differences in the vertical distribution of life-forms were evident, although these were probably largely due to the increased numbers of low shrubs, woody cushions, and vine tangles in Tennessee. The investigator of differences or preferences by animals in two widely separated areas is often caught up in a dilemma of interpretation. In habitat utilization or selection, for example, key factors inducing a species to select an area may gradually be isolated by demonstrating differences between non-key factors, arguing that the latter are irrelevant to the bird. However, such demonstrated differences could include key factors if geographic variation in response to potential habitat exists in the species. Such variation does apparently exist in some species (Mayr, 1963: 492). In the case of the Cardinal, I think that differences in frequencies of life-forms, which are outnumbered by the similarities, are not due to geographic variation in the species' response. The greater density of Tennessee cardinals (close to an increase of 60 times) probably forces birds to be more euryoecious through competition for space (see Figure 10). Also, a difference in frequency of vine-tangles between Elmira and Tennessee is obviously explained because that life-form was virtually absent from the northern area. Its ubiquitous presence in Tennessee may have been the very factor that made so many cover types habitable.

Likewise, I think that the many differences in frequencies of substrates (Table 13) reflect differences between Elmira and Tennessee rather than differences in response or preference of the birds of these areas.

It is interesting that the great decrease in home-range size in Tennessee is concomitant with only a slight decrease in the proportion of woody cover contained in the area (Table 7): 62.4 to 59.5 per cent. However, the total length of woody edge, 1,875 metres, in Elmira does not reduce proportionately to the 340 metres found in Tennessee. This

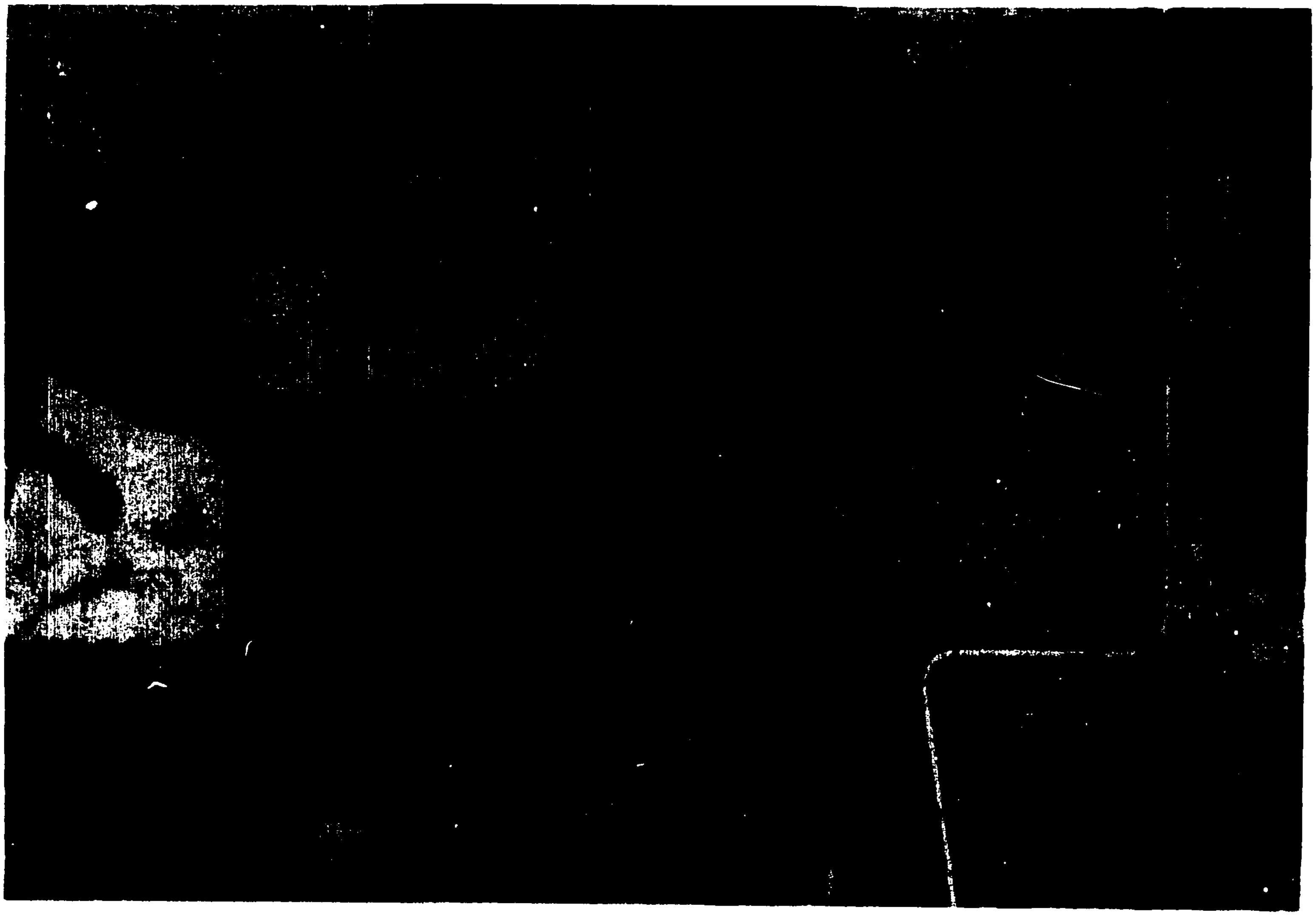


Figure 10. Approximate home-ranges of cardinals in Tennessee. Bird No. 1 (bottom in woodlot) was banded and the home-range plotted over several days. Other home-ranges were determined incidentally by observed encounters and simultaneous observations.

Figure 16. Approximate home-ranges of cardinals in Tennessee. Bird No. 1 (bottom in woodlot) was banded and the home-range plotted over several days. Other home-ranges were determined incidentally by observed encounters and simultaneous observations.

may reflect crowded conditions in Tennessee where birds are being forced into what might possibly be less favourable habitats, i.e., hedgerows. Occupancy of such cover types was absent at Elmira where birds have greater freedom of choice because of reduced competition, although, admittedly, such cover types were also less common. This interpretation is supported by the data of Table 6: 14.7 per cent of Tennessee cardinals were found in hedgerows and 20 per cent in narrowly wooded creek edges. In a population of lower density, this might represent strong selection for these cover types. In a high density population, it could represent the overflow from more preferred habitats.

Several authors (e.g., Svärdson, 1949; Hildén, 1965; Snow, 1954: 575) have pointed out the possible role of interspecific and intraspecific competition in habitat selection. Intraspecific competition, for food, nest-sites, or area in general -- and most often completely unspecified by the author discussing it -- is usually presumed to increase in response to an increase in population. There is evidence (Svärdson, 1949; Peitzmeier, 1960) that some species generally occupy "optimal habitats" when they first appear in a new area and that, under increased population pressure, some species colonize "suboptimal habitats". In other words, increased population pressure results in a more euryoecious population. This certainly seems to be true of the Cardinal where I studied it in Tennessee. These same authors contend that interspecific competition results in more stenoecious populations, a situation which ultimately reduces competition if the response to habitat becomes sufficiently stereotyped.

There are many examples of sympatric species with different habitat or ecological relationships in different parts of their range, a phenomenon particularly apparent from comparative studies of insular and mainland faunas (Lack, 1944; Lack and Southern, 1949; Mayr, 1951). However, actual descriptions of observed interspecific competition are rare.

I obtained no evidence to suggest that the Cardinal was a serious competitor with any other species in the parts of its range where I studied it. I have observed cardinals vigorously attacking male Baltimore Orioles (*Icterus galbula*) in Ontario and male Summer Tanagers (*Piranga rubra*) in Tennessee. Also, I have observed a male cardinal attacked by a male Red-winged Blackbird (*Agelaius phoeniceus*). Prescott (1965: 118) reported a male cardinal and a male Scarlet Tanager (*Piranga olivacea*) flying at each other in the vicinity of an empty tanager's nest. However, I think that all of these brief encounters can be explained simply as cases of mistaken identity. Of course, competition does not necessarily imply aggression. The Cardinal's most serious competitor for nest-sites may be the Catbird (*Dumetella carolinensis*). Nickell (1965: 449) cites one example of a pair of catbirds being chased from their nest, which was appropriated and used by cardinals. Hundley (1953: 89) states that Catbird interference led to two desertions in his study area. But I do not think that such competion for nest-sites, or for other obvious resource, is intense enough in Ontario to restrict the Cardinal's selection of habitat.

The differences in utilization of habitat between Tennessee and Elmira are of considerable interest. I am not convinced that the differences I observed in diversity of habitat elements used for foraging do not reflect a simple temporal relationship between foraging site and location of available food. Tennessee, being some 600 miles south, has an earlier spring growth of vegetation than Ontario. Cardinals there are reproductively active earlier in the year, probably by two to four weeks. Therefore, my observations are biassed to the extent that those at Elmira were concentrated on a relatively earlier period, perhaps while most available food was still on the ground. Also, a seasonal bias was introduced in both areas by my cessation of field observations before young had been produced. A single fledgling was produced by one pair in Tennessee during the period of my field observations, which ended on 23 July. No fledglings were produced in the Elmira area by 15 June. So, although the activities of foraging males in the two areas were comparable, males were not observed at the times when foraging activity might have been most intense.

It is not known whether the differential utilization of conifers and broadleaved vegetation (Table 22) for foraging indicated active avoidance of conifers or great preference for non-coniferous life-forms. It is possible that coniferous foliage supports less invertebrate food than broadleaved foliage. In Tennessee, cardinals were observed feeding on the fruit of red cedar. The most abundant conifer in the Elmira area was white cedar. I can find nothing in the literature comparing abundance of potential food on such foliage. Kluyver (1961) did not find the number of caterpillars to be lower in pine foliage than in oak, while Gibb (1962) found caterpillars in English pine woods to be scarce early in the season compared with the numbers available in oak-hazel woods.

The selection of non-coniferous life-forms for singing by Elmira birds was, I believe, directly due to preference. Most extensive tracts of white cedar contained many large dead elms, presumably victims of

Dutch elm disease (Figure 11). These provided high, conspicuous song-perches. Frequently, cardinals appeared to have difficulty in perching on the flexible tops of cedars and did not remain there for long. In Tennessee, conifers (red cedars) were isolated and rarely occurred in clumps or tracts as in Ontario. These appeared to be visited almost as frequently as other life-forms, and often provided relatively high perches, particularly along fence rows.

The fact that song-perches at Elmira were higher and less variable in height than in Tennessee suggests that males, in the absence of competitors, select areas with high life-forms suitable for song-perches. My impression of most forested areas in Tennessee was that their tallest trees were considerably higher than those found at Elmira. This is supported by Figure 4. If song-perches are selected on the basis of conspicuousness rather than height, the many dead elms at Elmira (Figure 11) may have resulted incidentally in greater height of song-perches. The greater variability of singing heights of Tennessee cardinals, as well as the knowledge that higher life-forms existed in their home-ranges than in those of Elmira birds, may be interpreted as additional evidence that song-perches are selected for their conspicuousness and that height per se is of little importance for the occupancy of a particular area. Supporting this conclusion is Crowell's (1963) report of populations occupying habitats with no foliage higher than 15 feet.

The use of conifers as nest-sites is a subject of considerable interest. All nests (8) found at Elmira were in white cedars, and three of 32 nests found in Tennessee were in red cedars. A high proportion of early nests at London, Ontario, are built in conifers (Scott, pers.

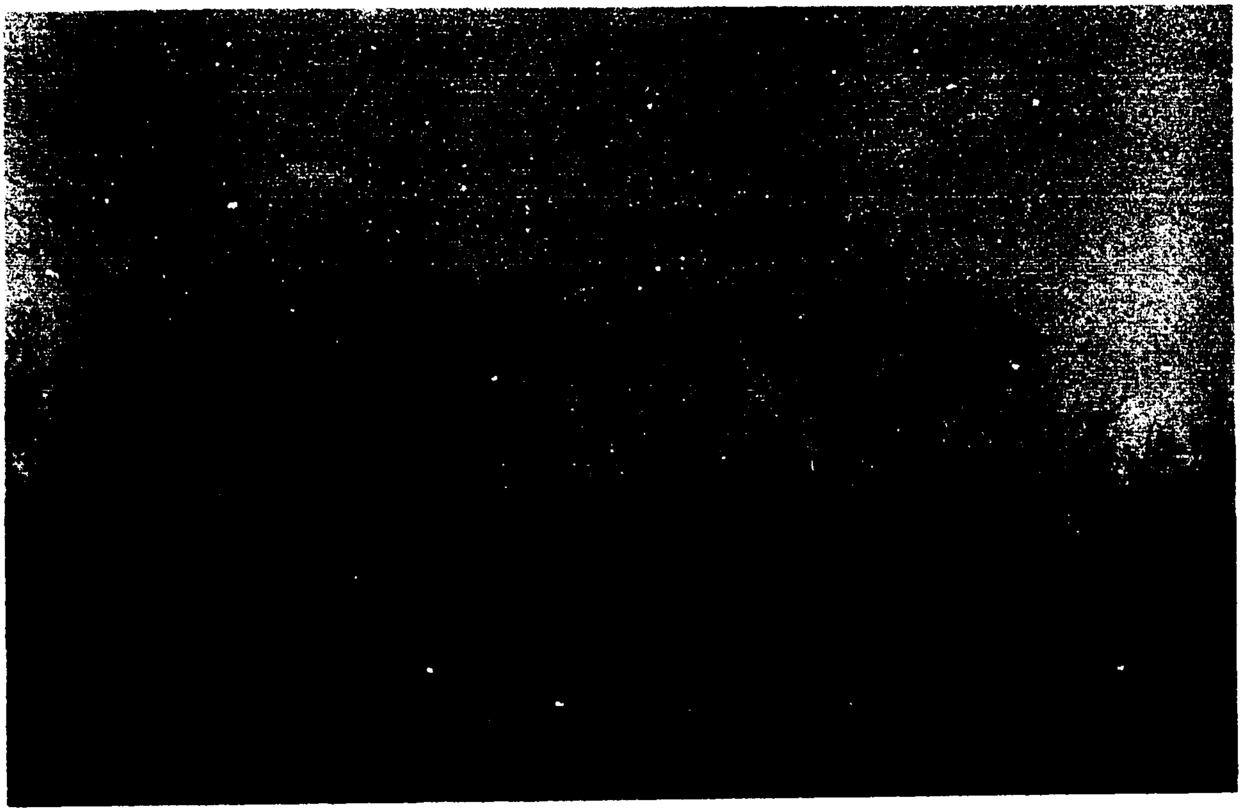


Figure 11. Vegetation typical of home-ranges at Elmira, Ontario. Dead elms provide high song-perches, low cedars nest-sites.

Figure 12. Cardinals were found in woods and swamp edges containing much birch and aspen. The one shown was situated in a pair's home-range near Fergus, Ontario, in the Elmira study area.

Figure 11. Vegetation typical of home-ranges at Elmira, Ontario. Dead elms provide high song-perches, low cedars nest-sites.

Figure 12. Cardinals were found in woods and swamp edges containing much birch and aspen. The one shown was situated in a pair's home-range near Fergus, Ontario, in the Elmira study area.

comm.), and conifers have been described as nest-sites by various authors (Shavers and Roberts, 1930; Laskey, 1944; Sutton, 1959; Burns, 1963). There is no evidence to suggest that such nests are more successful in producing young and, thus, no reasonable argument suggesting that they should be preferred sites. The breeding season of the cardinal begins early and is protracted to cover a period of four to five months. This may reflect the species' heritage, as tropical passerine breeding seasons tend to be longer than temperate ones (Klopfer, 1962: 77). Perhaps, in many areas, nesting activity of the Cardinal begins before sufficient cover has developed to provide a wide choice of nest-sites. Nest-site selection may be two-phased, the general site (life-form) being selected from afar by a bird moving through its habitat, and the specific site selected by inspection of the life-forms The attractive quality of the general site could be a dense patch of cover. Early in the season, conifers may be the most numerous of such patches and thus selected by chance. Such a hypothesis is consistent with the distribution of suitable nest-sites and their degree of utilization in the areas where I studied cardinals. Such a mechanism could neatly explain the "mistakes" made by cardinals in selecting nest-sites. I found one nest in Tennessee in a wire-fronted chicken-coop; Scott (pers. comm.) described a nest in a bale of wire inside an open-ended shed; also, see Harvey (1903).

Other than one unusually high nest in an American beech (_Fagus grandifolia_) in Tennessee, all that I found were between 1.5 and 13 feet above the ground. This range certainly includes the densest vegetation in most regions; but in the home-ranges that I studied, cover appearing to me as sufficiently dense for nest-sites was available at greater heights. If no increase in the nesting height of the Cardinal occurs during the breeding season, it probably indicates selection of cover for maximum density and concomitant concealment. A general shift in heights of nests may indicate selection of cover of a certain density, perhaps that which, in addition to providing necessary concealment, permits the female on the nest to survey the surrounding habitat. This function has been discussed in nest-site selection by the Catbird (Nickell, 1965: 453). An increase in both mean height and its variance may simply represent the higher nesting of a few birds in a population. I had hoped to investigate these aspects through series of photo-electric measurements in the vicinity of nest-sites in 1965 and 1966. However, this work was abandoned because of the great variability of measurements in the small samples of nests.

The ranges in nest heights reported by various authors are fairly similar to those that I found: southern Ontario, 19 inches to 24 feet, mean 6 feet 7 inches (Lemon, 1957); southern Michigan, 15 inches to 15 feet, mean 5.9 feet (Sutton, 1959); 25 inches to 15 feet, mean 5.96 feet (Nickell, 1963); Iowa, minimum 3 feet, mean 15 feet [sic](Hodges, 1949); Tennessee, 2½ to 12 feet, usually 4 to 5 feet (Laskey, 1944); 8 inches to 15 feet (Shaver and Roberts, 1930); Louisiana, 3.0 to 24.0 feet, mean 6.3 feet (Taylor, 1965); Arizona, 5 to 15 feet, mean 8 feet (Gould, 1961); Bermuda, 4 to 11 feet, mean 6.1 feet (Crowell, 1962). From these data, it appears evident that cardinals are opportunistic enough to utilize cover for nesting within a wide range of heights, but only rarely above 15 feet.

The evidence obtained and presented indicates that the Cardinal is a species with a very plastic response to habitat features. It may be this very plasticity that accounts for the success of the species in the areas that it has invaded in its rapid range expansion (Brown, 1920; Young, Stollberg, and Deusing, 1941; Hodges, 1949; Snyder, 1957; Burns, 1956, 1958; Boyd, 1962; Beddall, 1963; Boyd and Nunnely, 1964). In all parts of its range, the only vegetational requirement of the Cardinal seems to be a certain amount of woody cover; this must be adequate for nesting and must provide song-perches. However, the latter does not appear to be as critical a factor as it is for such open-country birds as the pipit (*Anthus trivialis*)(Lack, 1933: 247), and is apparently of much less importance than suitable nesting cover. Although there is evidence that high song-perches are preferred, height seems less important than conspicuousness.

A better evaluation of the species' requirements would be possible if the behavioural mechanisms of selection were understood. It is not known whether habitat is selected by male, female, or both. Possibly, males try to obtain areas with high song-perches. It is stated by some authors (Hodges, 1949:355; Sutton, 1959: 81) that the female selects the nest-site. A study of selection and occupancy of habitat early in the season when flocks are disbanding and breeding sites are being selected would be profitable. Do males select an area and try to attract a mate or are pairs formed prior to selection of breeding habitat? If the former, do males select an area on the basis of its song-perches? Do females accept a male on the basis of nest-site cover within his selected territory? I studied only one home-range suggesting that the latter might be the case. The only unmated male of those studied at Elmira occupied a habitat that was virtually devoid of low cover in the area where most singing occurred. This, a first-year bird, had a large area of riverbank pasture containing several widely separated high maples that it used as song-perches. It was of additional interest that this was one of those males (two of ten) whose home-range was in contact with that of another cardinal.

The total amount of woody cover does not seem to be a severe limiting factor to the Cardinal. Birds in the dense population studied in Tennessee had home-ranges containing as little as 0.64 acres of cover. Gould (1961: 252) suggested that the Cardinal must have some open fields within its territory for feeding. In my opinion, cardinals in most areas, at least during the breeding season, would have little trouble obtaining food in forested areas, both from the forest floor and canopy. It is more likely that these birds require a sufficiently dense tangle of vegetation for provision of nest-sites. Such dense vegetation, and its lush proliferation later in the season, seems most frequently associated with "edge" situations. These include the edges of woodlots, forest clearings, river and stream borders, and hedgerows, both planted and natural. Thus, the presence of open fields within a territory may merely reflect the bird's preference for the edge or interface between the field and some other type of vegetation.

I have remarked earlier that, in Tennessee, vegetation characteristic of woodland edge was found in almost every type of woody cover. It is likely that as long as sufficiently conspicuous song-perches accompany such vegetation, the species' basic habitat requirements are satisfied.

Unfortunately, we have no information on the species' preferred habitat at its centre of origin, but if we assume that its present centre of abundance, viz the lower Mississippi valley, is similar to that prior to man's extensive destruction of the original deciduous forest biome, then it suggests primitive association with the dense, tangled vegetation characteristic of riparian undergrowth. If this is, indeed, the ancestral habitat of the species, then its secondary, and perhaps less preferred, habitats include forest edge, hedgerows, and other fragmented patches of vegetation, all of which show structural, not physiognomical, similarity.

Most writers contend that the preferred habitat of a species is the one containing the highest population density. I would like to suggest that such a view may be erroneous and, in the case of the Cardinal in my Tennessee study area, most likely is. Because hedgerows are so obviously man-made and therefore recent in appearance and because I rarely saw them utilized in areas of sparse population, I would not consider them to be the preferred habitat of cardinals in Tennessee. Yet they are heavily occupied. I think that such cover types are absorbing the overflow of population from preferred habitats in this region. But based on land area occupied by the species, the population density in this non-preferred habitat is undoubtedly much higher than in forested riparian habitat. And surely the measure of "preferred" habitat, if it is to be defined as that to which the species is best adapted, is the degree of reproductive success attained in it rather than the number of birds attempting to reproduce. It may well be that cardinals in Tennessee, while reaching higher densities in non-preferred habitat, are reproductively unsuccessful in it. A closer study of these aspects would be worthwhile.

I have no information on the annual reproductive success of the cardinals that I studied. Most birds in my Tennessee area made many attempts at nesting (up to six before 18 June in one case). Only one pair succeeded to the point of having one fledgling before I terminated observations on 23 July. This low rate of success, at least early in the season, was typical of cardinals throughout the study area. Much nest destruction with most successful nests occurring late in the season is characteristic of the population at London, Ontario, (Scott, pers. comm.). It is also possible that in Tennessee dense hedgerow populations may have been younger birds forced into the most unfavourable habitats, if these extreme edge situations are in fact unfavourable.

The problem and investigation of edge effect on the distribution of birds is not new (Kendeigh, 1944; Udvardy, 1957; Wasilewski, 1961: 131). Most authors (e.g., Kendeigh, 1944; Nickell, 1963) consider the Cardinal to be an "edge species". Writers (e.g., Beddall, 1963; De Vos, 1964) have stressed the importance of man's forest-clearing as a factor in the range expansion of the Cardinal. Such clearing and cutting presumably produces a greater amount of forest edge than was previously available. However, as I have pointed out, it is likely not the edge per se that is important, but the type of cover that is permitted to grow. This low, dense cover, e.g., honeysuckle, wild grape, etc., is not confined to forest edges, but is characteristic of roadside hedgerows and riparian situations as well as natural clearings in extensive forests.

The Cardinal in Tennessee _is_ found in forested areas, not just along their edges, but well within them. It can be found in almost every wooded situation down to the sparsest of hedgerows. Admittedly, some resident males in such a dense population may be unmated; also, there may be a floating population of unmated birds of both sexes that is not associated with a specific area. However, the species in general is widely distributed among the varied types of vegetation.

Since my view of habitat is that of vegetation associated with an individual bird, it is important to realize that a considerable amount of individual variation should be expected in habitat selection. It is unknown, of course, whether the euryoecious population in Tennessee is composed of stenoecious subpopulations or whether there is great individual plasticity of selection. The result, in either case, is the same. Klopfer (1962: 40) has discussed nicely these theoretical implications with regard to feeding behaviour.

One type of habitat has been avoided in this study -- the urban area. It is only recently that the effects of this highly complex environment on birds have begun to be studied (see Novikov, 1964, and Ertz, 1966). Although the centres of large cities and industrialized areas have little to offer, small towns and the suburban regions of large cities with their parks and wooded riversides offer excellent cover, and the Cardinal is a common resident of such areas throughout eastern North America. Writers have stressed forest-clearing, climatic changes, possible increased reproductive capacity, and other factors as promoting the range expansion of the Cardinal, but few have considered the role of the urban habitat in such spread. There are few towns or cities throughout the northern edge of the Cardinal's range that do not boast several "feeding stations" for wild birds. Since vegetation does not appear to limit the species in the breeding season, what then limits expansion? At the northern part of the range, a definite limiting factor could be heavy snow cover, in turn limiting food. Certain upland regions are deeply snow-covered for much of the winter. In fact, Todd (in Hundley, 1953: 68-69), in the 1940's, suggested that the Cardinal's "ultimate range is conditioned by winter rather than summer" and "Being a seed eater and a ground feeder the Cardinal cannot maintain itself in force within the area of snow cap that in winter for weeks on end rests upon the northern states."

I can find no published quantitative information on the amount of accumulated snow cover in different parts of southern Ontario. Snow cover refers to the total depth of snow on the ground at any time, and is clearly the factor that would determine the ease with which birds might obtain food on or close to the ground. Meteorologists are still trying to improve methods of measuring fresh snowfall (Thomas, 1964). The relationship between snowfall and snow cover is not clear-cut; but, as the former is the only readily available information, the distribution of annual snowfall is shown in Figure 13. Comparison with Figure 6 shows reasonably good agreement between the mapped edge of the Cardinal's range and the area between the 64 and 80 inch iso-lines. The distribution of snowfall, producing the "snow belt" area of southern Ontario, is due to the effect of the Great Lakes: maximum snowfall occurs in the lee of the lakes and on the windward side of higher terrain (Richards and Derco, 1963). The same authors describe "precipitation shadows" on the lee side of higher ground and particularly in river valleys.

During times of maximum snow cover it is likely that river valleys may offer the most salubrious environment for the Cardinal. At such times, it is also conceivable that cardinals could move into the sheltered environs of the town, where food is available and garden plantings provide adequate cover. Likewise, pioneering cardinals could probably survive the winter by moving to farms where grain and cover are both readily available, and apparently such behaviour is exhibited by cardinals at farms near Elmira, Ontario. The few, small, extralimital

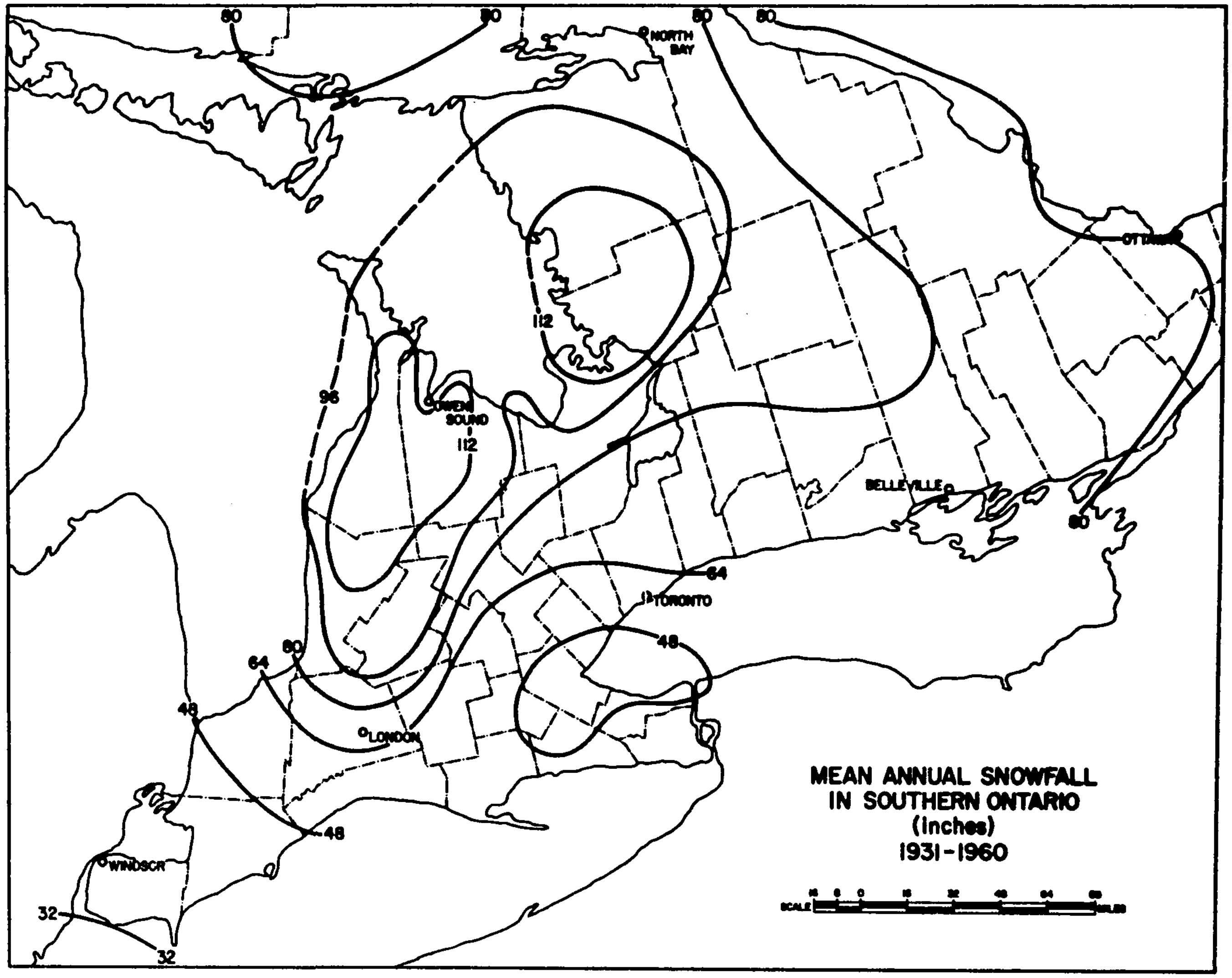


Figure 13. Mean annual snowfall in southern Ontario (from Thomas, 1964).

populations in Ontario seem to be established in small towns, e.g., Owen Sound, Meaford, Orillia, Tweed (Snyder, 1957), all well within the region of high snowfall. Therefore, it is quite likely that such urban areas play an important role in the maintenance of this species as it expands into less favourable areas.

My work suggests that although coniferous vegetation may be avoided for foraging and may not be preferred for singing, it is adequate for nesting and should not act as a barrier to the expansion of the species' range. If food is, in fact, severely limited in such vegetation, we should still expect the species much farther north and east of its present range. Extensive pockets of deciduous forest, mainly birch (Betula papyrifera) and aspen (Populus tremuloides), occur throughout the boreal forest biome. At Elmira, cardinals were found in similar forests (see Figure 12).

Since cardinals in peripheral populations are found more frequently in riparian vegetation, it seems reasonable to ask whether they are actively selecting this habitat or are found in it because it represents what might be called the historical avenue of approach to a new area. In Tennessee, where the species has existed presumably long before recorded history, it has had more than sufficient time to disperse and occupy any suitable cover. This seems to be exactly what it has done. The evidence I have presented after studying distribution with respect to vegetation along part of the edge of the range in Ontario supports the idea that cardinals remain close to rivers through "inertia", not because it is necessarily the best available habitat. Krause and Froiland (1956) showed a similar relationship between rivers and distributions of sight-records of cardinals in recently invaded regions of South Dakota. Such patterns of association with river systems and distribution of populations of expanding species have usually not been noted (e.g., Berndt and Henss, 1964; Peitzmeier, 1960; Warner, 1966), although Ulfstrand (1963) suggested that the Baltic Sea, which may be a guide line for migrants, may also guide species undergoing irruptive movements, and Keve (1963) clearly showed that three species, *Streptopelia decaocto*, *Dendrocopus syriacus*, and *Hippolais pallida*, had entered Hungary from the south along river valleys.

Thorpe (1945: 70) has pointed out that habitat selection could inhibit indiscriminate dispersal of a pioneer population. Even if the most favourable cover is not found near rivers, the simple mechanism of the Cardinal's following rivers and remaining in close association with them should inhibit indiscriminate dispersal. And if the attractiveness of an area is enhanced by the presence of conspecifics, it should result in the contiguous distributions that I have shown in sparse populations.

Related to the problem of present distribution is the one of dispersal. I have suggested on the basis of distributional evidence that cardinals use river systems in moving into new areas. It has not been established whether dispersal and range expansion by the Cardinal is effected largely through the efforts of immatures, as might seem logical, or whether adult birds are also involved.

Unfortunately, banding returns are not very helpful. The Cardinal is a sedentary species. Of 1,621 banded by Laskey (1944: 37) in Tennessee, none was recovered farther than four miles from the point of banding. From data supplied by the U.S. Bird Banding Laboratory, I have analyzed recoveries and foreign returns up to 1964. Using only birds of known age or sex, recovered outside of 10-minute blocks adjacent to that of banding, and recovered within one year of banding, I found no evidence of differential movement between age groups or sexes, the average distances lying between 43 and 58 miles. However, the high percentage (64) of mated first-year cardinals in a peripheral population (Elmira) strongly suggests that considerable recruitment comes from immature immigrants. It should be recalled that this percentage may be higher as not all first-year cardinals can be definitely identified. A proportion of this magnitude in such a peripheral population may be explained possibly in three ways. First, differential mortality may be affecting adults and immatures; more adults are dying than immatures. Secondly, reproductive success may have been greatly increased, resulting in more young being produced than in other areas. Thirdly, many first-year birds may be moving into the area to breed for the first time. Of course, it is possible that some or all of these suggested mechanisms may be interacting.

The first explanation seems untenable on logical grounds. Among passerines, it is usual for maximum mortality to occur before or during the first winter of life (Farner, 1955: 403). This presumably results from basic physiological weaknesses or behavioural inexperience. It is now necessary to postulate a mechanism that reverses this differential mortality. Perhaps such a mechanism may involve the adult's fidelity or tenacity to a particular region, which immatures leave. If winter conditions become severe enough, adults might be more frequently destroyed. However, this still leaves a population of wandering immature birds, and although their wintering conditions may be more moderate, considerable mortality must surely affect them. The second explanation seems untenable on physiological and ecological grounds. Reproductive statistics are fairly uniform in widely separated parts of the Cardinal's range, and most populations may have an annual production of two to three offspring per pair as they do at London, Ontario (Lemon, 1957: 43; Scott, pers. comm.), and Michigan (Batts, 1961). To reach my observed ratio of 64:36 or approximately 2:1 would require the annual production of four offspring per pair with <u>no</u> mortality of immatures before the time of first breeding. If a mortality of 50 per cent is assumed, then an annual production of at least eight offspring per pair would be required. This represents an increase of 2.5 to 3 times the production at London, 55 miles away. Therefore, I think that the third explanation is most plausible: recruitment to the breeding population is effected by first-year immigrants.

Thus, the situation at Elmira appears to be one of a rapidly expanding peripheral population. If strong tenacity is shown to territory from year to year, as it is at London (Scott, pers. comm.), then future years should show a more balanced ratio of first-year to older birds at Elmira, unless winter conditions annually reduce the population to very low levels. The latter may well be the case as evidence (W.W. Gunn, unpublished data) suggests that the species was present in the Elmira area, in small numbers, even before 1938 when widespread range expansion occurred. The first breeding record in Ontario was at Point Pelee in 1901 (Snyder, 1957). The Cardinal first bred at London in 1915, Brantford in 1919, and Toronto in 1922. It probably reached the Elmira region by entering the Grand River watershed from Lake Erie or crossing the height of land from the Thames River watershed.

Although wide rivers may act as barriers to dispersal, it seems certain that river banks and lake shores act as guide lines for the movement of cardinals. Such avenues of approach have been suggested in studies of the Cardinal's range expansion in several areas (Brown, 1920; Young et al, 1941; Krause and Froiland, 1956). These, along with my own detailed study of distribution, suggest that peripheral populations are comprised largely of young birds "pioneering" new areas via their river systems, which provide much food and cover.

Possibly these movements occur in fall or winter when birds are in flocks. Increases in population density or movements of cardinals have been noted in several regions in October and November (Trautman, 1940: 141; Hundley, 1953: 92; Graber and Graber, 1963: 494; Stoddard and Norris, 1967: 93). However, there is increasing evidence for marked spring movements, usually in March, (Trautman, 1940: 141; Hundley, 1953: 96; Stoddard and Norris, 1967: 93). Population increases have been noted for the same period at the Long Point Bird Observatory in Ontario (D.J.T. Hussell, pers. comm.) and in Maryland (C.S. Robbins, pers. comm.).

Dispersing birds probably take up residence close to the same river by which they entered an area and remain there until forced out by severe winter conditions. There is some evidence for such forced movements (Bordner, 1958). Thus, the ultimate factor limiting the Cardinal's spread may be winter snow cover and concomitant food shortage, or it may simply be a plateau or height of land devoid of wooded stream valleys.

LITERATURE CITED

Adkisson, C.S. 1966. The nesting and behavior of Mockingbirds in northern Lower Michigan. Jack-Pine Warbler, 44: 102-116.

Allard, H.A. 1930. The first morning song of some birds of Washington, D.C.; its relation to light. Am. Nat., 64: 436-469.

Batts, H.L.,Jr. 1961. Nesting success of birds on a farm in southern Michigan. Jack-Pine Warbler, 39: 72-83.

Bauer, H.L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology, 24: 45-60.

Beddall, B.G. 1963. Range expansion of the Cardinal and other birds in the northeastern states. Wilson Bull., 75: 140-158.

Bendell, J.F., and P.W. Elliot. 1966. Habitat selection in Blue Grouse. Condor, 68: 431-446.

Berndt, R., and M. Henss. 1964. Die Blaumeise, _Parus c. caeruleus_ L., als Invasionsvogel. Vogelwarte, 22: 93-100.

Bohl, W.H. 1956. Experiments in locating wild Chukar partridges by use of recorded calls. J. Wildl. Mgmt, 20: 83-85.

Bordner, D.L. 1958. Cardinal banded in Connecticut, retrapped in Pennsylvania. Bird-Banding, 29: 244.

Boyd, E.M. 1962. A half-century's changes in the bird-life around Springfield, Massachusetts. Bird-Banding, 33: 137-148.

Boyd, E.M., and S.A. Nunneley. 1964. Banding records substantiating the changed status of ten species of birds since 1900 in the Connecticut valley. Bird-Banding, 35: 1-8.

Brecher, L.C. 1943. The relation of vegetational life-forms to the distribution of breeding birds. Kentucky Warbler, 19: 41-49.

Brown, H.C. 1920. The Cardinal in north-central Iowa. Wilson Bull., 32: 123-132.

Burns, R.D. 1956. The Michigan Audubon cooperative Cardinal study. Jack-Pine Warbler, 34: 67-69.

Burns, R.D. 1958. A history of the entry of the Cardinal into Michigan. Jack-Pine Warbler, 36: 19-21.

Burns, R.D. 1963. Michigan cooperative Cardinal study: nesting data. Jack-Pine Warbler, 41: 56-61.

Clements, F.E., and V.E. Shelford. 1939. Bio-ecology. Wiley, N.Y. 425 pp.

Crowell, K.L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology, 43: 75-88.

Crowell, K.L. 1963. On determinants of insular faunas. Am. Nat., 97: 194-196.

Dansereau, P. 1951. Description and recording of vegetation upon a structural basis. Ecology, 32: 172-229.

Davis, J.H. 1960. Proposals concerning the concept of habitat and a classification of types. Ecology, 41: 537-541.

Davis, J. 1965. The "singing male" method of censusing birds: a warning. Condor, 67: 86-87.

De Vos, A. 1964. Range changes of birds in the Great Lakes region. Am. Midl. Nat., 71: 489-502.

Du Rietz, G.E. 1931. Life-forms of terrestrial flowering plants. Acta Phytogeographica Suecica, 3: 1-95.

Elton, C.S., and R.S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J. Ecol., 42: 460-496.

Emlen, J.T.,Jr. 1956. A method for describing and comparing avian habitats. Ibis, 98: 565-576.

Ertz, W. 1966. Ecological principles in the urbanization of birds. Ostrich, Suppl. 6: 357-363.

Farner, D.S. 1955. Birdbanding in the study of population dynamics. pp. 397-449. In A. Wolfson, Recent studies in avian biology. Univ. Ill. Press, Urbana. 479 pp.

Ficken, M.S., and R.W. Ficken. 1967. Age-specific differences in the breeding behavior and ecology of the American Redstart. Wilson Bull., 79: 188-199.

Finzel, J.E. 1964. Avian populations of four herbaceous communities in southeastern Wyoming. Condor, 66: 496-510.

Foote, L.E., H.S. Peters, and A.L. Finkner. 1958. Design tests for Mourning Dove call-count sampling in seven southeastern states. J. Wildl. Mgmt, 22: 402-408.

Frings, H. and M., J. Jumber, R. Busnel, J. Giban, and P. Gramet. 1958. Reactions of American and French species of *Corvus* and *Larus* to recorded communication signals tested reciprocally. Ecology, 39: 126-131.

Gates, J.M. 1966. Crowing counts as indices to cock pheasant populations in Wisconsin. J. Wildl. Mgmt, 30: 735-744.

Gibb, J.A. 1962. Tits and their food supply in English pine woods: a problem in applied ornithology. Festschrift der Vogelschutzwarte für Hessen, Rheinland-Pfalz und Saarland. pp. 58-66.

Goertz, J.W. 1964. The influence of habitat quality upon density of Cotton Rat populations. Ecol. Monogr., 34: 359-381.

Gould, P.J. 1961. Territorial relationships between Cardinals and Pyrrhuloxias. Condor, 63: 246-256.

Graber, R.R., and J.W. Graber. 1963. A comparative study of bird populations in Illinois, 1906-1909 and 1956-1958. Bull. Ill. Nat. Hist. Surv., 28: 383-528.

Greig-Smith, P. 1964. Quantitative plant ecology. 2nd edition. Butterworths, London. 256 pp.

Hamilton, T.H. 1962. The habitats of the avifauna of the mesquite plains of Texas. Am. Midl. Nat., 67: 85-105.

Harris, V.T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Contr. Lab. vert. Biol., Univ. Mich., No. 56: 1-53.

Harvey, G.F. 1903. The diary of a Cardinal's nest. Auk, 20: 54-57.

Hayne, D.W. 1949. An examination of the strip census method for estimating animal populations. J. Wildl. Mgmt, 13: 145-157.

Hewitt, O.H. 1963. Development of a roadside count method of census of breeding Redwinged Blackbirds (Agelaius phoeniceus). Angew. Orn., 1: 123-125.

Hildén, O. 1965. Habitat selection in birds. A review. Ann. Zool. Fenn., 2: 53-75.

Hodges, J. 1949. A study of the Cardinal in Iowa. Proc. Iowa Acad. Sci., 56: 347-361.

Hore-Lacy, I. 1964. Birds of the You Yangs, Victoria: habitat selection and status. Emu, 64: 29-32.

Howell, J.C. 1951. The roadside census as a method of measuring bird populations. Auk, 68: 334-357.

Hundley, M.L. 1953. Winter distribution of the Eastern Cardinal in the vicinity of Morgantown, West Virginia. J. Sci. Labs. Denison Univ., 43: 66-111.

Jones, R.E. 1960. The life-form concept applied to prairie chicken habitat in Oklahoma. Proc. 1959 Okla. Acad. Sci., 40: 134-136.

Jones, R.E. 1964. Habitat used by Lesser Prairie Chickens for feeding related to seasonal behavior of plants in Beaver County, Oklahoma. Southwestern Nat., 9: 111-117.

Kendeigh, S.C. 1944. Measurement of bird populations. Ecol. Monogr., 14: 67-106.

Kendeigh, S.C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk, 62: 418-436.

Kendeigh, S.C. 1954. History and evaluation of various concepts of plant and animal communities in North America. Ecology, 35: 152-171.

Keve, A. 1963. Peculiarities of range expansion of three European bird species. Proc. 13th Int. orn. Congr., pp. 1124-1127.

Kimball, J.W. 1949. The crowing count pheasant census. J. Wildl. Mgmt, 13: 101-120.

Klopfer, P.H. 1962. Behavioral aspects of ecology. Prentice-Hall, N.J. 173 pp.

Klopfer, P. 1963. Behavioral aspects of habitat selection: the role of early experience. Wilson Bull., 75: 15-22.

Klopfer, P.H. 1965. Behavioral aspects of habitat selection: a preliminary report on stereotypy in foliage preference of birds. Wilson Bull., 77: 376-381.

Klopfer, P.H. 1967. Behavioral stereotypy in birds. Wilson Bull., 79: 290-300.

Klopfer, P.H., and J.P. Hailman. 1965. Habitat selection in birds. pp. 279-303. In D.S. Lehrman, R.A. Hinde, and E. Shaw, Advances in the study of behavior. Vol. 1. Academic Press, N.Y. 320 pp.

Kluyver, H.N. 1961. Food consumption in relation to habitat in breeding chickadees. Auk, 78: 532-550.

Krause, H., and S.G. Froiland. 1956. Distribution of the Cardinal in South Dakota. Wilson Bull., 68: 111-117.

Küchler, A.W. 1949. A physiognomic classification of vegetation. Ann. Assoc. Am. Geog., 39: 201-210.

Lack, D. 1933. Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. J. Anim. Ecol., 2: 239-262.

Lack, D. 1934. Habitat distribution in certain Icelandic birds. J. Anim. Ecol., 3: 81-90.

Lack, D. 1944. Ecological aspects of species formation in passerine birds. Ibis, 86: 260-286.

Lack, D., and H.N. Southern. 1949. Birds on Tenerife. Ibis, 91: 607-626.

Lack, D., and L.S.V. Venables. 1939. The habitat distribution of British woodland birds. J. Anim. Ecol., 8: 39-71.

Laskey, A.R. 1944. A study of the Cardinal in Tennessee. Wilson Bull., 56: 27-44.

Lemon, R.E. 1957. A study of nesting cardinals (Richmondena cardinalis) at London, Canada. M.Sc. Thesis. Univ. Western Ont.,54 pp.

Lemon, R.E. 1966. Geographic variation in the song of cardinals. Can. J. Zool., 44: 413-428.

Lemon, R.E. 1967. The response of cardinals to songs of different dialects. Anim. Behav., 15: 538-545.

Leopold, A., and A.E. Eynon. 1961. Avian daybreak and evening song in relation to time and light intensity. Condor, 63: 269-293.

Levy, S.H., J.J. Levy, and R.A. Bishop. 1966. Use of tape recorded female quail calls during the breeding season. J. Wildl. Mgmt, 30: 426-428.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc. nat. Acad. Sci., 51: 1207-1210.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. Ecology, 42: 594-598.

MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. Am. Nat., 96: 167-174.

MacArthur, R., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Am. Nat., 100: 319-332.

Maher, W.J. 1959. Habitat distribution of birds breeding along the upper Kaolak River, northern Alaska. Condor, 61: 351-368.

Mayr, E. 1951. Speciation in birds. Proc. 10th Int. orn. Congr., pp. 91-131.

Mayr, E. 1963. Animal species and evolution. Oxford Univ. Press, London. 797 pp.

McKeever, C.K. 1941. Distribution and habitat selection of some local birds. Proc. Linn. Soc. N.Y. No. 52-53: 84-112.

McNemar, Q. 1962. Psychological statistics. 3rd edition. Wiley, N.Y. 451 pp.

Miller, A.H. 1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. Am. Nat., 76: 25-35.

Naylor, E., and I. Haahtela. 1966. Habitat preferences and interspersion of species within the superspecies Jaera albifrons Leach (Crustacea: Isopoda). J. Anim. Ecol., 35: 209-216.

Nice, M.M. 1941. The role of territory in bird life. Am. Midl. Nat., 26: 441-487.

Nickell, W.P. 1963. Cardinal habitats in southern Michigan. pp. 56-57. In R.D. Burns, Michigan cooperative Cardinal study: nesting data. Jack-Pine Warbler, 41: 56-61.

Nickell, W.P. 1965. Habitats, territory, and nesting of the Catbird. Am. Midl. Nat., 73: 433-478.

Norris, R.A. 1951. Distribution and populations of summer birds in southwestern Georgia. Occ. Publ. No. 3. Georgia orn. Soc. 67 pp.

Novikov, G.A. 1964. Changes in the species stereotype of birds nesting under the conditions of the cultural landscape [in Russian]. Zool. Zh., 43: 1193-1202.

Odum, E.P., and E.J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk, 72: 128-137.

Peitzmeier, J. 1960. Selbstselektion und Selbstisolation als Weg der intraspezifischen Differenzierung. Proc. 12th Int. orn. Congr., 2: 595-597.

Peterson, R.T. 1942. Life zones, biomes, or life forms? Audubon Mag., 64: 21-30.

Pitelka, F.A. 1941. Distribution of birds in relation to major biotic communities. Am. Midl. Nat., 25: 113-137.

Prescott, K.W. 1965. The Scarlet Tanager. New Jersey State Mus. Invest., No. 2. 159 pp.

Richards, T.L., and V.S. Derco. 1963. The role of "lake effect storms" in the distribution of snowfall in southern Ontario. [Paper presented at The 20th Meeting of The Eastern Snow Conference, Quebec City, February 14-15, 1963] Can. Dep. Transp. Met. Brch. 6 pp. 11 figs.

Rosene, W.,Jr. 1957. A summer whistling cock count of Bobwhite Quail as an index to wintering populations. J. Wildl. Mgmt, 21: 153-158.

Scott, D.M. 1967. Postjuvenal molt and determination of age of the Cardinal. Bird-Banding, 38: 37-51.

Shaver, J.M., and M.B. Roberts. 1930. Some nesting habits of the Cardinal. J. Tenn. Acad. Sci., 5: 157-170.

Shaver, J.M., and M.B. Roberts. 1933. A brief study of the courtship of the Eastern Cardinal (*Richmondena cardinalis cardinalis* (L.)). J. Tenn. Acad. Sci., 8: 116-123.

Shelford, V.E. [editor]. 1945. Bird distribution and ecological concepts. Wilson Bull., 57: 191-201, 243-252.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y. 312 pp.

Smith, R.H., and S. Gallizioli. 1965. Predicting hunter success by means of a spring call count of Gambel Quail. J. Wildl. Mgmt, 29: 806-813.

Snedecor, G.W. 1956. Statistical methods applied to experiments in agriculture and biology. 5th edition. Iowa State Univ. Press, Ames. 534 pp.

Snow, D.W. 1954. The habitats of Eurasian tits.(*Parus spp*.). Ibis, 96: 565-585.

Snyder, L.L. 1957. Changes in the avifauna of Ontario. pp. 26-42. *In* F.A. Urquhart, Changes in the fauna of Ontario. R.O.M., Univ. Toronto Press. 75 pp.

Southern, H.N., and L.S.V. Venables. 1939. Habitat selection among birds in a Lapland birch wood. J. Anim. Ecol., 8: 114-119.

Stebler, A.M., and S.D. Schemnitz. 1955. Habitat description and the life-form concept. Proc. Okla. Acad. Sci., 36: 154-157.

Stirling, I., and J.F. Bendell. 1966. Census of Blue Grouse with recorded calls of a female. J. Wildl. Mgmt, 30: 184-187.

Stoddard, H.L.,Sr., and R.A. Norris. 1967. Bird casualties at a Leon County, Florida TV tower: an eleven-year study. Bull. Tall Timbers Research Station, No. 8: 1-104.

Sutton, G.M. 1959. The nesting fringillids of the Edwin S. George Reserve, southeastern Michigan (Part III). Jack-Pine Warbler, 37: 77-101.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos, 1: 157-174.

Taylor, W.K. 1965. Nesting heights of some Louisiana birds. Wilson Bull., 77: 146-150.

Tennessee Conservation Needs Committee. [no date] Tennessee soil and water conservation needs inventory. 85 pp.

Thomas, M.K. 1964. Snowfall in Canada. Can. Dep. Transp. Met. Brch. CIR-3977. TEC-503. 16 pp.

Thorpe, W.H. 1945. The evolutionary significance of habitat selection. J. Anim. Ecol., 14: 67-70.

Trautman, M.B. 1940. The birds of Buckeye Lake, Ohio. Misc. Publ. Mus. Zool. Univ. Mich., No. 44. 466 pp.

Udvardy, M.D.F. 1957. An evaluation of quantitative studies in birds. Cold Spring Harbor Symp. quant. Biol., 22: 301-311.

Udvardy, M.D.F. 1959. Notes on the ecological concepts of habitat, biotope and niche. Ecology, 40: 725-728.

Ulfstrand, S. 1963. Ecological aspects of irruptive bird migration in northwestern Europe. Proc. 13th Int. orn. Congr. pp. 780-794.

U.S. Department of Commerce. 1966. Climatological data: Tennessee. Vol. 71: 59-70.

Van Tyne, J., and A.J. Berger. 1959. Fundamentals of ornithology. Wiley, N.Y. 624 pp.

Warner, A.C. 1966. Breeding-range expansion of the Scissor-tailed Flycatcher into Missouri and in other states. Wilson Bull., 78: 289-300.

Wasilewski, A. 1961. Certain aspects of the habitat selection of birds. Ekol. Polska Ser. A., 9: 111-137.

Wecker, S.C. 1964. Habitat selection. Sci. Am., 211(4): 109-116.

Weeden, J.S. 1965. Territorial behavior of the Tree Sparrow. Condor, 67: 193-209.

Weeden, J.S., and J.B. Falls. 1959. Differential response of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk, 76: 343-351.

Wiens, A.W. 1960. Sunrise, sunset, and the song of the Cardinal. Bull. Kansas orn. Soc., 11: 13-14.

Wilson, E.O., and G.L. Hunt. 1966. Habitat selection by queens of two field-dwelling species of ants. Ecology, 47: 485-487.

Winer, B.J. 1962. Statistical principles in experimental design. McGraw-Hill, N.Y. 672 pp.

Yapp, W.B. 1955. A classification of the habitats of British birds. Bird Study, 2: 111-121.

Yapp, W.B. 1957. Classification of avian habitats. Ibis, 99: 351-352.

Yapp, W.B. 1960. The colonization of coniferous plantations by birds. Proc. 12th Int. orn. Congr., 2: 801-803.

Yeager, L.E. 1960. Classification of North American mammals and birds according to forest habitat preference. J. For., 59: 671-674.

Young, F.N. 1958. In defense of the concepts of major and minor habitats in approaching biological problems. Q. J. Fla. Acad. Sci., 21: 92-100.

Young, H. 1946. Further studies on the Cardinal. Passenger Pigeon, 8: 104-109.

Young, H., B. Stollberg, and M. Deusing. 1941. The spread of the Cardinal through Wisconsin. Passenger Pigeon, 3: 1-4.

Zimmerman, J.R. 1960. Seasonal population changes and habitat preferences in the genus Laccophilus (Coleoptera: Dytiscidae). Ecology, 41: 141-152.

APPENDIX

INDEXING POPULATION DENSITIES OF THE CARDINAL WITH TAPE-RECORDED SONG

While studying habitat utilization by the Cardinal, I wanted to obtain information about the relative densities of populations in different regions. As the indexing of population density was not the primary objective of the study, I sought a method that would yield consistent and comparable results with a minimum expenditure of time.

As I was working with large areas, 15 by 15 miles and larger, many standard techniques of measuring population density, such as those described by Kendeight(1944)*, were impracticable. Roadside counts (Kendeigh, 1944; Howell, 1951; Hewitt, 1963) did not appear promising as cardinals are seldom seen along roadways in southern Ontario where I began this work. As I had had much previous success in trapping cardinals using a recorded song and a mounted bird as a lure, and as the species is a loud singer, I developed a modified roadside count method utilizing responses to tape-recorded song.

Listening counts along roadways are well known to workers in game bird management (Kimball, 1949; Rosene, 1957; Foote, Peters, and Finkner, 1958; Smith and Gallizioli, 1965; Gates, 1966). Tape-recordings have been used to locate birds (Bohl, 1956; Levy, Levy, and Bishop, 1966). Stirling and Bendell (1966) used tape-recordings to stimulate calling of the Blue Grouse (_Dendragapus obscurus_) in a census method,

---

* Literature cited in this appendix is included in the thesis bibliography.

but I am unaware of such a technique having been used for indexing population densities of passerine birds.

BASIC TECHNIQUE

The method of sampling is as follows. An automobile is driven to a predetermined point on a road, it is stopped, and an amplified tape-recording of Cardinal song is played. Three songs are played in 15 seconds. This is followed by a listening period of 30 seconds when the number of birds responding are counted. The procedure is repeated four times, bringing the total listening time to two minutes. A "response" is defined as the singing of a bird or the approach of a non-singing male. I found it possible to sample about 20 points in two to three hours if the points were selected at random from a grid of one-mile cells where the sampled cells represented about 60 per cent of the total study area and the shortest route connecting them was followed. In other applications when sample points were non-random, e.g., a line transect with points one mile apart, sampling was somewhat faster, and about 10 points could be sampled per hour. The index value is the average number of birds responding at the sampled points.

Songs were broadcast from a continuous loop of tape on the recorder, amplified by a 12 watt transistorized unit, and fed through a 7.5 watt loud speaker fitted with a horizontal, circular baffle and mounted vertically on a car window. The baffle and vertical mounting were used to distribute the sound as uniformly as possible. A large VU meter was connected across the voice coil for monitoring the output level of the signal. The volume level used was empirically determined as that which a listener could just hear at one-quarter mile, this being approximately the average distance that a singing cardinal can be heard.

Urban areas and heavily travelled paved roads were avoided because of the noise usually associated with them.

INCREASE IN RESPONSE OVER NORMAL SINGING

Figure A1 shows the effect of continuing listening periods beyond the four normally used. The cumulative percentage increase shows almost no levelling off even by the eighth period, and the greatest percentage increase of successive listening periods occurs in the second period. My selection of four listening periods is, therefore, arbitrary; it is not a meaningful biological unit. Instead, it represents a compromise between a large number of listening periods and the maximum number of points that can be sampled in a reasonably short time. It should be obvious from Figure A1 that the index value is conservative and not that which could be obtained if listening were prolonged.

There can be no doubt that the use of tape-recordings increases the number of birds heard or seen (Table A1). The difference in percentage increase between April and July is typical; the spontaneous singing of the species is decreasing throughout this period, whereas the responses to recordings remain about the same. The very large increase (160 per cent) in July resulted from playing recordings later in the day than usual. This increase is analagous to the seasonal one just described. A similar comparison in Tennessee showed a relatively small increase of 37 per cent. This may be an artifact of a very high population density and will be discussed later.

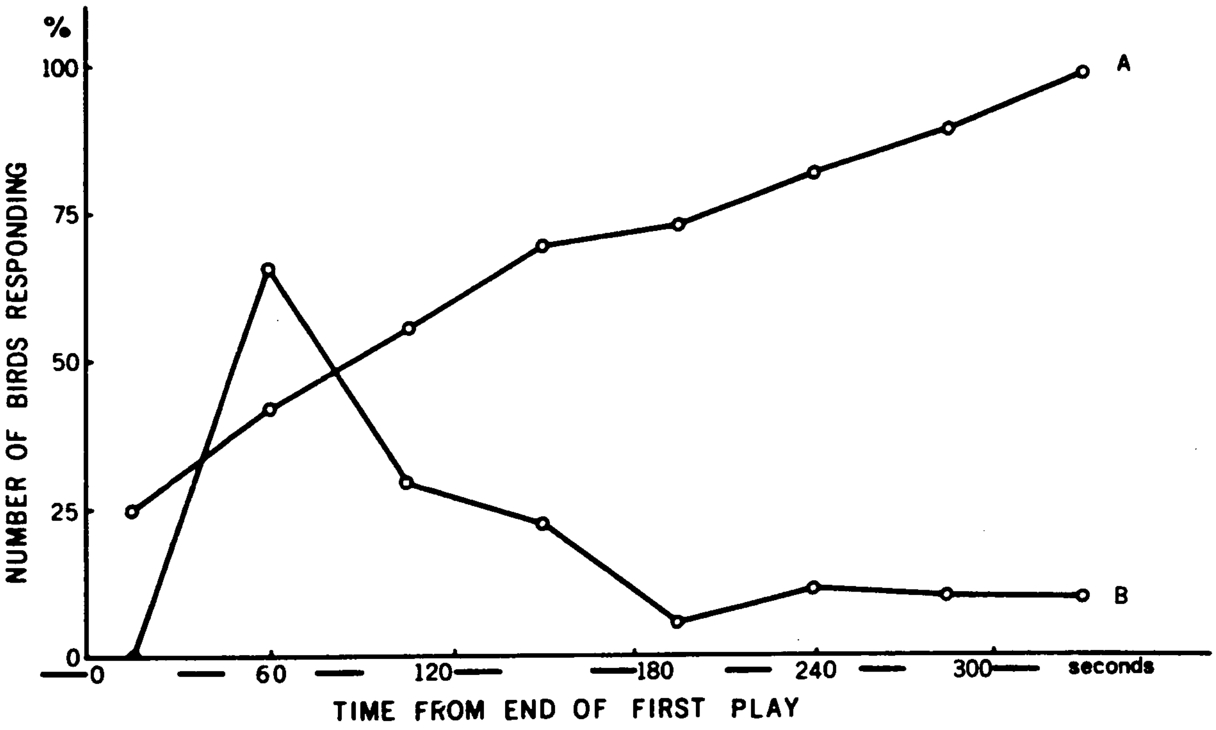


Figure A1. (A) Cumulative percentage increase in number of cardinals responding with extended listening periods. The total number of birds responding was arbitrarily assigned the value of 100 per cent. (B) Percentage increase from previous to next listening period. Points plotted represent the average of 20 points sampled on 27 and 28 March 1966 near Lambeth. Ontario. Solid lines on time scale indicate playing of tape-recorded song.

TABLE A1

INCREASE IN RESPONSE ATTRIBUTABLE TO THE USE OF TAPE-RECORDINGS

Locality (nearest town)	Sampling dates	Index value		Percentage increase	No. of points sampled	P*
		Without tape	With tape			
Lambeth, Ontario	18-19 April	0.600	1.000	67	20	NS
Melbourne, Ontario	21-22 July	0.290	0.613	111	31	<0.025
Melbourne, Ontario	15-16 July†	0.161	0.419	160	31	<0.01
Dresden, Tennessee	22-23 June	2.95	4.05	37	20	<0.005

* Significance level of one-tailed Wilcoxon Signed Rank Test of difference between dependent means (Siegel, 1956).

† Sampled between 1030 and 1330 hours. All others were sampled just after sunrise.

FACTORS INFLUENCING RESPONSE

The importance of standardizing as many conditions as possible in order to increase confidence in interpreting the results obtained by a technique such as this is obvious. The method is not only susceptible to vagaries of weather, as are most field experiments, but to almost any distracting sound: crowing of roosters, awakening roosts of blackbirds, barking of dogs, bellowing of cattle, and, worst of all, traffic and tractor noise.

Additional factors influencing response can be roughly categorized as climatic, temporal, and physiological or psychological. The acoustic influence of topography and cover on both broadcast songs and responses presents too formidable a complex of factors for investigation here. It is assumed that such factors cancel each other over a large area. Also, they are largely mitigated in successive comparisons of the same areas. Under climatic factors are included temperature, cloud cover, wind, rain, snow, and fog. Temporal factors include daily and seasonal changes. Physiological or psychological factors are more subtle in effect. For example, there may be differential response to local and foreign recordings or perhaps to different songs of the same population. The volume level of the broadcast song might affect response. Also, there is the biassing influence of several simultaneous songs on the perceptive ability of the listener.

I have examined the effects of some of these factors. The only main climatic factors that appear to appreciably influence responses are wind and rain. As wind increases, the recorded responses decrease. Light to moderate rain seems to inhibit singing, and the drumming of rain on roads and nearby vegetation makes listening impossible. There was no evidence that even very dense fog had any influence on response, although spontaneous singing seemed somewhat suppressed under such conditions.

The time of day is critical. The distribution of responses obtained at different times of day is shown in Figure A2. The response drops from a morning peak to a low level in mid-afternoon, then rises again in the evening, but not to the same high level as morning song. This is similar to the pattern of spontaneous singing of most passerine birds (Van Tyne and Berger, 1959: 147). From this preliminary work, I considered a possible correction factor for evening sampling. However, subsequent sampling indicated that the ratio between means of morning and evening samples was not constant enough for reliable estimation. This inconstancy was probably attributable to the greater chance of wind in the evening and also to the increase in human activity in some areas. Thus, all further sampling was restricted to morning hours; each sample route was begun between the onset of civil twilight and sunrise, which is about the time that most individuals of this species normally begin to sing (Allard, 1930; Leopold and Eynon, 1961; Wiens, 1960).

The order of sampling is of some interest. Davis (1965) has pointed out that in censuses of singing birds more may be noted at the beginning of the observation period than at the end. I have found the same to be true using tape-recordings. This, of course, was predictable from Figure A2. But by repeating several sample routes in reverse order at the same time on different days, I discovered that although more birds are counted in the early half of sampling, the average number remains

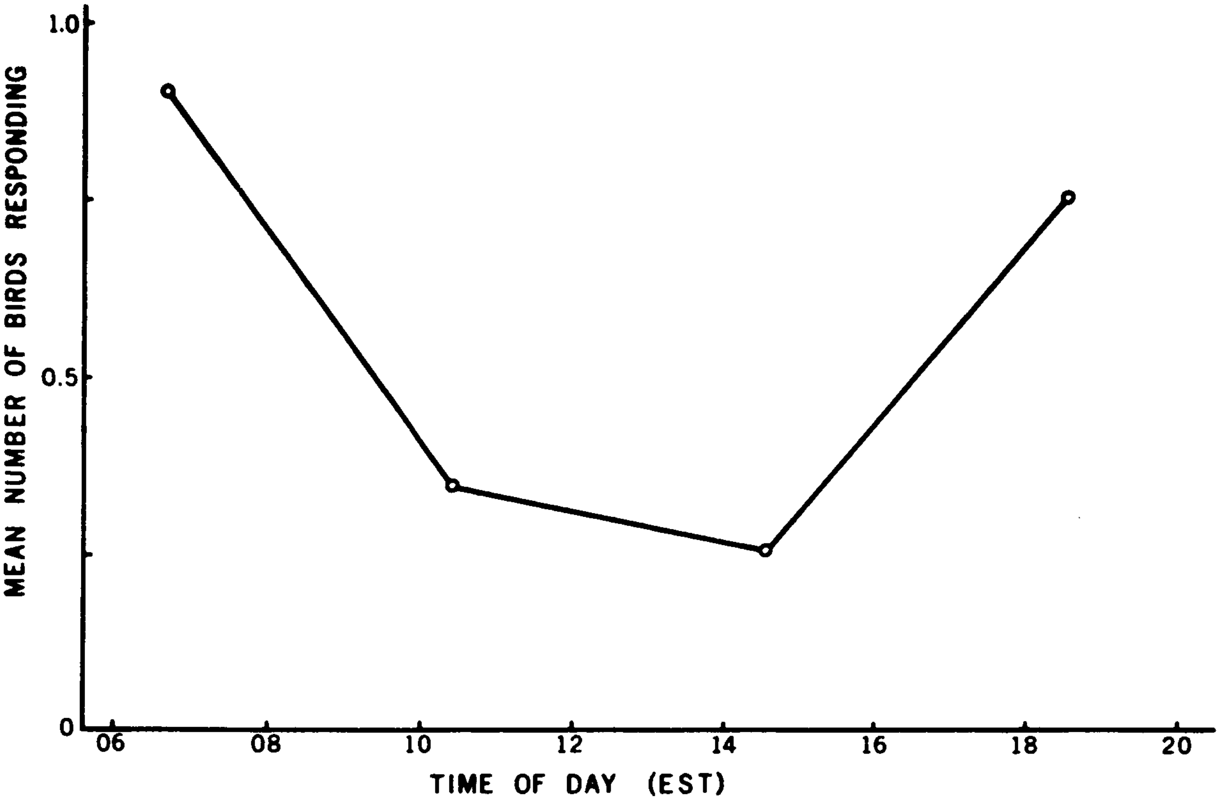


Figure A2. Distribution of responses obtained from sampling the same 84 points at four different times of day near Melbourne, Ontario, between 2 and 13 August 1964. (P<0.01 in Friedman two-way analysis of variance.)

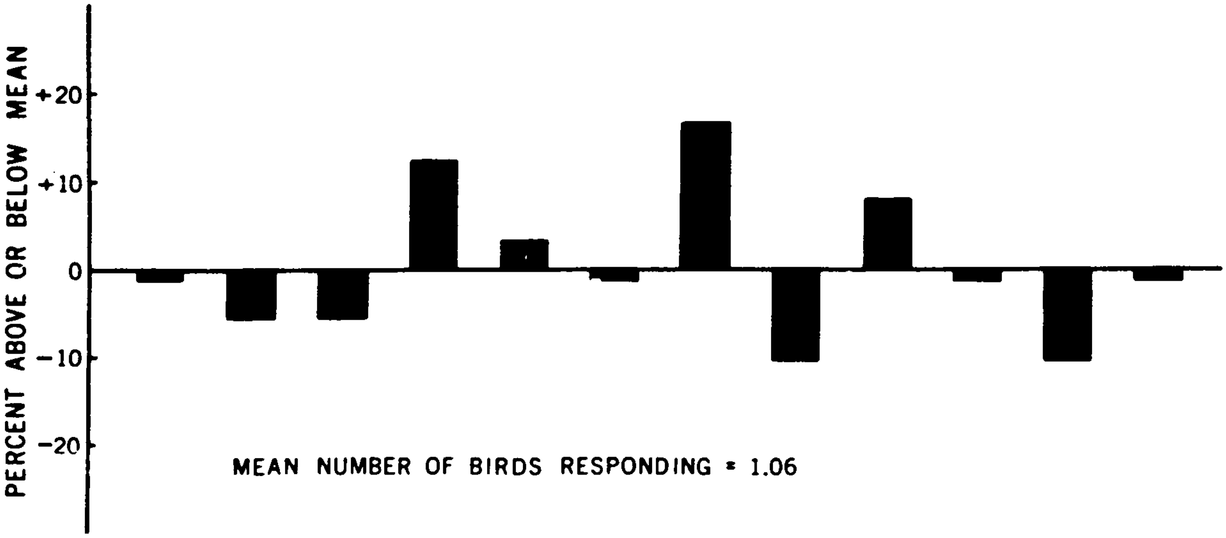


Figure A3. Variability of index among 12 samples of the same 20 points near Lambeth, Ontario. Points were sampled approximately every 14 days between 1 March and 10 August 1965.

constant.

Changes in response are abrupt in early spring at the onset of seasonal singing and again late in the summer when reproductive activity wanes. However, during the intervening period, responses remain fairly constant (Figure A3) while spontaneous singing steadily declines. Herein lies one of the principal advantages of using tape-recordings to stimulate song. The method is not restricted to the spring when birds are most active, as are many censusing techniques, but will yield fairly consistent results late in the season. In Ontario, it was possible to obtain comparable results between late February and mid-August. In Tennessee, a sudden decline of spontaneous singing and concurrent reduction of response to tape-recorded song occurred in late June. However, as spontaneous singing begins somewhat earlier in the season (Laskey, 1944), it is likely that the technique would also be applicable early in the year.

I did not experiment with the volume of playback song, but used a standard level previously described. The Cardinal, in Ontario, has a vocal repertoire consisting of some 10 to 19 recognizable song types (Lemon, 1966). I used a song that is widespread throughout the species' range; it corresponds approximately to type WBW of Lemon's classification.

It is well known that the reaction of a bird upon hearing a foreign conspecific song may be quite different to that upon hearing a neighbour's song (Frings et al, 1958; Weeden and Falls, 1959). I compared responses at sets of 20 points to determine if differences existed when I played tapes of foreign birds rather than local ones. Slightly fewer Ontario birds responded to songs recorded 17 miles to the west and 37 miles to the east (mean values of 0.85 versus 1.15 and 0.90

versus 1.15 respectively); whereas, slightly more Tennessee birds responded to an Ontario song recorded 627 miles NNE (Ontario, 3.65; Tennessee, 3.52). A reciprocal test in Ontario showed similar results (Ontario, 1.22; Tennessee, 1.32). This suggests that there may be slight differential response associated with different populations. However, as none of these differences are statistically significant, they appear negligible for this application. Lemon (1967) has shown that there are quantitative differences in the singing of cardinals responding to different local dialects, but his work shows no appreciable difference in numbers of birds responding to recordings.

Perhaps the greatest disadvantage of this, and of any technique involving listening, is its limited applicability in regions of high population density. In high density regions, where larger numbers of birds can be expected to respond at a point, I think that close singers tend to mask more distant ones. Thus, in such areas, too few birds are scored. I believe that the low increase in Tennessee (Table A1) resulted because not all birds responding to the tape were actually counted (I differentiated up to eight individual birds at a point.); whereas, birds singing spontaneously had a higher probability of being noted because there were fewer singing.

It should be noted that the female Cardinal also sings occasionally. In low density populations, I was able to see most of the responding birds. The incidence of female song during such sampling was below one per cent. Furthermore, I have found that if the female of a pair responds to a recorded song, it is generally many minutes after the male has done so. Therefore, the bias introduced by singing females is considered to be negligible.

A further consideration should be kept in mind by anyone using this or any technique involving tape-recording. A recorded song or call, unless played at a volume well below the normal singing level of the species, can never be regarded as a *constant* stimulus. The stimulus value of the song is likely modified in a complex manner by the members of the population to which it is being played. Thus, two or more birds responding to a recording probably increase the stimulus value for themselves, through feedback, as well as for other conspecifics within hearing range. Consequently, in a dense population, which may only be a very local condition, a recording may have a higher effective stimulus value than in a sparse population if few birds are singing prior to the broadcast; the opposite may be true if most of the birds are already singing.

It should be clear from the above discussion that in order to obtain truly comparable results, as much control as possible should be exercised. Sampling should be confined to the same relative time of day, noisy locations such as heavily travelled highways or urban and industrial areas should be avoided, and mornings with considerable wind or rain should not be used.

Of course, sufficiently large samplessizes should be used in making statistical comparisons. I generally used routes containing 20 points, a convenient number for a morning's work. However,aa sample of 60 to 100 or more points is preferable for comparative purposes.

Also, the technique seems better suited to moderate population densities than to very high ones.

RELATION OF INDEX TO POPULATION DENSITY

It should be recalled that this technique was developed to yield a relative index, not an absolute measure of density. It is unlikely that the relationship between the index value and the real density is linear. Possibly, it is linear in low densities and becomes logarithmic as density increases. This seems reasonable because of the masking effect that I previously suggested in very high densities. Although the actual measurement scale of the index has not been elucidated, it is undoubtedly at least ordinal, i.e., an increase in index value under similar environmental conditions indicates an increase of unspecified magnitude in population density. The particular relationship could be established through independent, empirical estimates of population densities. To obtain such information for two of my study areas, I made 14 strip censuses, each one mile long, randomly selected and randomly oriented. Each male seen was plotted on an aerial photograph, and the density was then computed from the average of the 14 counts using the method of Hayne (1949). In Tennessee, the density was 30 males per 100 acres (o.74 per hectare). In Ontario (Elmira), the density was 0.48 males per 100 acres (0.012 per ha.). Of course, many more areas of different density would require sampling by the two methods to establish a continuous relationship.

I foresee no reason why a similar technique could not be used to advantage with other species. I have not experimented with many passerine species, but I have played amplified songs of the Indigo Bunting (<u>Passerina cyanea</u>) in areas of high density for that species and found it to respond in a manner very similar to that of the Cardinal. So, I would expect the technique to work particularly well for any species with a loud or distinctive song or call.