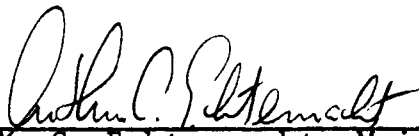


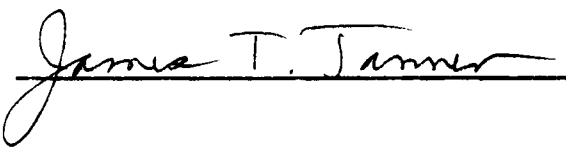
To the Graduate Council:

I am submitting herewith a thesis written by Reed Frederick Noss entitled "The Avifauna and Its Diversity in Sugarcreek Reserve: Component Trends over a Summer and Implications for Sanctuary Management." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

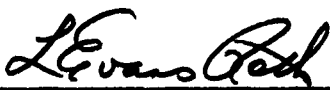

A. C. Echternacht, Major Professor

We have read this thesis
and recommend its acceptance:





Accepted for the Council:



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THE AVIFAUNA AND ITS DIVERSITY IN SUGARCREEK
RESERVE: COMPONENT TRENDS OVER A SUMMER
AND IMPLICATIONS FOR SANCTUARY
MANAGEMENT

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Reed Frederick Noss
June 1979

1390022

DEDICATION

I dedicate this thesis to my parents,
Jim and Peggy Noss,
who have forever encouraged and supported me
in my study of nature.

ACKNOWLEDGMENTS

I am particularly grateful to my major professor, Dr. A. C. Echternacht, and graduate committee members, Dr. J. T. Tanner and Dr. E.E.C. Clebsch, for their encouragement and critical evaluation during the course of this study and writing. I am also beholden to the eternal mirth and fellowship of Moon Enterprises, and especially to the warm companionship of my fiancée, Miss Myra Wilson.

ABSTRACT

Despite the plethora of literature on the theoretical implications of species diversity and the measurement and expression of diversity in ecological communities, sample size dependence and controversy over the relationships between the diversity components have invalidated comparisons between studies and obscured ecologically meaningful conclusions. In this study, the avifauna of an internally heterogeneous 228 ha nature reserve (Sugarcreek Reserve) in southwestern Ohio was censused from May 31 to August 9, 1978, to discern trends in species composition and diversity components over the breeding and postbreeding seasons. Three-hour fixed strip censuses, averaging three censuses per week, were conducted each week over the 11-week study period. Species diversity was calculated by the Shannon formula on both a discrete daily basis and on a cumulative basis over the span of the study. It was concluded that species diversity variables show distinctly different trends and relationships to one another when analyzed cumulatively from when analyzed discretely. Although the discrete measurement system is useful for illuminating component trends over time, the cumulative system allows quantification of sample size effects and is more likely to generate predictive relationships between diversity variables. The association

between species richness and species diversity was found to be significantly positive in both the discrete and the cumulative data, but the correlation is stronger in the cumulative data. The relationship between evenness and species diversity is directionally opposite in the two data sets. While the discrete measurement system found diversity and evenness to be positively correlated, with parallel variation attributable to the occasional occurrence of large monospecific flocks, the cumulative system found diversity and evenness to be negatively correlated. Opposing trends result from the addition of rare species to the sample with increasing sample size, which lowers the evenness value while increasing diversity. While there was no significant correlation between evenness and richness in the discrete data, a negative correlation in the cumulative data is again related to the addition of rare species to the sample. Null hypotheses predicting constancy of diversity components over the summer were supported by the discrete data. Significant increases in both cumulative species richness and cumulative species diversity were found as cumulative sample size increased over the study period. The increase in species diversity was significant only up to the second week of study, while richness increased significantly up to the fourth week. Cumulative species evenness decreased significantly with increasing cumulative sample size up to

the third week of study. Approximately 42 hours of observation (14 three-hour censuses) with a cumulative sample size of 3030 was deemed sufficient to accurately assess true breeding bird composition and diversity of the study area.

Sugarcreek Reserve, with 61 species assumed to be breeding, contains a more diverse avifauna than comparable temperate areas for which diversities have been reported in the literature. This high bird species diversity results from high internal habitat heterogeneity and edge effect, the comparatively large size of the study area, and the recent insularization and concomitant supersaturation of the reserve as surrounding habitat has given way to intensive agriculture and housing subdivision and thus become unsuitable for many species. Future management of Sugarcreek Reserve should emphasize preservation of extinction-prone species assemblages rather than high habitat and species diversity per se. Such policy is most conducive to the long-term maintenance of regional diversity in a deteriorating landscape.

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CHAPTER I

INTRODUCTION

The problem of species diversity, its measurement and its meaningfulness in the ecological-evolutionary context, has for several decades been a source of sometimes heuristic, sometimes tedious debate among those interested in theoretical community ecology and, more recently, in island biogeography and practical applications for the design of natural reserves. Species diversity is by definition an attribute of all biological collections, but why one community should contain more or fewer species than another is as yet enigmatic. Empirical observations of latitudinal gradients in species diversity (see Pianka, 1966) and variability in within-habitat and between-habitat diversity have prompted some fundamental questions concerning the stability and predictability of different ecosystems, the relation of the structural complexity of the environment to the number of species present, and the apportionment of resources among the members of guilds over ecological and evolutionary time. The myriad hypotheses offered in explanation for these intra- and interregional disparities have not yet succeeded in providing sound predictive formulae; inconsistencies, exceptions, and contradictions are uncomfortably ubiquitous and, increasingly, the very basis

of the equilibrium theory of community structure upon which most assumptions have at least implicitly rested is being challenged (Connell, 1978; Huston, 1979).

Birds have been the most frequently studied group of animals in relation to the diversity problem probably because they are the best known and most easily observed and identified animals (Diamond, 1973), and because their esthetic appeal is universal. The relationship between vegetation structure and bird species diversity has been studied most intensively and it is well documented that the structural characteristics of the vegetation can be used to accurately predict the diversity of bird species within a given biogeographic region (MacArthur and MacArthur, 1961; MacArthur et al., 1962; MacArthur, 1964, 1965; MacArthur et al., 1966; Karr, 1968, 1971, 1975; Recher, 1969; Karr and Roth, 1971; Willson, 1974; Roth, 1976), although the predictability fails for comparisons between biogeographic provinces (Terborgh and Weske, 1969; Terborgh, 1977). It is now apparent that structural complexity can not alone account for the increased diversity observed in such habitats as tropical forests. If one is concerned with ultimate explanations for regional diversity patterns, the heterogeneity hypothesis, while supported by convincing evidence for animals, is clearly inadequate since it pushes the problem on to the plant ecologists; that is, "the complexity

and diversity of plants may explain part of the diversity of animals, but this still leaves us with the problem of plant diversity" (Huston, 1979). It has been assumed in many cases that the high diversity of tropical systems relates to their more "stable" condition (Klopfer, 1959) which allows for species coexistence through increased niche overlap or niche compression, with the relative "equitability" of the physical environment assuring a stable food supply (Karr, 1971). That there is a more precise resource subdivision in space, and perhaps also in foraging strategies, in the tropics has been substantiated in a variety of studies of tropical avifaunas (Orians, 1969; Terborgh and Weske, 1969; Karr and Roth, 1971, among others) and in New Guinea by Diamond (1973). Orians (1969) and Karr (1971, 1975) have advanced the hypothesis that there is a greater range of resource types (particularly fruits, large insects, and nectar) permanently above threshold levels in tropical forests, allowing the addition of bird species with no temperate counterparts. It is evident above all that no single hypothesis can account for all the observed patterns in bird species diversity and that the "relative influence of factors varies among environments and differs among taxonomic groups due to differences in morphology, population dynamics, biology, and complexity of interspecific interactions" (Karr, 1975). Recently, however,

a general hypothesis of species diversity has been proposed by Huston (1979) which identifies the common elements of previous hypotheses (e.g., competition, predation, environmental stability, predictability, and productivity) and demonstrates that the observed patterns may be harmoniously explained by a dynamic equilibrium (competitive non-equilibrium) theory which asserts that diversity may be maintained by a dynamic balance between the rate of competitive displacement and the frequency of population reduction. Huston's model is uncommonly robust and is certain to spark interest among theoretical ecologists.

The measurement and expression of species diversity has been the arena of considerable mathematical theorizing since Gleason (1922) first discussed the concept, though Fisher et al. (1943) were apparently the first to introduce the term into the literature (DeJong, 1975). Since then the concept of species diversity has been multifariously defined with several different indices developed to express it. The value of a given diversity index is that it permits comparison of species-number distributions between communities, or of a certain community over time. Shannon (in Shannon and Weaver, 1949) is primarily responsible for the formulation of a diversity measure for use in the information theory of communication. Shannon's formula and similar "informational measures" have since been widely used by

ecologists in the measurement of diversity (e.g., Margalef, 1958). Such measures are especially applicable in that they do not require that species conform to any strict numerical distribution (Kricher, 1973). Informational measures are also of considerable theoretical appeal because they relate to uncertainty, the information content of a community being equivalent to the uncertainty involved in predicting which species a freely-wandering animal would be confronted with by the next random encounter (Lloyd, Zar, and Karr, 1968).

In Shannon's formula (also called the Shannon-Weaver or Shannon-Wiener formula)

$$H' = -\sum_{i=1}^S p_i \log p_i$$

where H' is species diversity (information content of the community), S is the number of species in the sample (species richness), and p_i is the proportion of the total sample belonging to the i th species. Lloyd and Ghelardi (1964) have pointed out that this measure has two separate components: species richness (S), and the "equitability" or "evenness" ($J' = H'/H'_{\max}$, the ratio of the observed diversity to the maximum diversity possible for that number of species) of relative abundances. Evenness is highest when all species in the sample are equal in population size.

There are various mathematical and interpretational problems inherent in the informational measurement of diversity and the relevance and usefulness in the practical sense of information theory has been questioned (e.g., Hurlbert, 1971; Peet, 1975; Smith and Grassle, 1977). It has been noted that the nature of the informational measure of diversity is such that the addition of a large number of rare species to the sample makes little contribution to the diversity index for the community as a whole (Peet, 1974). Sager and Hasler (1969) and Karr and Roth (1971) have criticized this insensitivity of the Shannon formula to the rare species of the community since, although the individual importance of a rare species is generally less than that of a common species, the collective importance of all rare species in a community can be considerable. In their study of several New World avifaunas, Karr and Roth (1971) found that the rare species (those which each contribute less than 2% to total sample size) in tropical areas make up 36-37% of the number of individuals in the community and are, therefore, quite important in community energetics; yet these species are overlooked by the informational measure of diversity. Hurlbert (1971), however, characterizes this sort of criticism as "as invalid as complaints that the weight of a tree is an inadequate measure because it is insensitive to the tree's functionally important leaves"

since diversity indices do not assume that the most abundant species in the community are likewise the most important. A species' importance is better defined as "the sum, over all species, of the changes (sign ignored) in productivity which would occur on removal of the particular species from the community" (Hurlbert, 1971). Informational measures of diversity are not the only indices which have been criticized for paying too little attention to the rare species. Simpson's index (Simpson, 1949), derived from probability theory, is for example, even more strongly affected by the most abundant species in a community than are the informational measures (Hill, 1973; DeJong, 1975).

Although Shannon's formula is the least sensitive to sample size of the various informational measures (Karr, 1968; Kricher, 1973), it still tends to underestimate the true amount of information in the statistical population at small sample sizes (Bowman et al., 1971). Smith and Grassle (1977) have indicated that differences in diversity estimates from samples from two different statistical populations can result from three distinct effects: true differences in species diversity, random sampling error, or a sample size dependent bias of the index. When the sample size is small (particularly if less than about 50 individuals), it is often impossible to separate these three effects. The two components of informational diversity

are also sample size dependent, indeed much more so alone than when incorporated into the H' measure. Not only is there the intuitively obvious increase in species richness with sample size, which necessitates that comparisons between communities be based on similar numbers of individuals, but the manner in which sample species richness increases with sample size varies according to the number of species and their relative abundances; it is possible that at one sample size collection A will have a larger richness value than collection B, while at another sample size collection B has the larger value. Therefore "species richness comparisons made at a single sample size (n) permit only limited conclusions" (Hurlbert, 1971).

Whereas species richness tends to increase with increasing sample size, species evenness often does just the opposite, in accordance with the trend that larger collections have more rare species, the addition of which will always lower the J' value (Hurlbert, 1971). Evenness is a relative diversity index component in that J' , for example, is defined as the ratio of the observed diversity to the maximum diversity possible for a given collection (Lloyd and Ghelardi, 1964; Pielou, 1966). Peet (1975) has shown that all relative diversity indices, whether scaled to maximum diversity with a variable species number or with a fixed species number, are sample size dependent and in as much as

they fail to approach constant values with infinite sample size are "inappropriate for most studies of ecological diversity." Peet (1975) notes, however, that the Shannon index, based on percentage composition by species, will approach a constant value with increasing sample size in a hypothetical community with an infinite number of individuals but with the number of species and their relative abundances predetermined, as will also the indices of Simpson (1949) and McIntosh (1967). We can infer from the above indications that although the H' value is not overly sensitive to sample size above some crucial minimum, its relativized component of evenness (J') is. It appears then that the opposing sample size dependent effects of richness and evenness may balance each other when incorporated into an informational diversity measure like Shannon's, but that extra caution must be taken to adjust for sample size differences before comparisons are made between communities for the components S and J' , and also for H' when sample sizes are small or the sample not truly random (Hill, 1973).

The problem remains with diversity indices in general of the lack of any objective way to assign relative weights to the richness and evenness components of the index. Hurlbert (1971) doubts that any objective way will ever be found since "diversity . . . has never had a single,

unequivocal definition." Generally the two components are not independent variables in ecological systems (Sheldon, 1969), partly because the added species at high values of species richness tend to be rare and thus to depress the evenness of relative abundances. The result is the plateau effect of the H' value at increasing sample sizes mentioned above. Of course, in sampling real ecological communities within finite boundaries, if H' never plateaued such extreme sample size dependence would certainly make the value of little worth as a sampling measure and the whole concept of species diversity horribly chaotic, a situation it already approaches. A curvilinear correlation between H' and S has similarly been attributed to decreasing evenness with the rare species appearing at high sample sizes (Monk, 1967; Kricher, 1972). This plateau effect, however, may only be a consequence of plotting H' against S on an arithmetic scale. Transformations have shown that when diversity values (either Shannon's, Simpson's, or McIntosh's) are plotted against the $\log_2$ of species richness, the plot is linear (Tramer, 1969; DeJong, 1975); the plateau effect may be merely a mathematical rather than an ecological phenomenon. Furthermore, DeJong (1975) compared the above three indices for the relative influence of evenness and richness on the diversity value for identical data and found that Shannon's index is more strongly influenced by

its richness component than by its evenness component when compared to Simpson's or McIntosh's index.

Despite the problems associated with the informational measurement of diversity, I agree with Hill (1973) that Hurlbert's despair in the "nonconcept of species diversity" (Hurlbert, 1971) is premature and "when carefully defined according to an appropriate notation, diversity can be as unequivocal as any other ecological parameter" (Hill, 1973). Which diversity index is best for a particular analysis may always be disputed. Willson and Moriarty (1976) used the Shannon index "solely so that our data would be cast in the same terms as most previous work concerned with bird species diversity, not because it is particularly good." I too consider the comparative value to be sufficient justification for my use of the Shannon index in this study and moreover agree with Tramer (1969) and Kricher (1972) that it is worthwhile to evaluate the index in terms of its component parts since the components can vary independently of one another to the extent that two samples having identical H' values may in fact be very different. Tramer (1969) found that changes in bird species diversity were closely correlated with species richness, while the equitability component remained stable, in a comparison of different bird communities. He concluded from this that "the factors which regulate bird species diversity do so by

determining the number of species which can coexist in a given habitat" and suggested that "the regulation of diversity by either the species richness or relative abundance components represent alternative strategies which are suited to predictable/nonrigorous and unpredictable/rigorous environments, respectively." Kricher (1972), in a comparison of summer and winter avifaunas, found higher equitabilities in summer, suggesting as Tramer (1969) did that territoriality in nesting passerines influences them to distribute themselves evenly among their own species. Austin and Tomoff (1978), in an analysis of Nevada and Arizona avifaunas, found that evenness remained at a high level throughout the year and that species richness and diversity varied. But instead of attributing the consistently high evenness values to territoriality, which in most birds is limited to the breeding season, they proposed that trophic diversity in bird communities is the fundamental basis for high relative abundances year round and that in most terrestrial avian communities species counts of birds alone may provide a fairly good prediction of bird species diversity at any time of the year. But while species richness alone might be all that is required to describe diversity in many avifaunas, important ecological factors can be elucidated through consideration of equitability trends.

Studies such as the above provide some reassurance to those ecologists haunted by the question of just what significance does that diversity figure have ecologically. One of the most elusive and controversial relationships is that between species diversity and ecosystem stability, a topic beyond the scope of this study. Kricher (1973) sums up the problem succinctly when he states that "the entire question of how diversity and stability are related could prove to be an ecological 'chicken or the egg.'" Finally, species diversity is undeniably important in human esthetic appreciation of natural areas, as any "birder" will testify. It is naive science to assume that such subjective, esthetic human sentiments are unimportant to considerations of environmental quality and proper ecosystem management. On the contrary, the attitudes of society toward natural areas, as influenced by the variety of "interesting" species, are paramount to the ultimate protection and preservation of these areas for whatever purpose. The holistic maintenance of organic diversity as a fundamental precept of conservation ethics is unequivocally justified.

Despite the plethora of literature on the theoretical implications as well as the measurement and expression of species diversity, the need remains for further empirical testing of the relation of the informational diversity index and its components to sample size (and/or study time) for a

given taxocene using a specified census method in a given study area. These variables must be qualified and, ideally, quantified before valid comparisons can be made between communities. Although tests for variability in bird species diversity and its components over time have been conducted (e.g., Tramer, 1969; Kricher, 1972, 1973; Adams and Barrett, 1976) with illuminating results, these studies have not been properly concerned with sample size dependence or with determination of the sample size or amount study time required to obtain a reasonable estimate of the true species diversity, richness, and evenness of an avian community.

The purpose of this study was to test for species diversity (H' , S , and J') trends over a summer in a structurally heterogeneous 228.25 hectare (564 acre) nature reserve in southwestern Ohio and to explain observed trends in terms of ecological, sampling, and/or stochastic variables. Measurements of both discrete daily census diversities and cumulative diversities were calculated to divulge such trends and to provide for estimation of the sample size or study time required for a researcher using similar methods in a similar environment to assure a portrayal of true bird species diversity of a given level of accuracy. Examination and comparison of discrete census trends versus cumulative data trends in the association of diversity variables is particularly heuristic since much confusion in the literature may stem simply from failure to separate sample size effects

which can obscure ecologically meaningful relationships between variables; additionally, the sample size dependencies can be interesting in themselves. Following informational characterization of the Sugarcreek avifauna, speculations concerning future diversity and compositional trends and implications for sanctuary management and regional land use planning are discussed in light of the habitat island character of the reserve. Specifically, the following sets of hypotheses were tested:

I. Null Hypothesis: Over the span of the study period, weekly mean Shannon diversity (H') values calculated from discrete daily census measurements will not vary significantly. This hypothesis, if accepted, would support the findings of Kricher (1973) and Adams and Barrett (1976) for constancy of H' values for temperate woodland birds over the summer.

Alternative Hypothesis: Over the span of the study period, calculated mean weekly diversities will vary due to intrinsic (e.g., differential population recruitment, movements) or extrinsic (e.g., changes in detectabilities) factors.

II. Null Hypothesis: Over the span of the study period, weekly means of daily census species richness values will not change significantly.

Alternative Hypothesis: Over the span of the study period, species richness will change due to intrinsic

(e.g., movement of species in or out of the study area) or extrinsic (e.g., changes in detectabilities) factors.

III. Null Hypothesis: Evenness values will remain high and constant during the study period, as Tramer (1969) found, perhaps because most species are nesting passerines which tend to distribute themselves evenly among their own species and remain on territory throughout the breeding season (Kricher, 1972), or because birds occupy a diverse number of consumer trophic levels (Austin and Tomoff, 1978).

Alternative Hypothesis: Evenness values will vary significantly during the course of the study. This could be due to postbreeding flocking and movement patterns (Kricher, 1972; Austin and Tomoff, 1978).

IV. Null Hypothesis: Cumulative bird species diversity (means for weeks) will not change significantly over the study period, indicating that one week of sampling is adequate to accurately assess true bird species diversity.

Alternative Hypothesis: Cumulative bird species diversity will increase during the study period due to sample size dependence at small sample sizes (Bowman et al., 1969; Smith and Grassle, 1977), and will either plateau at a sample size which is an objective of this study to determine, or will increase indefinitely.

V. Null Hypothesis: Cumulative bird species richness will not increase significantly during the course of

the study. Acceptance of this hypothesis virtually demands that all species in the reserve are observed during the first week of censusing.

Alternative Hypothesis: Cumulative bird species richness will increase with increasing sample size due to the universally observed sample size dependence of this component (Hurlbert, 1971), and will either eventually stabilize when all summer resident species within the finite limits of the reserve have been observed, or else keep rising indefinitely. Incremental species late in the study period must be evaluated as to whether they are nesting or resident species in the reserve or vagrants or transients from elsewhere.

VI. Null Hypothesis: Cumulative evenness values will not change significantly during the course of the study, the true evenness of the avian community being assessed in the first week of study and with no significant changes in relative abundance over the summer.

Alternative Hypothesis a: Cumulative evenness values will increase over the course of the study as observed evenness gradually approaches the high and constant equitability characteristic of most bird communities (Tramer, 1969; Kricher, 1972; Austin and Tomoff, 1978).

Alternative Hypothesis b: Cumulative evenness values will decrease as sample size increases, as predicted by

Hurlbert (1971), since larger collections have more rare species which depress the J' value.

VII. Null Hypothesis: There is no significant relation between species richness and species diversity; that is, increases in species diversity will not follow consistently with increases in species richness, since positive correlation of species diversity and species richness is neither a biological nor a mathematical necessity (Hurlbert, 1971). This hypothesis and its alternative will be tested separately with data from discrete daily and cumulative censuses.

Alternative Hypothesis: Increases in species richness will be accompanied by increases in species diversity, indicating that species counts alone are sufficient to predict species diversity in this type of avian community. In particular, species richness should be an accurate predictor of bird species diversity in ecosystems where the majority of birds are nesters (Tramer, 1969).

VIII. Null Hypothesis: There is no significant relation between evenness and species diversity. This might be found if diversity trends are observed but evenness remains constant as predicted above. This hypothesis and its alternatives will also be tested separately with both discrete and cumulative census data.

Alternative Hypothesis a: There is a positive correlation between evenness and species diversity, indicating that

variation in species diversity is positively associated with variation in evenness. This hypothesis would more likely be supported with the discrete census data than with cumulative data, for opposing trends due to increasing sample size effects would not be expected in the former. The occurrence of large monospecific flocks in particular censuses would be expected to significantly affect the discrete diversity values for those censuses.

Alternative Hypothesis b: There is a negative correlation between evenness and species diversity, a strong possibility in the cumulative census data since, while diversity values can be expected to rise and plateau with increasing sample size, evenness is predicted to drop with increasing sample size (Hurlbert, 1971), at least until the rare species in the community have been added.

IX. The previous hypothesis and its alternatives will be tested for the relationship between evenness and species richness, which is expected to be similar to that between evenness and species diversity.

CHAPTER II

THE STUDY AREA

Sugarcreek Reserve in southwestern Ohio (Greene County), about 24 km southeast of Dayton and immediately southwest of the small town of Bellbrook, is a nature reserve administered by the Dayton-Montgomery County Park District (DMCPD) and the site of my bird species diversity censuses. The reserve (Figure 1) comprises approximately 228.25 ha (564 a) of old farmland and woodlot in varying stages of secondary succession. Topographically the area is dissected upland descending to the valley of Sugar Creek, with a high of over 275 m near Wilmington Road, the western boundary of the reserve, to a low of less than 243 m in the main valley of Sugar Creek. The valley slopes, mostly heavily wooded with second growth to mature forest, are fairly steep and the creek has cut through the underlying bedrock to expose walls of shale and limestone strata as thick as 3 to 6 m in some places. This sedimentary bedrock is of Ordovician age, formed in shallow seas approximately 425-500 million years ago, and represents some of the oldest bedrock occurring near the surface in Ohio. The bedrock outcroppings are composed of Richmond shale and limestone, sometimes highly fossiliferous. Small caps of Brassfield limestone and Niagra limestone of the early Silurian Period

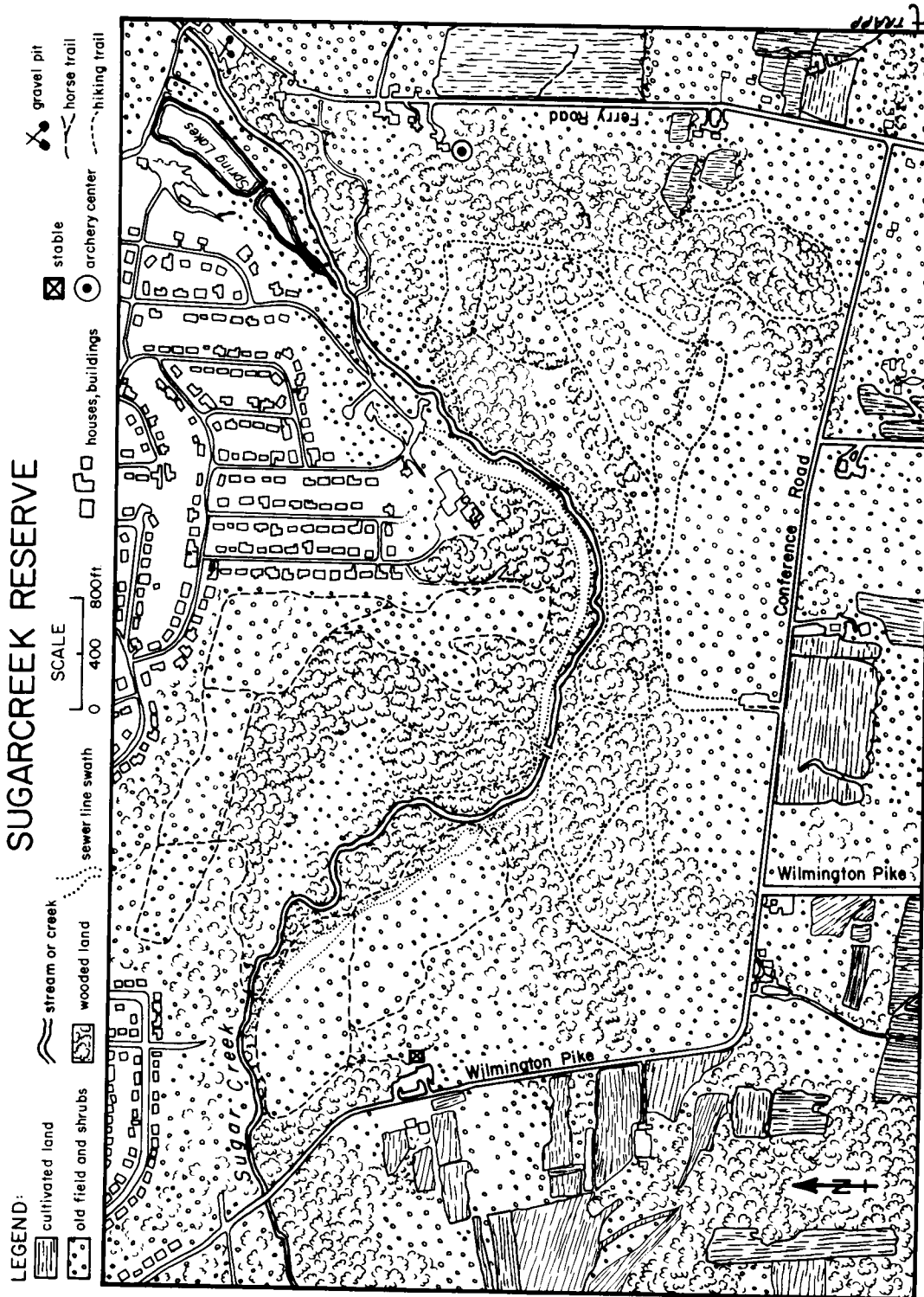


Figure 1. Sugarcreek Reserve and immediately surrounding habitat.

occur just west of the reserve area and fragments of these formations undoubtedly occur along the stream bed. Glacial till, composed primarily of an unsorted, unstratified mixture of clay, sand, silt, and coarser material deposited discontinuously as ground moraine, overlies the bedrock to a depth of approximately 6 to 46 m in the Sugarcreek area except where eroded away by the creek branches (Miami Valley Regional Planning Commission [MVRPC], 1971). Additionally, the reserve is distinguished by a prominent esker, a glacial meltwater deposit formed in tunnels in the ice and observable today as an east-west line of gravel hills just south of the main valley of Sugar Creek. Although Sugar Creek, which flows generally west to east, is the only stream of considerable size in the reserve, two permanently flowing tributaries traverse the reserve and enter Sugar Creek from the south, one near the western edge of the reserve and the other near the eastern edge. Numerous springs and several small marshes, the largest marsh arising from a spring by the western tributary, contribute further habitats to the reserve. In addition to the land within the legal confines of Sugarcreek Reserve, one census each week included the area around the ponds visible in the northeast corner of the study area (Figure 1) which comprises Spring Lakes Park and is contiguous with Sugarcreek Reserve. Domestic ducks, mallards, and Canadian geese sighted in and around these ponds were not included in the censuses.

The original pre-settlement vegetation of the Sugar-creek area consisted of beech forests (the beech-sugar maple association described by Gordon, 1969, after Braun, 1947) with mixed oak areas and elm-ash swamps, the latter located along creeks and floodplain areas (DMCPD, unpublished). Several small to moderate sized stands of mature beech-maple and mixed mesophytic associations remain on the reserve, and the bottomlands bordering the creek branches are dominated by mixed stands of sycamore, cottonwood, hackberry, chinquapin oak, box elder, slippery elm, and buckeye. The DMCPD has identified American beech, sugar maple, wild black cherry, black walnut, shagbark hickory, bitternut hickory, white ash, flowering dogwood, pawpaw, Virginia creeper, and hackberry as the primary woody components of the beech woods in the reserve today, with red oak, white oak, tulip poplar, black oak, black walnut, and sugar maple dominating the drier areas where beech is not present, as well as an oak-hickory complex containing white oak, shagbark hickory, pignut hickory, mockernut hickory, shellbark hickory, and bitternut hickory. Woody species found in the grazed and heavily disturbed areas include honey locust, basswood, slippery elm, sugar maple, hackberry, osage orange, and white ash (DMCPD, unpublished). A plant check list composed of species identified from April to July, 1968 (DMCPD, unpublished) includes 54 woody species,

122 species of flowering herbaceous plants, and seven species of non-flowering herbaceous plants. This list is most certainly incomplete as, for example, I have identified three fern species in addition to the five ferns and two horse-tails listed under non-flowering herbaceous plants. The majority of the Sugarcreek Reserve acreage today is made up not of woodland but of successional patches of variable age, the youngest being less than ten years into secondary succession. Some mowed areas are maintained by the DMCPD for group camping, picnicking, etc., and an approximately 20 m wide swath extending west to east was cut through the bottomland about six years ago for the installation of a sewer line and has subsequently grown up to wet meadow. In late summer, 1978, shortly after the completion of my field work, a large portion of the front (south) meadow, which was growing up in box elder and wild black cherry, was cut and burned with the intention of introducing a tallgrass prairie community. Islands of prairie, some of considerable size, were widespread through much of Ohio in presettlement times but have been largely destroyed (Gordon, 1969).

The fauna of Sugarcreek Reserve has been inadequately surveyed. To my knowledge the only printed account is an unpublished bird check list compiled by the DMCPD of species sighted from April, 1968 to June, 1969. The list includes only 96 species and is certainly incomplete, for my bird

counts in the reserve, both in this present study and in previous informal observations over the last few years, have yielded all those species listed plus an additional 38, for a grand total of 134 species observed over all seasons.

My reasons for choosing Sugarcreek Reserve as the site for a study of bird species diversity are the following:

1. The reserve was easily accessible for field work, located only 12 km from my parents' home and therefore providing a convenient and economically affordable study site. I am also quite familiar with the reserve and its natural history and avifauna, having visited it innumerable times in the past 10 years.

2. Sugarcreek Reserve is structurally varied with a heterogeneous assortment of vegetation stands providing several habitat types relevant to the distribution and abundance of birds. Most other studies of bird species diversity have seemingly used homogeneity of vegetation structure as a primary criterion for selection of census areas, then comparing the results from these definitive habitat types (e.g., Karr, 1968, 1976; Tramer, 1969; Recher, 1969; Orians, 1969; Kricher, 1972). It has been noted repeatedly that the spatial heterogeneity of the habitat is crucial in regulating bird species diversity, but the majority of studies have been concerned with complexity or diversity of vegetation in the vertical plane (Roth, 1976); the horizontal component of habitat diversity has been

largely ignored. MacArthur et al. (1962), however, recognized the importance of "within-plot variability" and concluded that habitat patchiness was the prime factor affecting bird species diversity and that its effect was much more important than the addition of vegetation layers. Sugarcreek Reserve, being a mosaic of habitat patches due largely to variable land use history patterns as well as variation in water relations and edaphic factors, has high horizontal complexity with a diversified resource base and thus would expectedly contain a heterogeneous and rich fauna. The study of a heterogeneous complex of habitats is legitimate and particularly valid today when "pure" stands are scarce and small. Although containing numerous habitat types, Sugarcreek Reserve is relatively distinct as an island of more or less "natural" vegetation in a sea of intensive-use farmland and, increasingly, housing subdivisions.

3. As the fragmentation and isolation of forests continues, the study of community structure and function of the resulting habitat islands is imperative if we are to preserve regional diversity. MacArthur and Wilson (1963, 1967) have shown that the number of species on an island is influenced by the island's size, internal environmental heterogeneity, age, and distance from a species source. Generally the fauna and flora of islands tend to be depauperate or disharmonious when compared with similar mainland

habitats, the number of species representing a balance between extinction of indigenous species populations and replacement through immigration by the same or other species. Diversity remains constant "only under the improbable conditions that the gain and loss components of the equation are equal" while "the day is rapidly approaching when the remnants of the natural environment will be contained in a patchwork of parks and reserves" (Terborgh, 1974). Sugarcreek Reserve is such an insular refuge; the surrounding landscape is, with continuing development, becoming increasingly inhospitable to many species and suitable dispersal corridors are being severed. From the map of the study area (Figure 1, page 21), which was made from an aerial photograph taken in 1975, it is evident that the major wooded corridor extending from the reserve is along Sugar Creek to the west of the reserve. Indeed this corridor connected Sugarcreek Reserve to another forest island less than a mile to the west and of a size comparable to the forested portion of Sugarcreek. The fate of this other forest, concerning potential development, is not known but it is significant as well as quite unfortunate that in 1978 development began south of Sugar Creek in the forest corridor that linked these two forest islands, and it appears that such destruction will sever any continuous wooded extension between the two. Moreover, "for sale"

signs are becoming increasingly prevalent on the farm lots surrounding the reserve on all sides except the north, which is already completely developed with housing subdivisions. What impact this habitat alteration and severance of suitable dispersal corridors will have on the faunal and floral composition of Sugarcreek Reserve remains to be seen, but Whitcomb et al. (1976) and Whitcomb (1977) indicate that many of the neotropical migratory birds that were once dominant in the interiors of eastern forests tend to disappear from fragmented forests and are not replaced by other species. Permanent resident passerines are less affected and often profit from such changes. Unless measures are taken to preserve forest systems of adequate size and continuity ("thousands of contiguous acres may be required to assure the long-term survival of the forest interior bird species"), regional extinctions of many neotropical migrants may be imminent (Whitcomb, 1977). Data from this study on the relative abundances of bird species in Sugarcreek Reserve can therefore be a valuable assessment for sanctuary management and the land use planning of the surrounding area, particularly if continuing study can be implemented in forthcoming years. Indeed such a follow-up dynamic approach is absolutely imperative to generate conclusions of biogeographic validity. The Dayton-Montgomery County Park District, which manages the local reserves, has at least informally expressed the need for such an appraisal.

CHAPTER III

METHODS

Two preliminary bird censuses were conducted on May 10 and 11 in Sugarcreek Reserve to test the study method and to measure bird species diversity during the peak spring migration for comparison with later summer resident breeding and postbreeding measurements. The latter censuses, which form the basis of this analysis, consisted of 33 censuses conducted from May 31 to August 9, 1978, a time period during which the resident bird patterns should be most stable, with nearly all breeding birds in territories (Trautman and Trautman, 1968; Adams and Barrett, 1976). Three censuses were conducted each week (defined as a Sunday to Saturday interval) except one week (June 4-10), when five censuses were conducted, and two weeks (June 25-July 1, and August 6-August 12) when only two censuses were conducted due to inclement weather. All censuses began within one half hour of sunrise and continued for precisely three hours. Censuses were conducted only on fair (rain-free) mornings to control for possible weather effects on avian activity and detectability. The census method was an auditory/visual fixed strip technique wherein I walked slowly (averaging perhaps 1 mph) with frequent brief pauses to look and listen, a method described by Emlen (1971).

I invariably worked alone and avoided all interruptions, my intent being to cover as much of the study area as possible each week, striving idealistically to detect every individual bird within my fixed study strip at all times. To this end I walked different parts of the reserve on different days in an alternating fashion so that over a week's time all parts of the reserve received approximately equal coverage. This was done because weekly means were used for analysis of variance in diversity calculations and I desired to achieve correct proportional coverage of all habitat types within the reserve each week. Inevitably, however, certain sections of the reserve were slighted; in particular, much of the areas around the horse barns on the western end of the reserve and the archery ranges on the eastern end of the reserve were not censused as thoroughly, nor did I normally traverse open fields or thickets except when a path led through them. Generally I followed maintained trails wherever possible but departed from trails when necessary to adequately cover back areas or other important habitat types. My daily censuses followed a loop course so that the same sections were not duplicated. Although I made no attempt to locate nests during the three hour censuses, since such diversion could result in missing birds within the study strip, nests found fortuitously were noted, as were also any definitive signs of breeding such as

persistent territorial behavior, consistently paired individuals, or the incidence of fledglings. In addition, observations made outside the census time but within the study period helped confirm breeding indications.

The differential conspicuousness (detectability) of different species presents a problem. Species vary in the readiness with which they attract an observer's attention due to differences in size, flight habits, habitat in which observed, flocking tendencies, loudness and frequency of songs and calls, flushing distance, and ease of recognition (Kendeigh, 1944). To deal with this variation, some investigators have devised coefficients of conspicuousness or detectability for species to effect more realistic estimation of abundances (Colquhoun, 1940a, 1940b; Kendeigh, 1944; Emlen, 1971). These efforts vary in their arbitrariness and to my knowledge none have been tested adequately; in fact, direct tests of the accuracy of such measures are impossible as there is no known way to obtain a complete and accurate census of nonflocking land birds as a reference (Emlen, 1971). From my experience, I find that individuals of most species in almost all habitats encountered in the reserve can be detected and identified equally up to a distance of approximately 20 m from the observer in the summer season, especially when the observer progresses slowly and makes a concerted effort to search the

vegetation for secretive, non-vocalizing individuals. Emlen (1971) notes also that plotting the frequency of detection values for successive parallel strips on either side of the route results in a distribution curve that maintains a high level for from 40 to 100 ft. (12.2 to 30.5 m) for most species before declining precipitously. I, therefore, kept my strip width constant at 40 m, recording all birds observed within 20 m in both lateral directions of my path. For completeness I included birds flying directly over the strip as well as those seen or heard within the strip width in front of or behind me, since many of these individuals will become quite silent and unnoticeable or quickly depart as the observer appears. This is particularly true for such wary species as raptors, crows, pheasant, and bobwhite. I also uttered chirping and "spshing" sounds to lure inconspicuous birds such as warblers and vireos out of hiding, as did Emlen (1971), and gave barred owl and great horned owl calls on several occasions to determine the presence and location of individuals of these species; although such tactics are inadequate to assess the abundance of owls relative to other species and may introduce bias, any bias incurred is probably less than that which would result from making no special attempt to determine the presence of such nocturnal species and they were therefore omitted from the species list. Despite these

measures to ensure completeness, some birds (e.g., non-vocalizing warblers and vireos of the canopy, ground birds in dense cover, all nocturnal species) are bound to be underrepresented and would be by any single census method or practical combination of methods. Such observational bias is inevitable whenever a supposedly random sample is drawn from a biological community in which there is a large number of species with small abundances (Engen, 1975). Emlen (1971) summarizes factors which limit the accuracy and efficiency of census methods for non-flocking terrestrial birds. According to his scheme, the present method ("count in narrow strip") may potentially be biased by the identification skill of the observer, observation conditions (weather, etc.), screening effect of the habitat, differential conspicuousness of birds, changes during the season, birds missed, and distances misjudged. Obviously I attempted to control as many of these factors to as high a degree as was reasonable, and moreover contend that the present census method was most adequate to assess relative abundances of birds over a large area. Though estimates of absolute abundance are necessary for determinations of biomass and energy functions (Kendeigh, 1944; Emlen, 1971), such methods require controlled measurements of area as well as population and are therefore intractable when large areas must be covered by a single observer in a limited

amount of time. Relative abundance data clearly suffice for diversity calculations.

The assumption that there will be no significant changes in auditory or visual conspicuousness of individual birds of the various species as the summer progresses is probably not strictly warranted, for as Welty (1975) notes, the highest frequency of singing is in the spring during territory establishment and courtship, and "after a pair is mated and the duties of rearing a family begin, song generally wanes or may cease altogether." Since different species have different detectability peaks and species that produce more than one brood will be expected to have bimodal to multimodal peaks, the abundance trends for individual species seen in the data may reflect simply detectability trends rather than variations in actual abundance. Population recruitment through reproduction, however, might compensate for decreasing detectabilities over the summer. If total sample size per census declines over the study period, it can be inferred that population recruitment is failing to compensate for decreasing post-breeding detectabilities.

Bird species diversity was calculated with the aid of the computer program for the Shannon measure described by Zar (1968) and used at The University of Tennessee, Knoxville, by my colleague Mike Sherman for tree species

diversity of Savage Gulf, Grundy County, Tennessee. The program computes informational diversity (H') and the components species richness (S) and evenness (J') as well as the maximum diversity ($H'_{\max}$) and minimum diversity ($H'_{\min}$) possible for the collection, and standard error ($s_{\bar{x}}$) of H' . For all calculations $\log_2$ was used rather than the alternatives $\log_e$ or $\log_{10}$, for mostly arbitrary reasons; all three logarithm bases have been used in the literature and indices based on different logs can easily be converted to one another by multiplication by constants (Shugart and James, 1973).

Statistical analysis consisted of one-way analysis of variance to test for significant variation among weekly means of the diversity and sample variables, as used by Kricher (1973) and Adams and Barrett (1976) for variation in bird species diversity with time. Pearson correlations, scattergrams, and linear regressions were performed to illuminate relationships between paired variables. All statistical analysis was executed by computer using the SPSS package (Nie et al., 1975) and interpreted with the aid of Sokal and Rohlf (1969).

CHAPTER IV

RESULTS

The Summer Birds of Sugarcreek: Species Composition

Eleven continuous weeks of study (May 31 - August 9, 1978) with an average of three three-hour censuses per week yielded a total count of 77 species. Appendix A lists these species in taxonomic order and supplies the following information: (1) Status, as determined by range maps in Robbins et al. (1966), information from Trautman and Trautman (1968), and Whitcomb et al. (1979), and my own observations. PR designates permanent resident (assumed to be resident in the reserve year round), SM = short migrant, and LM = long migrant. Short distance migrants are those species which winter not far south of their summer ranges, generally in the southern United States. Long distance migrants are neotropical migrants, wintering from southern Florida south to Central and South America. Distinguishing between short distance and long distance migrants is useful because it has been shown (Whitcomb et al., 1976; Whitcomb, 1977; Whitcomb et al., 1979) that neotropical migrant species tend to disappear from small isolated forest tracts, which are then dominated by species that are either permanent residents or short distance migrants. (2) Cumulative number of individuals after (x) weeks study time. This denotes

sample size for each species and increases with time in accordance with the occurrence of individuals of each species as determined by movement patterns and detectability trends. Since each week of censusing covered the same study area and most species counted are assumed to be territorial and remain on territory throughout the study period, the cumulative number of individuals refers only to cumulative sample size, not population size, for it was not intended to distinguish between individual birds of a species or map territories. (3) Relative abundance (density) and importance values. Relative abundance denotes percent of the total number of individuals (total sample size = 7613) each species comprises; the relative abundance value for a given species can be thought of as the proportion of potential encounters that is intraspecific for an individual of that species wandering freely through the study area. The importance value (Kricher 1973, 1975) is defined as the relative abundance plus the relative frequency (percent of the total number of censuses in which a given species appeared). The maximum value that a species could have would therefore be 200. The importance value allows the consideration of species that are periodically common along with species that may be consistently uncommon but nevertheless regular members of the community. The numbers in parentheses after each relative abundance and

importance value in Appendix A indicate each species' position in the ranking for each value. A "t" indicates that a species tied with at least one other for that position in the ranking. Table 1 provides a comparison of relative abundance and importance value rankings for Sugarcreek birds, listing the top 30 species in each category. Note that the first six species in each category are in identical order, indicating that these species were both highly abundant in terms of numbers of individuals and regularly recorded in censuses. In fact, these six species were each recorded in all 33 censuses, as were the top 16 species in the importance value ranking. Concerning the comparative utility of these two measures of species magnitude in the community, it is obvious that the relative abundance ranking gives, with my study method, what is probably disproportionately high weight to those flocking species that are periodically found in extremely high abundance on particular censuses when the flocks just happen to pass over the observer's transect. For example, the June 10 census recorded 120 starlings, almost all of which comprised a single flock departing the roosting area in the bottomland forest at about dawn. This flock was possibly of the type described by Bent (1950), consisting primarily of juveniles from the first brood which band together and forage in fields by day and return to roost

Table 1. Comparison of relative abundance and importance value rankings for Sugarcreek birds--top 30 species in each ranking.

By Relative Abundance (%)	By Importance Value*
1. Common Grackle	1. Common Grackle
2. Cardinal	2. Cardinal
3. Carolina Chickadee	3. Carolina Chickadee
4. Red-winged Blackbird	4. Red-winged Blackbird
5. American Goldfinch	5. American Goldfinch
6. Blue-gray Gnatcatcher	6. Blue-gray Gnatcatcher
7. Starling	7. Indigo Bunting
8. Indigo Bunting	8. Field Sparrow
9. Field Sparrow	9. Red-eyed Vireo
10. Brown-headed Cowbird	10. Acadian Flycatcher
11. American Robin	11. Rufous-sided Towhee
12. Red-eyed Vireo	12. Common Yellowthroat
13. Acadian Flycatcher	13. Tufted Titmouse
14. Rufous-sided Towhee	14. Song Sparrow
15. Common Yellowthroat	15. Eastern Wood Pewee
16. Tufted Titmouse	16. Yellow-billed Cuckoo
17. Common Crow	17. Common Crow
18. Song Sparrow	18. Chimney Swift (nn)
19. Chimney Swift (nn)	19. Common Flicker
20. Downy Woodpecker	20. American Robin
21. Cerulean Warbler	21. Downy Woodpecker
22. House Wren	22. Cerulean Warbler
23. Yellow-breasted Chat	23. House Wren
24. Eastern Wood Pewee	24. Yellow-breasted Chat
25. Common Flicker	25. Starling
26. Yellow-billed Cuckoo	26. Blue Jay
27. Rock Dove (nn)	27. Red-bellied Woodpecker
28. Brown Thrasher	28. Brown-headed Cowbird
29. Blue Jay	29. Willow Flycatcher
30. Willow Flycatcher	30. White-eyed Vireo

*See text for explanation (p. 37).

nn = no good evidence for nesting within the study area.

in the woods for the night. Such flocks have been reported to number in the thousands by mid-July. As a result of this flocking behavior, the starling ranks seventh in relative abundance but only 25th in importance value. The importance value thus corrects somewhat for the periodic occurrence of flocks which may bias relative abundance rankings. Birds such as the red-eyed vireo, Acadian flycatcher, rufous-sided towhee, common yellow-throat, song sparrow, eastern wood pewee, and yellow-billed cuckoo, all consistently common but not found in high numbers, accordingly rank higher in importance values than in relative abundances. Neither of the two values, however, can realistically be considered to provide more than a rough estimate of the true ecological importance of a species in the community. Such real importance is conceptually better defined by the sum of the ecological changes that would take place should the particular species be removed from the community (Hurlbert, 1971) but is not generally amenable to testing when so defined.

Of the 77 species of birds observed in Sugarcreek Reserve during the study period, good evidence for breeding and/or nesting within the study area was found for only 61 species. For the remaining 16 species, either the evidence for breeding was insufficient or, judging from considerations of temporal occurrence over the study period (Appendix A),

spatial location (e.g., consistently by a reserve boundary), or from various observed behavioral or known life history characteristics, the birds are assumed to have bred outside the study area and utilized the reserve only for foraging, or were nonbreeding or postbreeding transients or vagrants. These nonbreeding species are the great blue heron, wood duck, turkey vulture, red-tailed hawk, American kestrel, killdeer, spotted sandpiper, rock dove, chimney swift, red-headed woodpecker, eastern kingbird, tree swallow, purple martin, mockingbird, cedar waxwing, and scarlet tanager. Although these species probably did not nest within the study area, the persistent appearance of some (e.g., chimney swift) in the censuses suggests ecological importance in the community. Furthermore, the number of breeding bird species in this 1978 study may be lower than that of most years within the last decade. In particular, I have observed evidence of nesting in the following species in previous years: Cooper's hawk, red-tailed hawk, mockingbird, Carolina wren, and bluebird. The latter two species disappeared abruptly from the avifauna during the severe winter of 1976-77, indicating the importance of critical events in the nonbreeding season to the structure of the breeding community.

Appendix B lists the 80 species which were recorded during two three-hour censuses on May 10 and 11, 1978, when

the census method was tested and species diversity values were calculated for comparison with the summer data. The bird list for these two days of peak spring migration indicates the wealth of bird species which depend on wooded habitat islands like Sugarcreek as crucial resting and feeding areas during migration. Over the past few years of birdwatching in Sugarcreek Reserve, I have recorded a total of 134 species over all seasons.

Variation in Discrete Values of Diversity Components over the Summer

Table 2 and Figures 2-5 illustrate the observed variation in weekly means of daily census H' , J' , S , and sample size over the summer. Calculation of coefficients of variation ($CV = s \times 100/\bar{y}$, where s = standard deviation of the variable, and $\bar{y}$ = mean of the variable), useful for comparing the amount of variation in populations having different means (Sokal and Rohlf, 1969), indicates that sample size varied most ($CV = 15.5893$), followed by species richness ($CV = 7.4048$), species diversity ($CV = 4.1632$), and lastly, evenness ($CV = 3.8245$). These coefficients were calculated from daily census values for these variables, which obviously had higher standard deviations than weekly means of the same components. Analysis of variance (Table 3) indicates that there are no significant differences between weekly means for any of these variables

Table 2. Weekly means and standard deviations for discrete daily census values of diversity components.

Weeks	Sample Size	H'	S	J'
1 (5/31-6/2) 3 censuses	179.00 (s=19.69)	4.869 (s=.179)	42.33 (s=6.03)	.903 (s=.003)
2 (6/4-6/10) 5 censuses	241.20 (s=53.09)	4.626 (s=.389)	41.60 (s=2.70)	.861 (s=.076)
3 (6/11-6/13) 3 censuses	226.00 (s=22.34)	4.834 (s=.101)	42.00 (s=1.00)	.896 (s=.014)
4 (6/20-6/23) 3 censuses	223.00 (s=47.69)	4.748 (s=.268)	42.33 (s=2.52)	.879 (s=.047)
5 (6/27-7/1) 2 censuses	225.00 (s=28.28)	4.771 (s=.034)	43.00 (s=1.41)	.879 (s=.014)
6 (7/3-7/5) 3 censuses	244.00 (s=31.75)	4.843 (s=.091)	44.33 (s=3.06)	.885 (s=.006)
7 (7/10-7/12) 3 censuses	251.00 (s=30.81)	4.842 (s=.021)	41.33 (s=1.15)	.902 (s=.003)
8 (7/16-7/18) 3 censuses	247.67 (s=51.96)	4.899 (s=.104)	45.00 (s=3.61)	.893 (s=.022)
9 (7/26-7/28) 3 censuses	237.00 (s=19.47)	4.984 (s=.053)	45.67 (s=.58)	.904 (s=.012)
10 (8/1-8/4) 3 censuses	218.67 (s=18.50)	4.921 (s=.118)	43.33 (s=5.50)	.906 (s=.014)
11 (8/8-8/9) 2 censuses	293.00 (s=5.66)	4.915 (s=.131)	47.00 (s=2.83)	.885 (s=.009)
Mean of means	230.69 (s=35.96)	4.828 (s=.201)	43.24 (s=3.20)	.889 (s=.034)

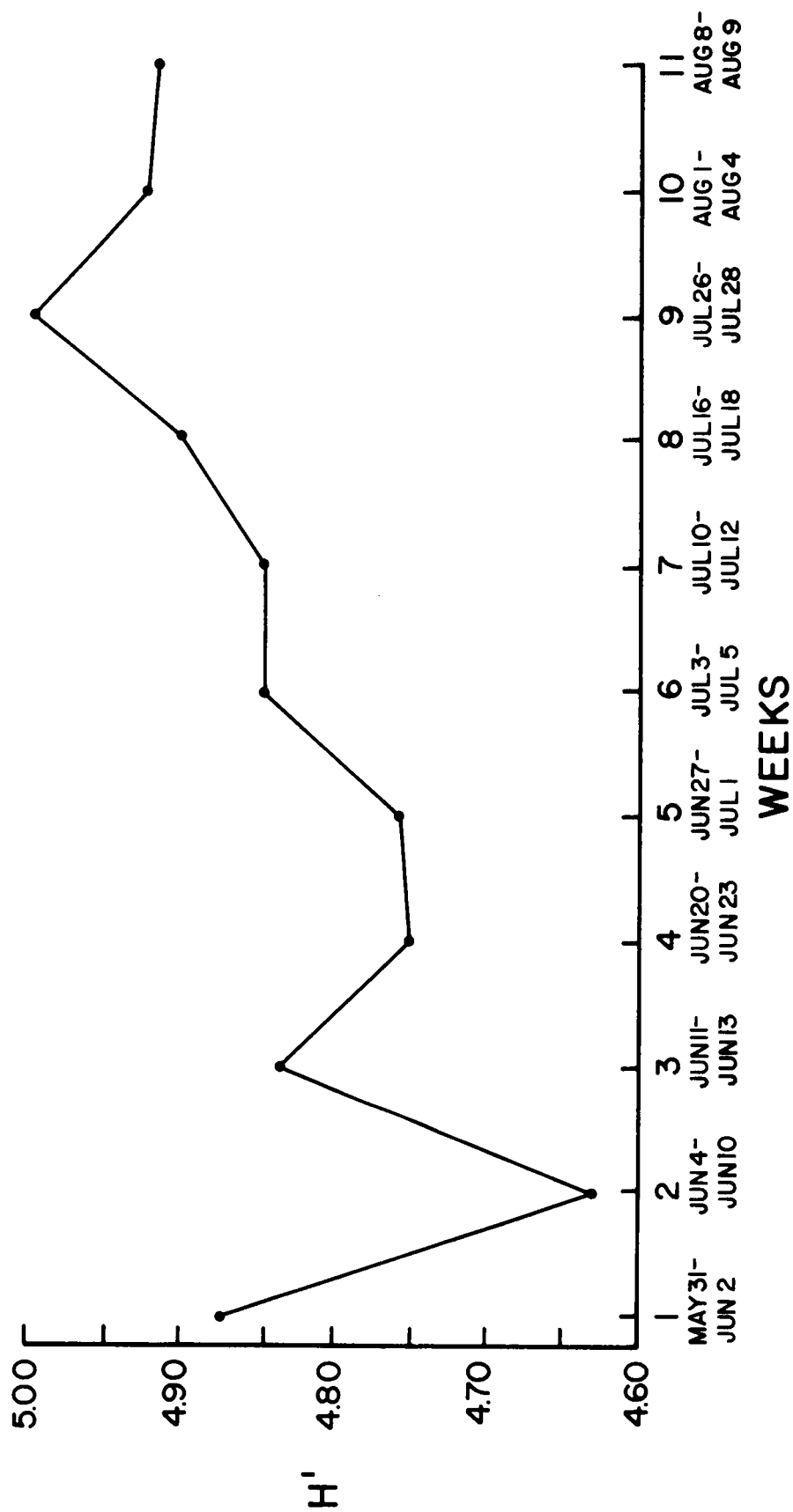


Figure 2. Weekly means of discrete bird species diversity (H') over the summer.

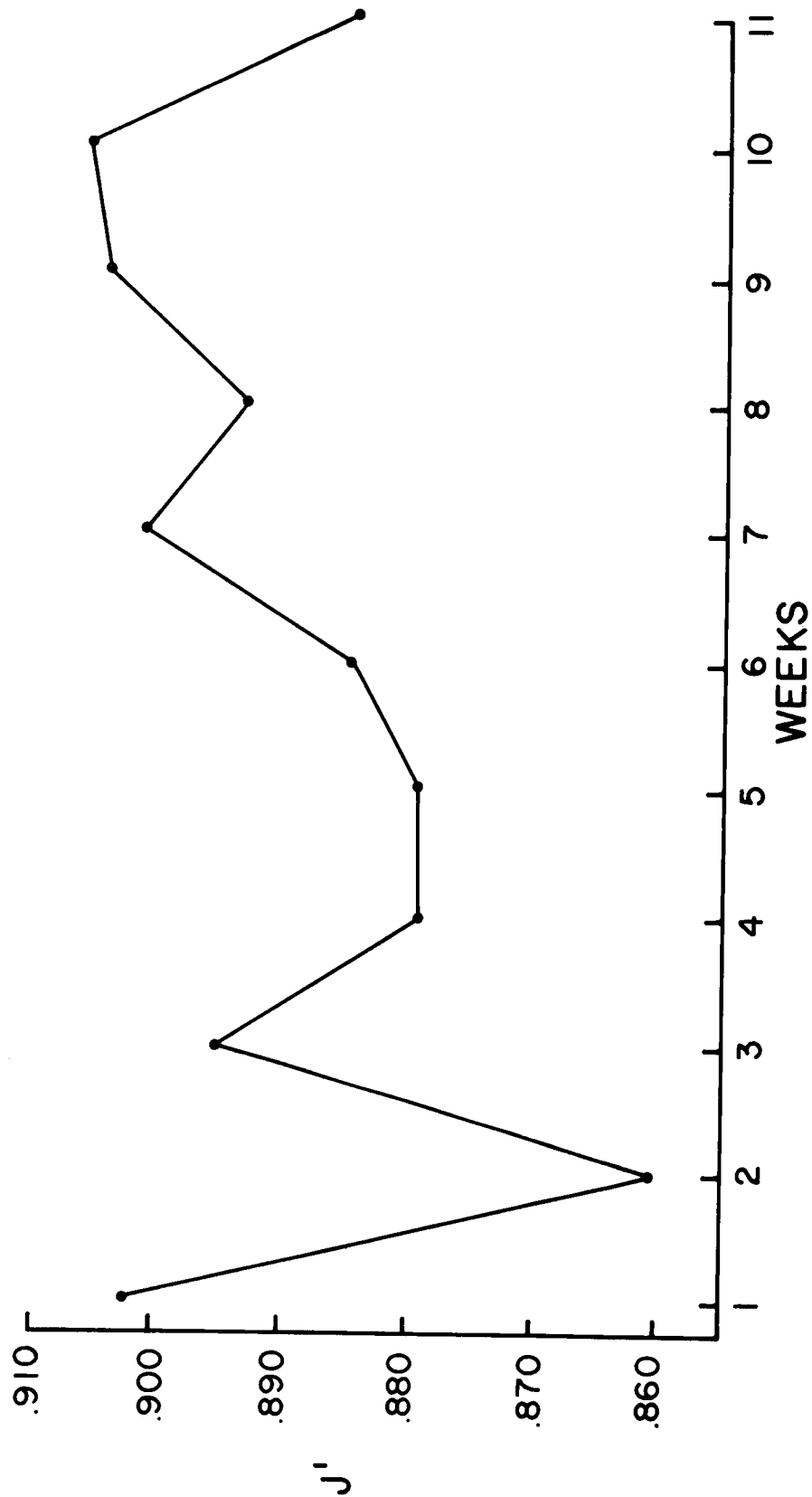


Figure 3. Weekly means of discrete species evenness (J') over the summer (abscissa legend as in Figure 2, page 44).

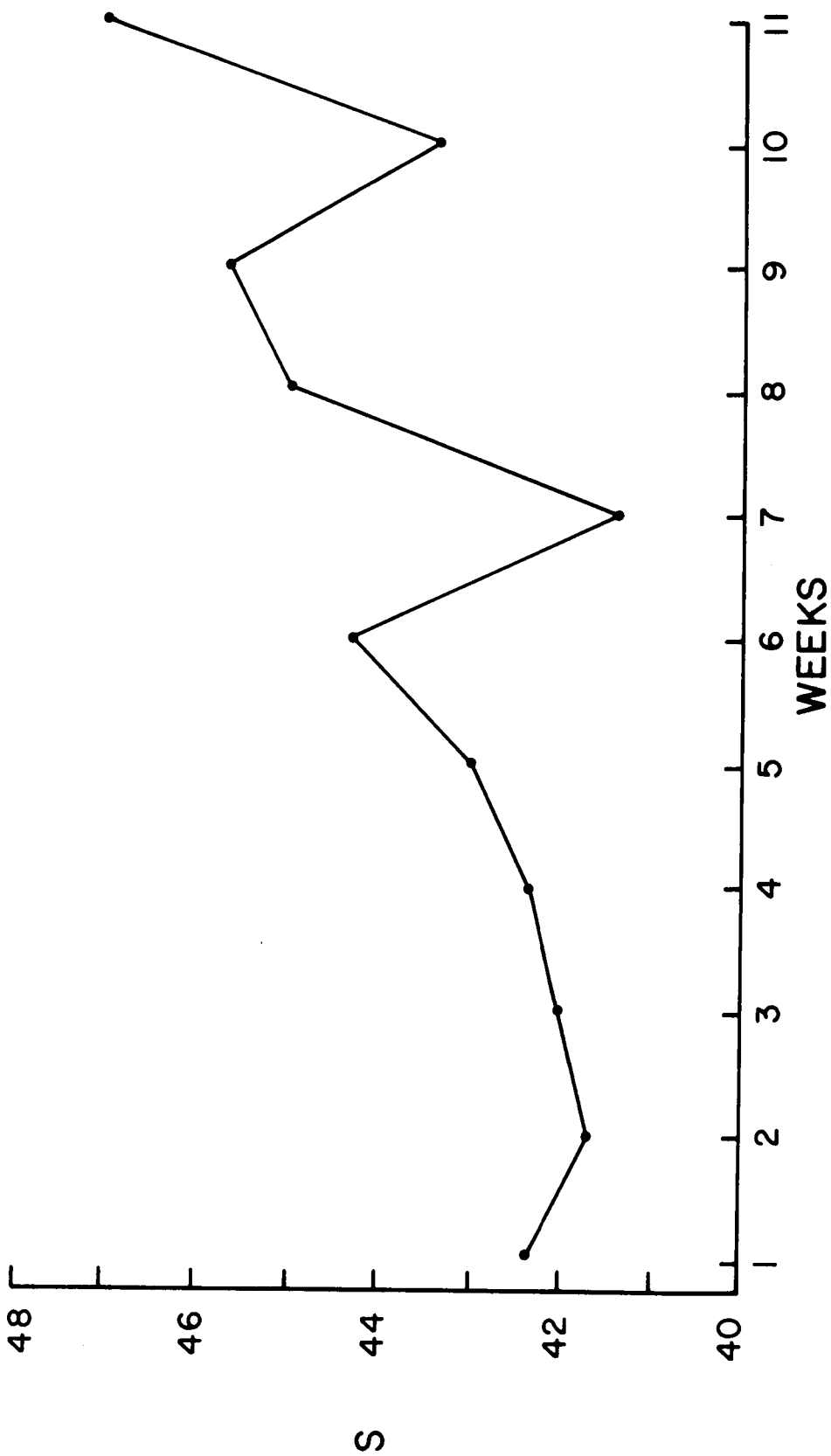


Figure 4. Weekly means of discrete species richness (S) over the summer (abscissa legend as in Figure 2, page 44).

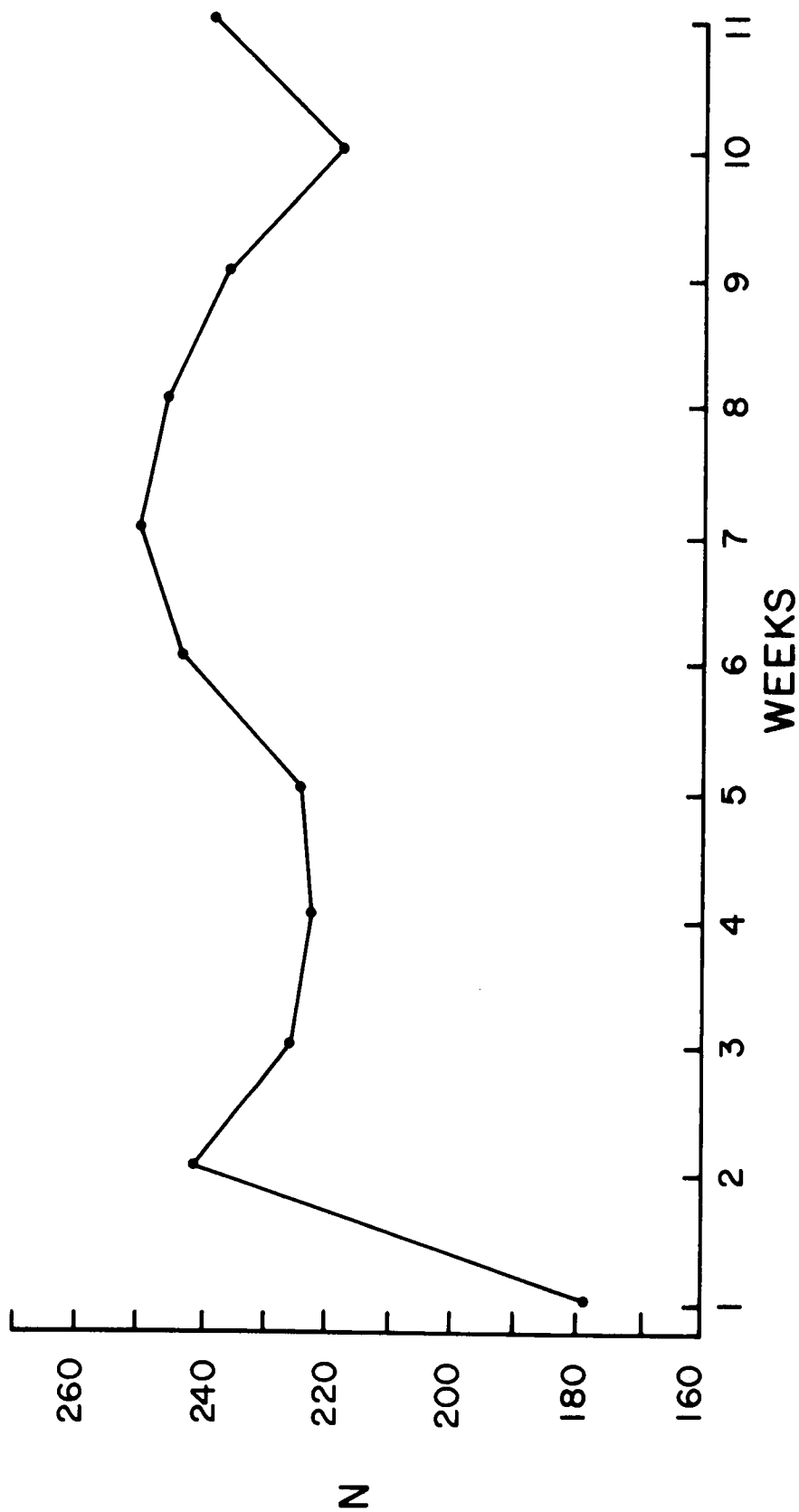


Figure 5. Weekly means of sample size (N) per discrete daily census (abscissa legend as in Figure 2, page 44).

Table 3. One-way analysis of variance (ANOVA) summaries for discrete daily census data: variation over the summer.

Source	D.F.	S.S.	M.S.	F-Ratio	F-Prob.
<u>Species Diversity(H')</u>					
Between Groups	10	.3648	.0365	.867	.5753 (NS)
Within Groups	22	.9258	.0421		
Total	32	1.2906			
<u>Evenness(J')</u>					
Between Groups	10	.0073	.0007	.539	.8440 (NS)
Within Groups	22	.0300	.0014		
Total	32	.0373			
<u>Species Richness(S)</u>					
Between Groups	10	2337.1131	233.7113	.770	.6556 (NS)
Within Groups	22	6677.9190	303.5418		
Total	32	9015.0321			
<u>Sample Size</u>					
Between Groups	10	691.4912	69.1491	1.562	.1836 (NS)
Within Groups	22	973.7610	44.2619		
Total	32	1665.2522			

(H' and J' met the criterion of homogeneity untransformed while S and sample size required arcsine transformation to meet the parametric assumptions). The Student-Newman-Keuls multiple range a posteriori test indicates that, for each variable, the means can be grouped into one homogeneous subset. Despite the lack of any statistically significant variation in these variables with time, Pearson (product-moment) correlations computed from daily values indicate significant associations between species diversity and time ($r = .3776$, $P = .015$) and between species richness and time ($r = .3908$, $P = .012$), in accordance with the general rising trends of H' and S seen in Figures 2 and 4, respectively. The diversity component evenness, however, showed no significant correlation with time ($P = .122$), nor did sample size ($P = .107$). The latter indicates that average species detectabilities did not at least fall to the point where they failed to keep pace with population recruitment through reproduction over the season, though changes in detectabilities in some individual species can be described in the data (Appendix A). Evenness and daily census sample size were negatively correlated ($r = -.6231$, $P = .001$), as might be expected since the occurrence of large monospecific flocks (starlings, for example) tends to increase sample size while depressing the J' value. In accordance with this decline in evenness with larger

sample size, species diversity showed a similar relationship, though not as strong ($r = -.3902$, $P = .012$); as Figure 6 shows, the scatter is considerable and the relationship hardly predictive. Species richness, on the other hand, showed a significant positive association with sample size ($r = .3665$, $P = .018$).

In general, the results of this study support the null hypotheses and the findings of Kricher (1973) and Adams and Barrett (1976) that species diversity and its components, when measured discretely over the season for a community of mostly breeding birds, do not vary significantly as the season progresses. As will be discussed, the significant correlations of H' and S with time appear to arise from increments in species richness which occur during the last seven weeks of the study period (weeks 5-11, or June 27 through August 9), and the additional species are classifiable as non-nesters in the reserve. Increases in species richness therefore tend to support the alternative hypothesis in hypothesis set II: species richness varies with time due to movement of species into the study area; the essential qualification is that these species do not appear to be part of the breeding avifauna of the reserve.

Variation in Cumulative Diversity Components over the Summer and Relation of Diversity Components to Cumulative Sample Size

Calculated coefficients of variation indicate that species richness varied most ($CV = 14.2641$) as cumulative

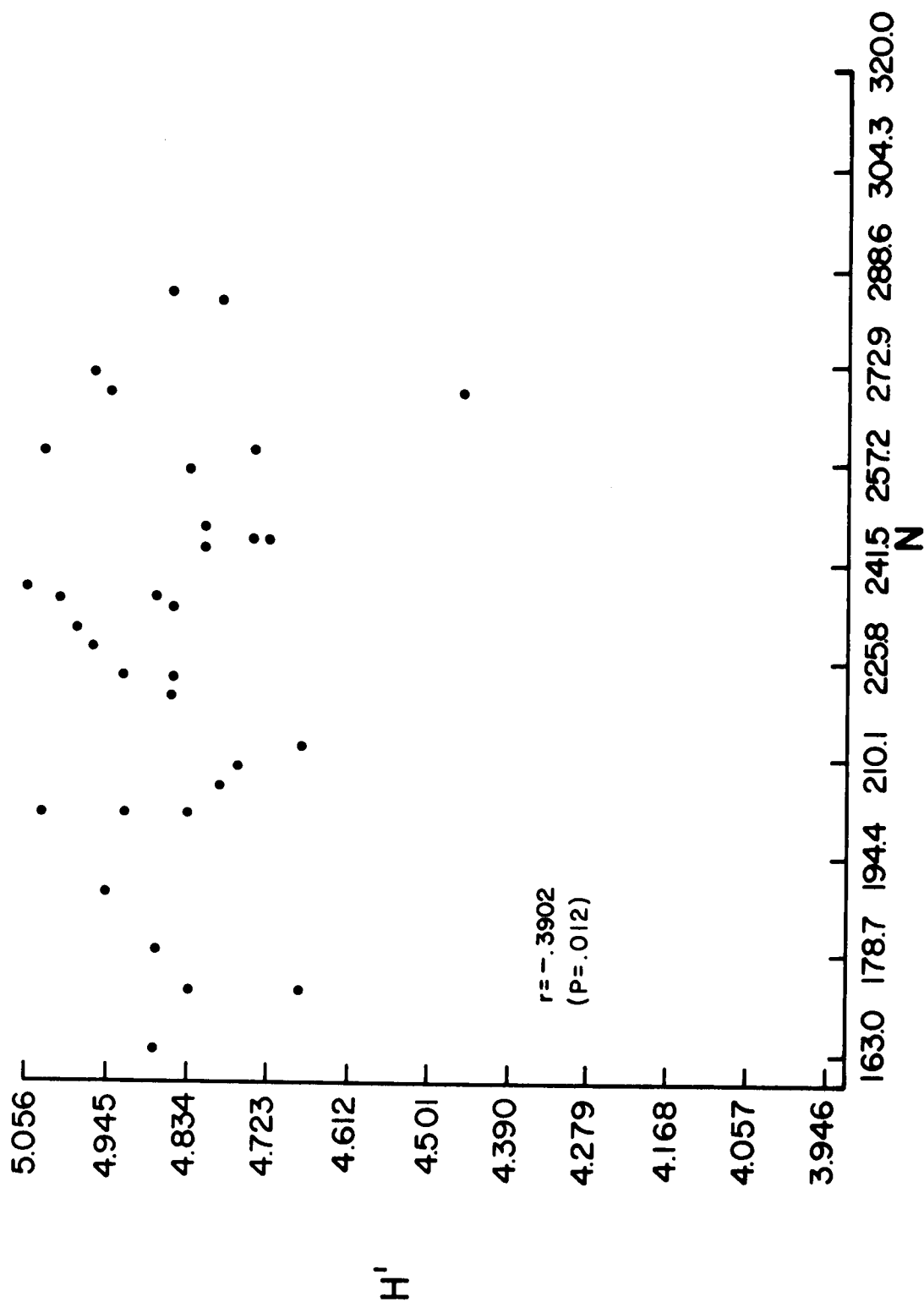


Figure 6. Relationship between discrete species diversity (H') and discrete census sample size (N).

sample size increased over the span of the study period, accompanied by quite small variations in evenness ($CV = 2.8777$) and species diversity ($CV = 1.7248$). The CVs for the latter two variables are lower in the cumulative data than in the discrete data, indicating that variation by this measure was greater from census to census than it was when associated with steadily increasing cumulative sample size. Table 4 and Figures 7-9 illustrate the cumulative trends for species diversity and its components as the study progressed. Analysis of variance (Table 5) indicates significant variation for all three components. Species diversity values are grouped by the Student-Newman-Keuls procedure into just two subsets, with the mean for week one ($H' = 4.864$) alone in the first subset, denoting that the mean cumulative H' values in weeks 2 through 11 were not significantly different from each other at the .05 level. The SNK procedure applied to cumulative species richness means, however, groups the values into four homogeneous subsets, with week 1 in subset 1, week 2 in subset 2, weeks 3 to 8 in subset 3, and weeks 4 to 11 in subset 4. The SNK procedure groups cumulative evenness values into three subsets, with subset 1 comprising weeks 3 through 11, subset 2 including only week 2, and subset 3 only week 1. The reversed sequence is in accordance with the observation that cumulative J' values fall with increasing sample size over the summer (Figure 8). The SNK groupings are thus

Table 4. Weekly means and standard deviations for cumulative values of diversity components.

Week	Sample Size	H'	S	J'
1 (5/31-6/2)	348.67 (s=182.33)	4.864 (s=.168)	44.33 (s=7.64)	.892 (s=.012)
2 (6/4-6/10)	1199.40 (s=404.04)	5.019 (s=.030)	58.60 (s=4.72)	.855 (s=.019)
3 (6/11-6/13)	2195.67 (s=221.59)	4.993 (s=.038)	65.67 (s=.58)	.827 (s=.004)
4 (6/20-6/23)	2828.67 (s=219.90)	5.022 (s=.014)	68.67 (s=1.15)	.823 (s=.006)
5 (6/27-7/1)	3386.00 (s=217.79)	5.036 (s=.026)	70.50 (s=.71)	.821 (s=.002)
6 (7/3-7/5)	4012.00 (s=262.02)	5.061 (s=.007)	71.33 (s=.58)	.822 (s=.001)
7 (7/10-7/12)	4761.33 (s=254.11)	5.075 (s=.004)	72.00 (s=.00)	.822 (s=.001)
8 (7/16-7/18)	5415.00 (s=215.00)	5.063 (s=.024)	72.67 (s=.58)	.819 (s=.006)
9 (7/26-7/28)	6229.67 (s=244.64)	5.119 (s=.009)	74.67 (s=.58)	.823 (s=.001)
10 (8/1-8/4)	6832.33 (s=152.43)	5.122 (s=.010)	75.67 (s=.58)	.820 (s=.003)
11 (8/8-8/9)	7422.00 (s=270.11)	5.155 (s=.037)	76.50 (s=9.60)	.824 (s=.004)
Mean of means	3802.52 (s=2265.71)	5.004 (s=.087)	67.33 (s=9.60)	.823 (s=.024)

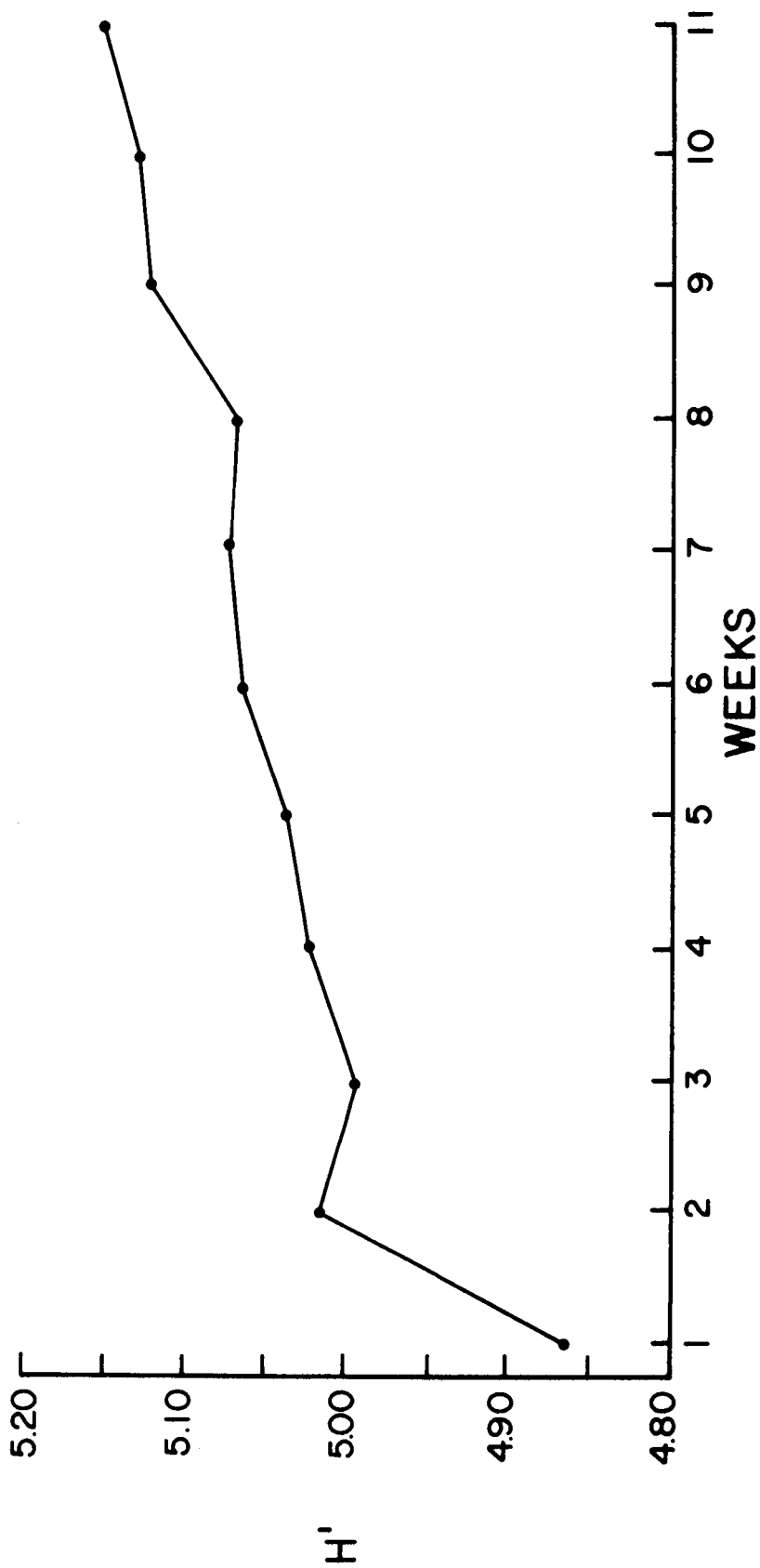


Figure 7. Weekly means of cumulative bird species diversity (H') over the summer (abscissa legend as in Figure 2, page 44).

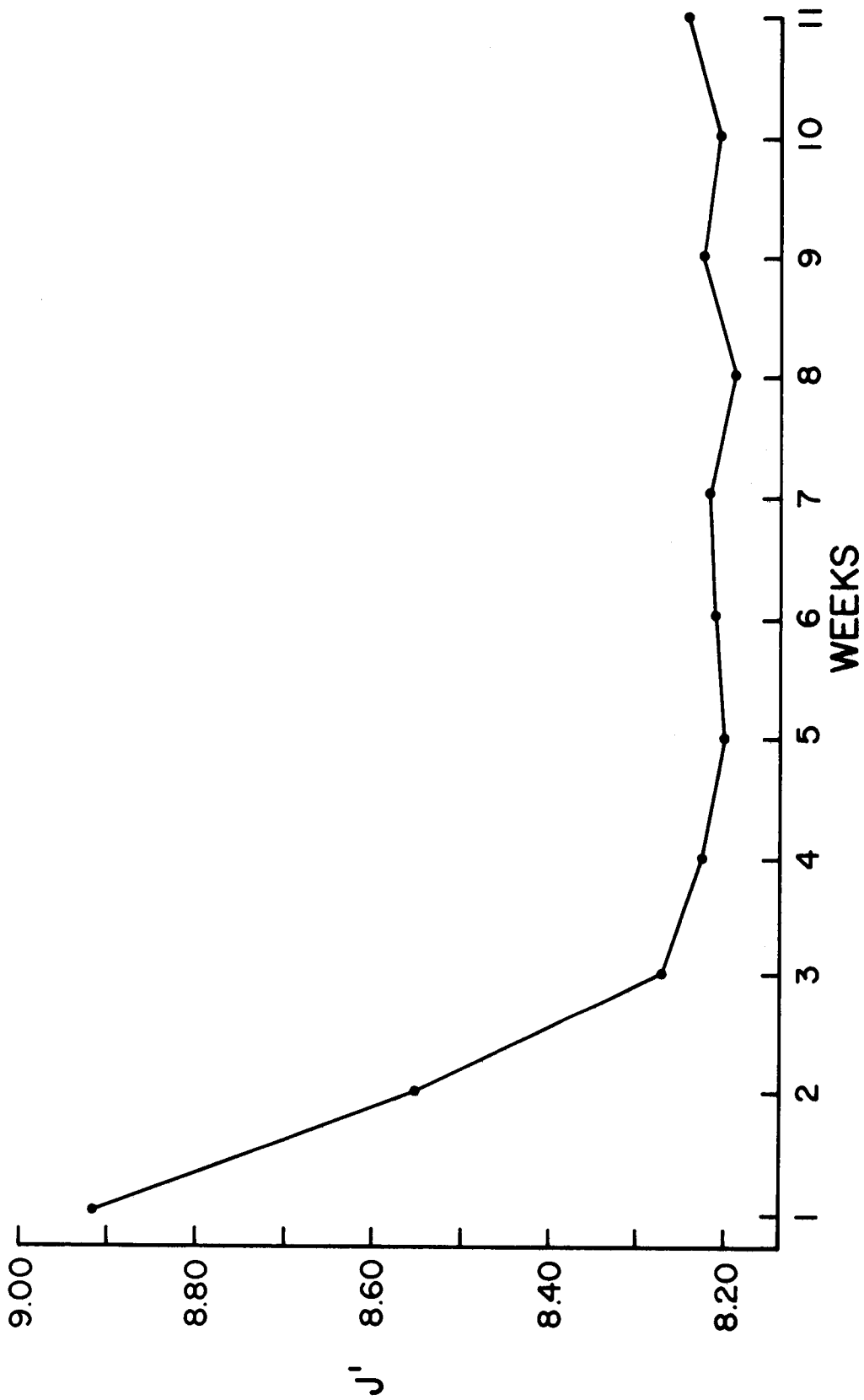


Figure 8. Weekly means of cumulative species evenness (J') over the summer (abscissa legend as in Figure 2, page 44).

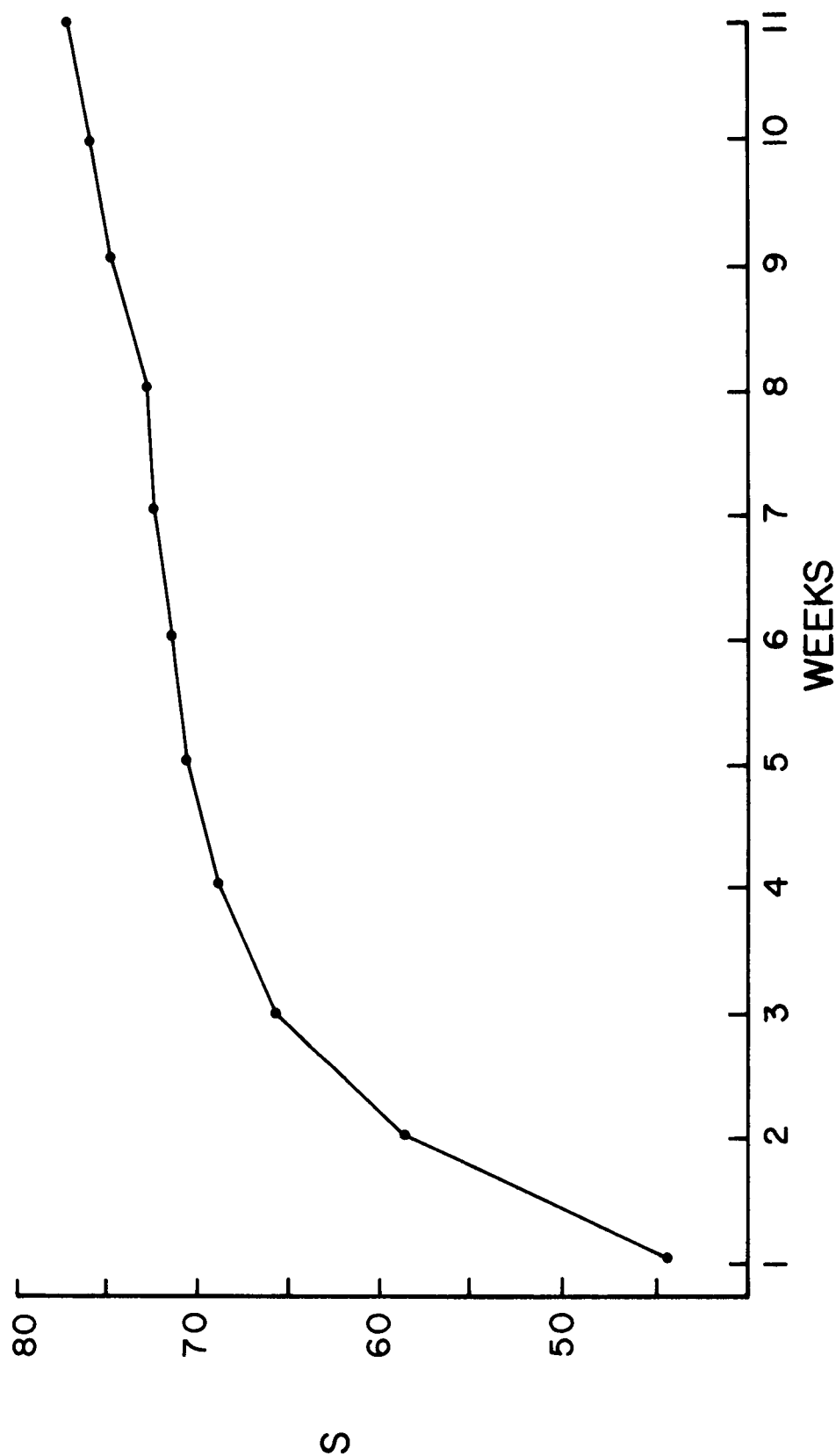


Figure 9. Weekly means of cumulative species richness (S) over the summer (abscissa legend as in Figure 2, page 44).

Table 5. One-way analysis of variance (ANOVA) summaries for cumulative census data: variation with increasing sample size.

Source	D.F.	S.S.	M.S.	F-Ratio	F-Prob.
<u>Species Diversity(H')</u>					
Between Groups	10	.1745	.0175	5.703	.0003(S)
Within Groups	22	.0673	.0031		
Total	32	.2419			
<u>Evenness(J')</u>					
Between Groups	10	.0158	.0016	17.110	<.0001(S)
Within Groups	22	.0020	.0001		
Total	32	.0179			
<u>Species Richness(S)</u>					
Between Groups	10	2738.4676	273.8468	28.302	<.0001(S)
Within Groups	22	212.8667	9.6758		
Total	32	2951.3343			

consonant with the punctuated rise in H' only up to the second week, followed by a gradual increase, and the more extended increments in cumulative S and decrements in cumulative J' to plateaus, as shown in Figures 7-9.

The apparent nonrandom responses of species diversity, richness, and evenness to increasing sample size suggest functional relationships of these variables to the number of individuals in the sample. In all cases, correlations were higher between the diversity components and cumulative sample size than between the components and study time per se (Table 6, cumulative data). Therefore linear regressions were run for each of the components against cumulative sample size to test for predictive relationships. Transforming either or both variables in regression may simplify a curvilinear relationship to a linear one; specifically, a logarithmic transformation of the independent variable in regression is effective when proportional changes in the independent variable produce linear responses in the dependent variable (Sokal and Rohlf, 1969). For these data, correlations between the diversity components (H' , S , and J') and the $\log_2$ of sample size were consistently higher than correlations between the diversity components and untransformed sample size. Figures 10-15 portray the relationships between the diversity components and untransformed versus logtransformed sample size. It is clear that

Table 6. Correlation matrices for discrete daily and cumulative census diversity variables.

	Sample Size	Study Time	Species Richness	Species Diversity
Discrete Data				
Study time	.2222			
Species richness	.3665*	.3908*		
Species diversity	-.3902*	.3776*	.4079**	
Evenness	-.6231***	.2086	-.0811	.8766***
Cumulative Data				
Study time	.9938***			
Species richness	.8656***	.8329***		
Species diversity	.7639***	.7513***	.8445***	
Evenness	-.7180***	-.6717***	-.9488***	-.6660***

* = $p < .05$; ** = $p < .01$; *** = $p < .001$.

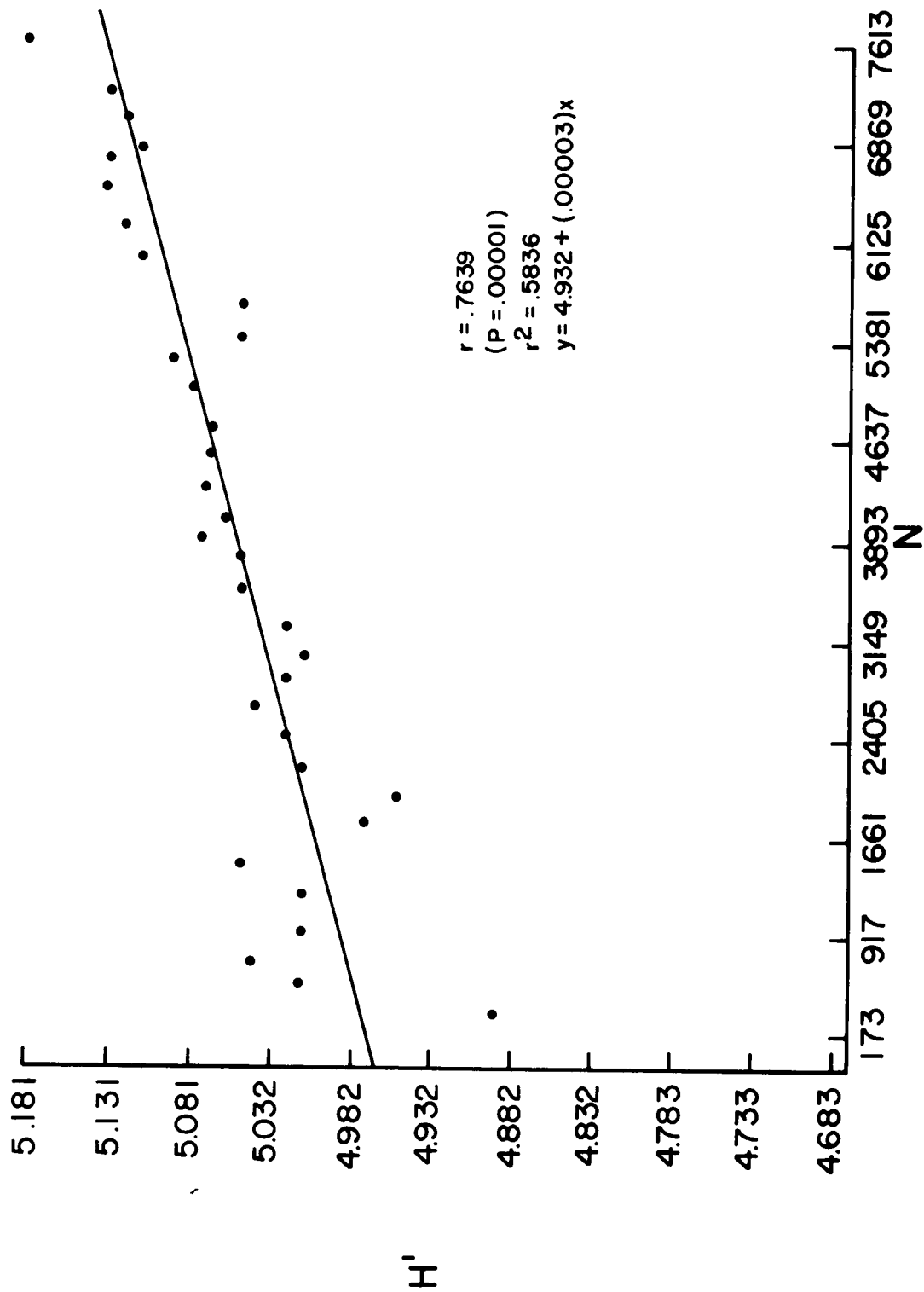


Figure 10. Regression of cumulative species diversity (H') against cumulative sample size (N).

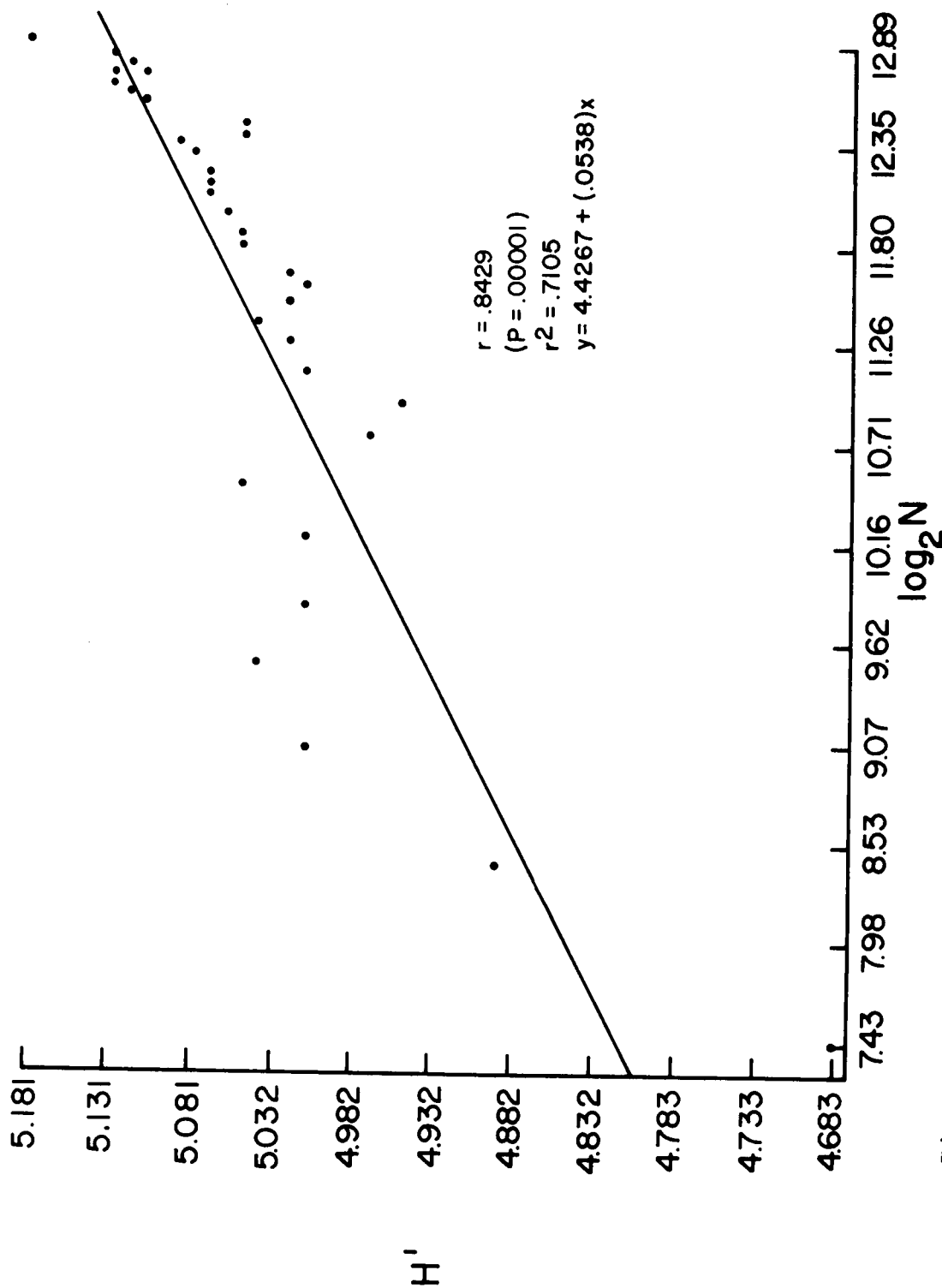


Figure 11. Regression of cumulative species diversity (H') against $\log_2$ cumulative sample size ($\log_2 N$).

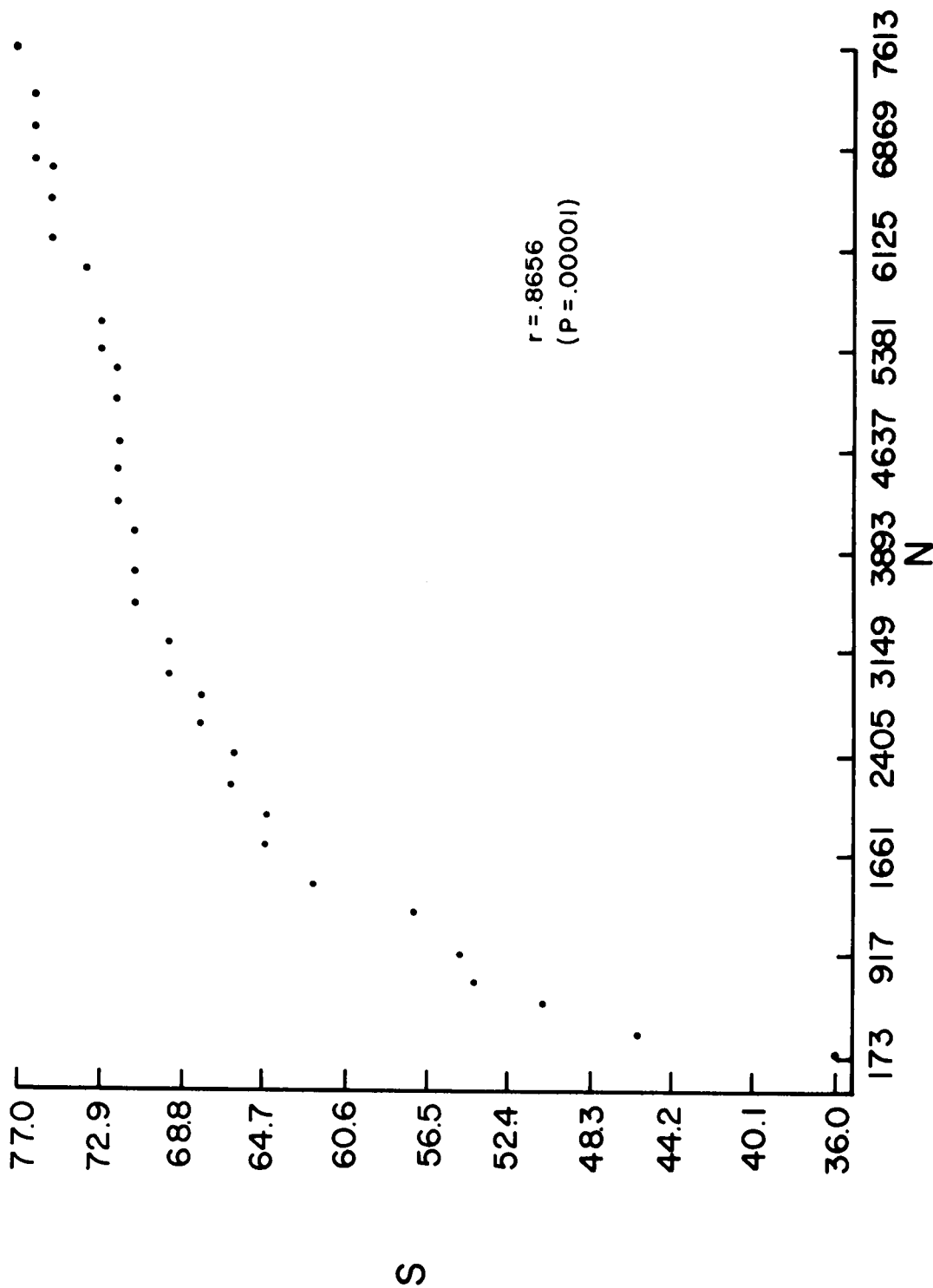


Figure 12. Relationship between cumulative species richness (S) and cumulative sample size (N).

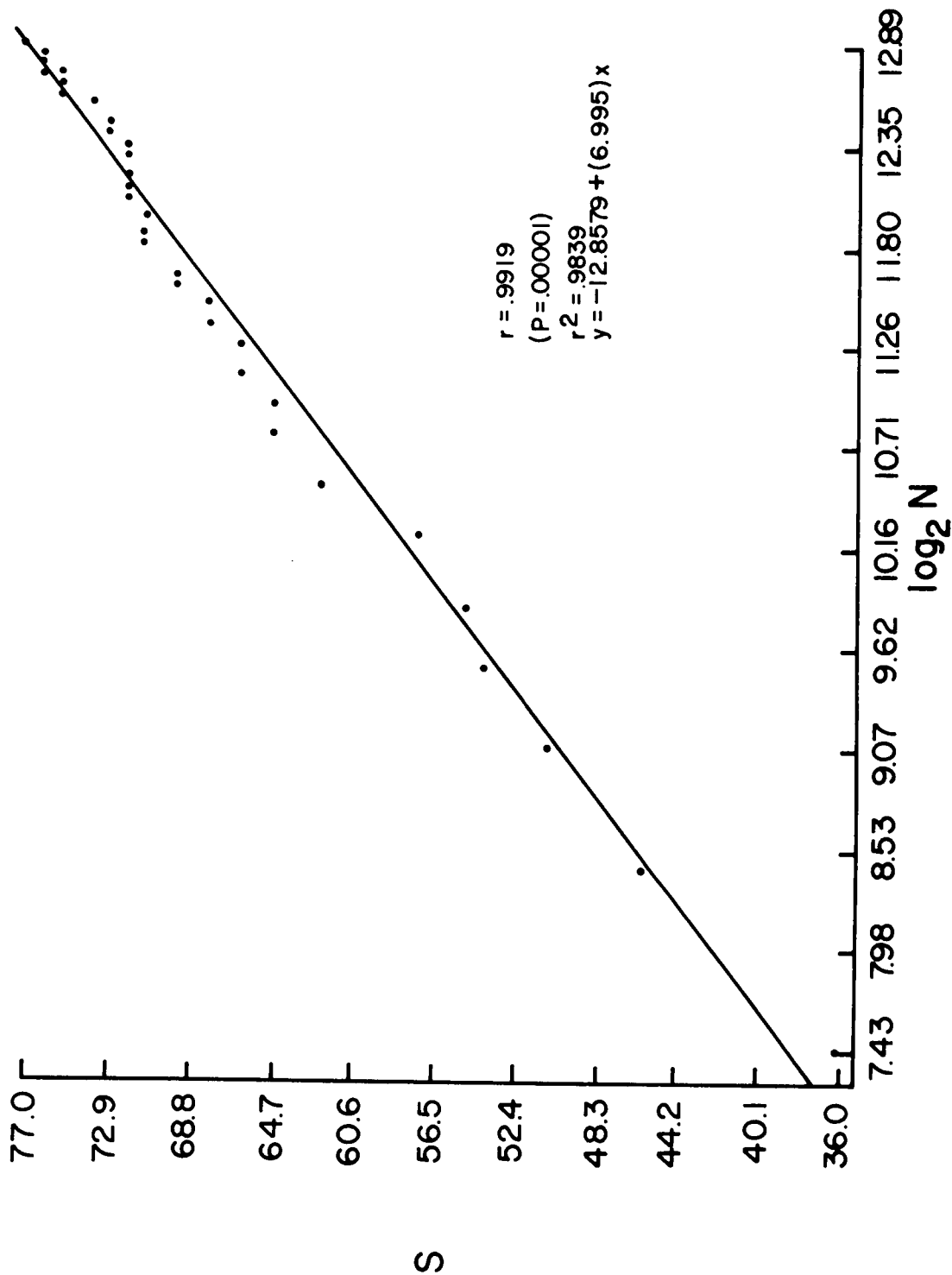


Figure 13. Regression of cumulative species richness (S) against $\log_2$ cumulative sample size ($\log_2 N$).

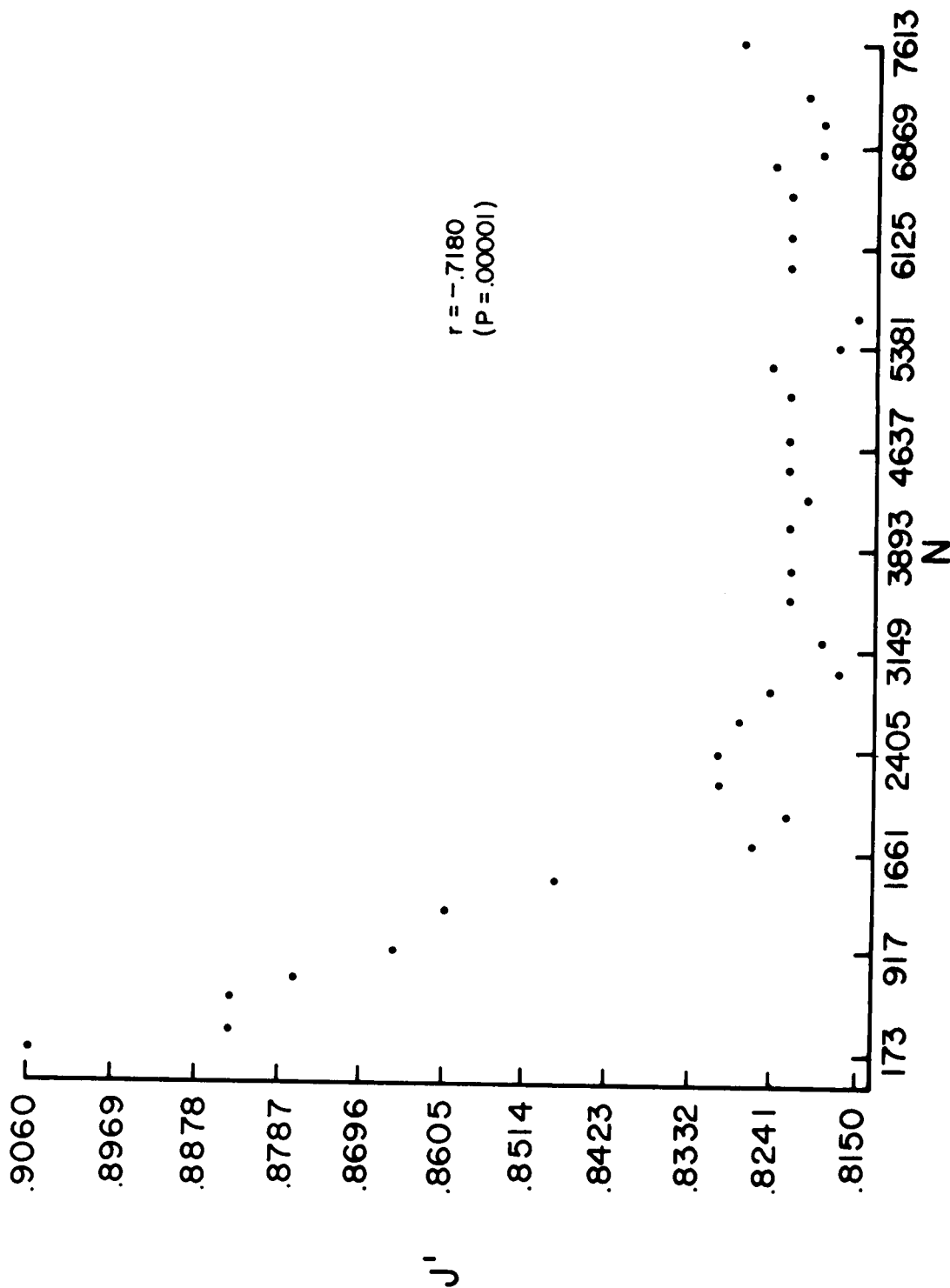


Figure 14. Relationship between cumulative evenness (J') and cumulative sample size (N).

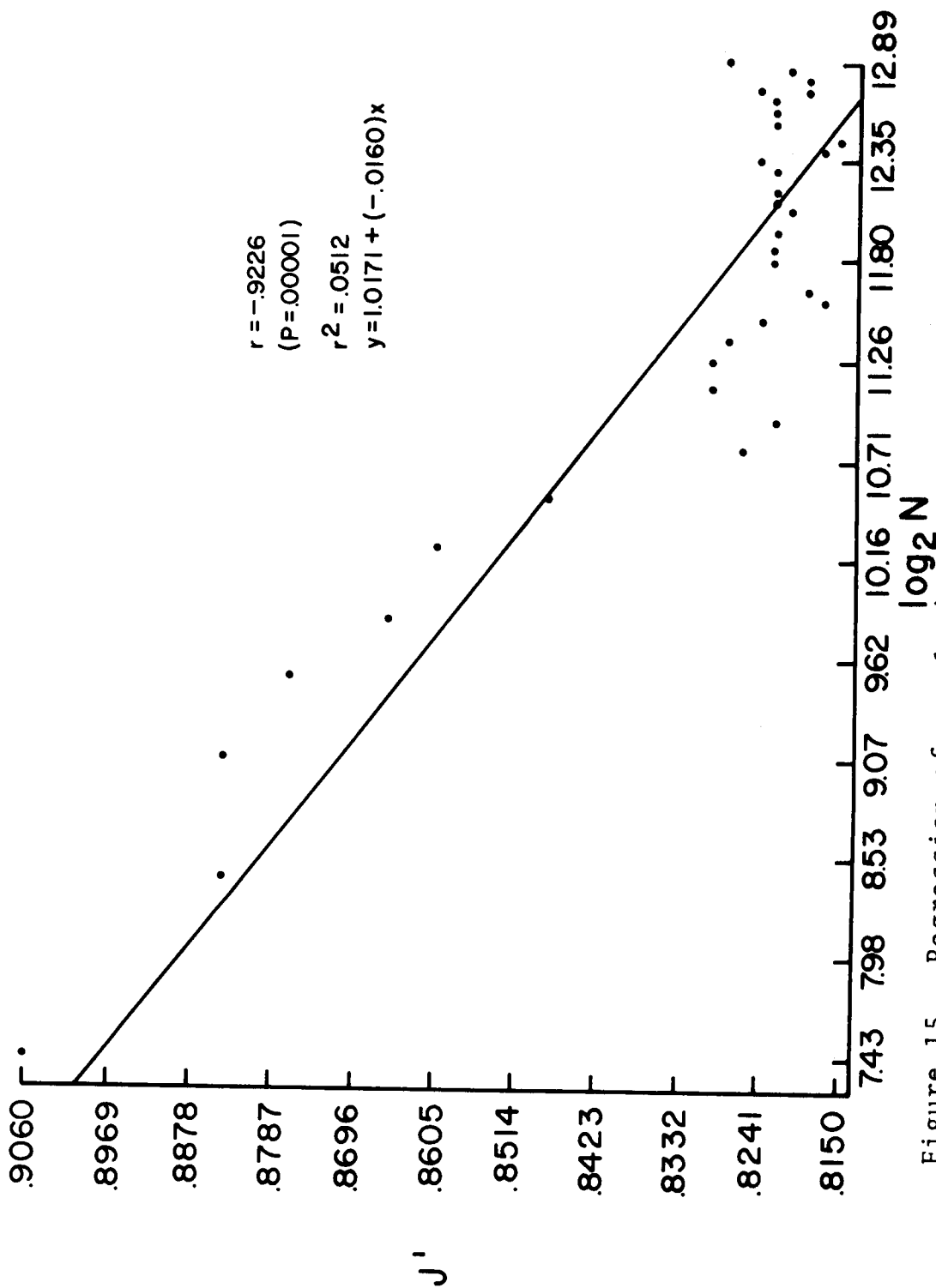


Figure 15. Regression of cumulative evenness (J') against $\log_2$ cumulative sample size ($\log_2 N$).

logtransformation can dramatically augment predictive ability in these cases.

It would be of tremendous value to know beforehand how many study hours or what cumulative sample size with a given census method are necessary to obtain close estimation of true community diversity parameters. My results to this end are preliminary, in that they arise from but a single study. Table 7 indicates change in some parameters over the span of the study period and shows percentages of the final cumulative species diversity and species richness generally rising with the percentages of the total study hours and total sample size. From a table of this sort, plus some additional information on species composition of the breeding avifauna and on the particular species responsible for the percentage increments, one can choose a level of completeness for H' and S and tailor the study accordingly. For my purposes, 42 cumulative hours would have been sufficient. By that time (June 23), with 3030 birds observed in 14 censuses apportioned over four weeks of the breeding season after the passing of transients, species richness was 70, or 90.9% of its final cumulative value and species diversity was 5.010, or 96.7% of its final value. These proportions were reached after just 42.4% of the final study hours and 39.8% of the final sample size. I choose this cut-off point more from the criteria of species richness and composition than from

Table 7. Changes in cumulative species richness and species diversity with increasing study hours and sample size, and percentages of final values.

Censuses	Study Hours	% Final Hours	Sample Size	% Final Sample Size	Cum.H'	% Final H'	Cum.S	% Final S
1	3	3.0	173	2.3	4.683	90.4	36	46.8
2	6	6.1	336	4.4	4.893	94.4	46	59.7
3	9	9.1	537	7.1	5.016	96.8	51	66.2
4	12	12.1	716	9.4	5.046	97.4	54	70.1
5	15	15.2	928	12.2	5.009	96.7	55	71.4
6	18	18.2	1187	15.6	5.016	96.8	57	74.0
7	21	21.2	1423	18.7	5.050	97.5	62	80.5
8	24	24.2	1743	22.9	4.976	96.0	65	84.4
9	27	27.3	1978	25.9	4.949	95.5	65	84.4
10	30	30.3	2188	28.7	5.010	96.7	66	85.7
11	33	33.3	2421	31.8	5.019	96.9	66	85.7
12	36	36.4	2594	34.1	5.038	97.2	68	88.3
13	39	39.4	2862	37.6	5.019	96.9	68	88.3
14	42	42.4	3030	39.8	5.010	96.7	70	90.9
15	45	45.5	3232	42.5	5.017	96.8	70	90.9
16	48	48.5	3540	46.5	5.054	97.5	71	92.2
17	51	51.5	3748	49.2	5.054	97.5	71	92.2
18	54	54.5	4016	52.8	5.062	97.7	71	92.2
19	57	57.6	4272	56.1	5.068	97.8	72	93.5
20	60	60.6	4518	59.3	5.072	97.9	72	93.5
21	63	63.6	4741	62.3	5.074	97.9	72	93.5
22	66	66.6	5025	66.0	5.080	98.1	72	93.5
23	69	69.7	5213	68.5	5.090	98.2	72	93.5
24	72	72.7	5391	70.8	5.052	97.5	73	94.8
25	75	75.8	5641	74.1	5.047	97.4	73	94.8
26	78	78.8	5990	78.7	5.109	98.6	74	96.1
27	81	81.8	6220	81.7	5.121	98.8	75	97.4
28	84	84.8	6479	85.7	5.127	98.9	75	97.4

Table 7 (Continued)

Censuses	Study Hours	% Final Hours	Sample Size	% Final Sample Size	Cum.H'	% Final H'	Cum.S	% Final S
29	87	87.9	6698	87.9	5.134	99.1	75	97.4
30	90	90.9	6801	89.3	5.114	98.7	76	98.7
31	93	93.9	6998	91.9	5.119	98.8	76	98.7
32	96	97.0	7231	95.0	5.129	98.9	76	98.7
33	99	100.0	7613	100.0	5.181	100.0	77	100.0

species diversity, for H' was 97.4% of its final value after only 12 cumulative study hours and then proceeded to dip somewhat before slowly rising to its final value of 5.181. Cumulative evenness declined from its peak first week value and remained approximately constant after four weeks and did not contribute to increasing cumulative H' . Moreover, the very slow increases in S and concomitantly H' over the last seven weeks of the study were brought about wholly by the addition of supposed transient or vagrant individuals of species that were almost certainly not breeding in the study area and thus were not directly germane to a study of the breeding avifauna.

Relationships between Diversity Components

Though it is clear that there is no biological or mathematical necessity for species diversity and richness to be positively correlated, the assumption that one can adequately estimate bird species diversity from bird species richness, at least in communities where the majority of birds are nesters, is nevertheless becoming rather firmly fixed in the literature (e.g., Tramer, 1969; Kricher, 1972; Forman et al., 1976; Austin and Tomoff, 1978). Table 6, page 59, shows that species diversity and species richness in this study are positively correlated in both the discrete ($r = .4079$) and the cumulative ($r = .8445$) data. The correlation is much stronger in the cumulative data as

variation in species diversity as measured discretely over the summer was seen to more closely parallel variation in the evenness of relative abundances ($r = .8766$), as can be seen by comparing Figures 2 and 3, pages 44 and 45. Variations in evenness and hence in species diversity in the discrete data can be largely ascribed to the sporadic occurrence of large monospecific flocks, particularly of starlings and secondarily of grackles, red-winged blackbirds, and sometimes robins and cowbirds. Flocks of the latter two species generally contained only about a dozen birds or fewer. Kricher (1972) noted similar effects on evenness and diversity from large itinerant starling flocks. This obnoxious introduced species has an ecological importance probably commensurate with its effect on the discrete evenness and diversity values in this study (note the dip in H' and J' in week 2 in Figures 2 and 3--this is the week when 120 starlings appeared in a single census), since it is an important (and generally successful) nest site competitor with native hole-nesting birds, as well as perhaps the most destructive component in the extremely large "blackbird" flocks that plague the southeastern states in winter. Starlings and other flockers may also play a primary role in the redistribution of nutrients between ecosystems since they feed to a large extent in the farmlands surrounding Sugarcreek, for example, and nest and roost in the Sugarcreek woods, depositing nutrients there in the form of

fecal matter. The function of birds in the redistribution of nutrients has been discussed by Sturges et al. (1974).

The relationship of bird species diversity to species richness has been shown to be linear when H' is plotted against the $\log_2$ of S (Tramer, 1969; DeJong, 1975). Tramer (1969), in an analysis of 267 breeding bird communities, found a correlation of .972 between the two variables and calculated the regression equation as $H' = -.251 + .94 (\log_2 S)$. For my single summer bird community, the correlation of H' with $\log_2 S$ in the discrete data is lower ($r = .3988$) than the correlation between H' and untransformed S ($r = .4079$). Figure 16 shows the scatter in the relation of H' to S for the discrete measurement of diversity over the summer. In this case, regression would account for only about 17% of the variation in H' and is not warranted. If $\log_2 S$ was used as the independent variable, regression would account for only 16% of the variation in H' . For the cumulative data, however, comprising the continual refinement of diversity component values over 33 censuses with increasing sample size, the correlation of H' with $\log_2 S$ is slightly higher than the correlation of H' with untransformed S ($r = .8610$ compared to $r = .8445$) and regression (Figure 17) on $\log_2 S$ accounts for 74% of the variation in species diversity. Nonetheless it appears that species richness is not as good a predictor

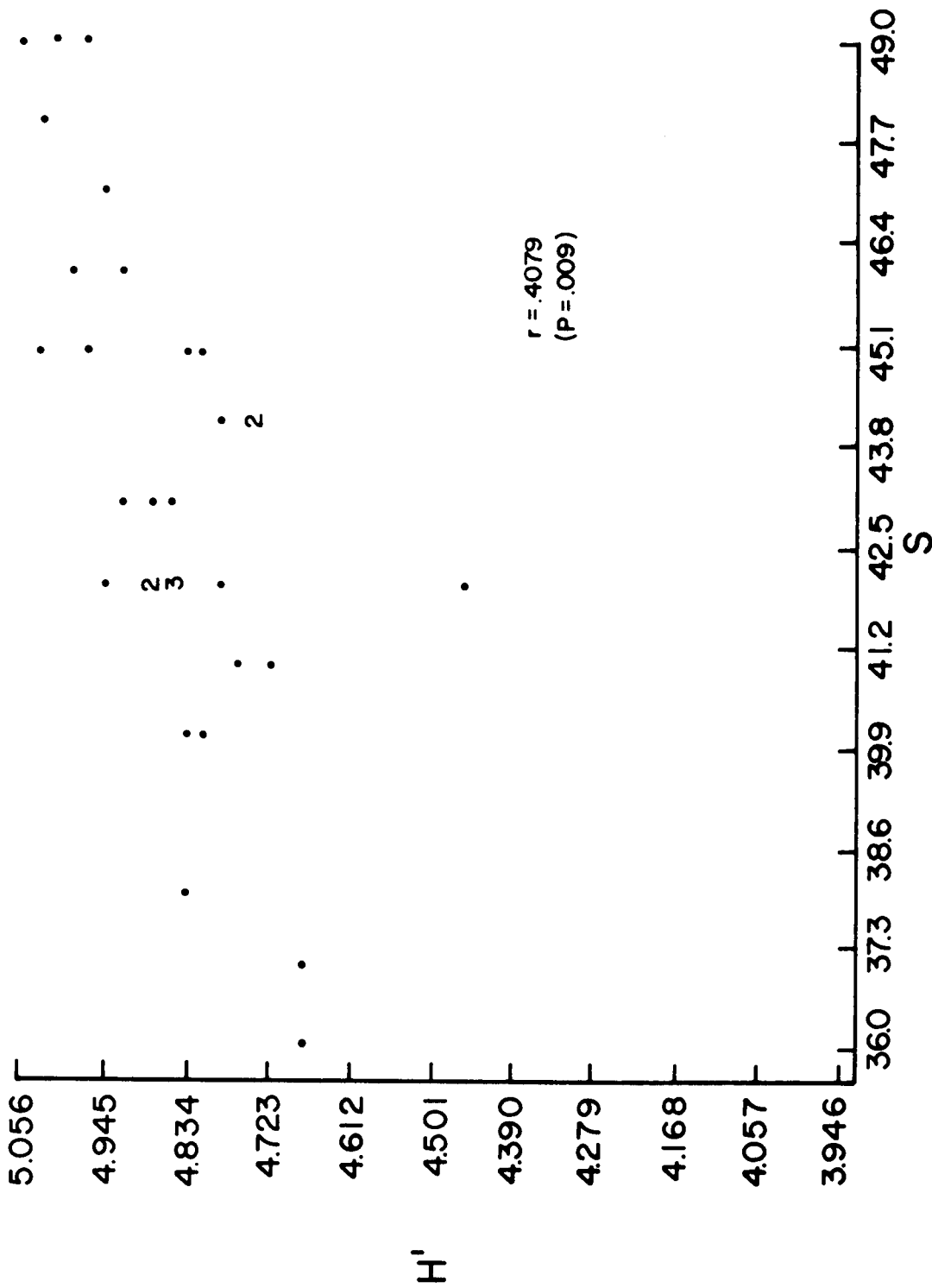


Figure 16. Relationship between species diversity (H') and species richness (S) for discrete census data.

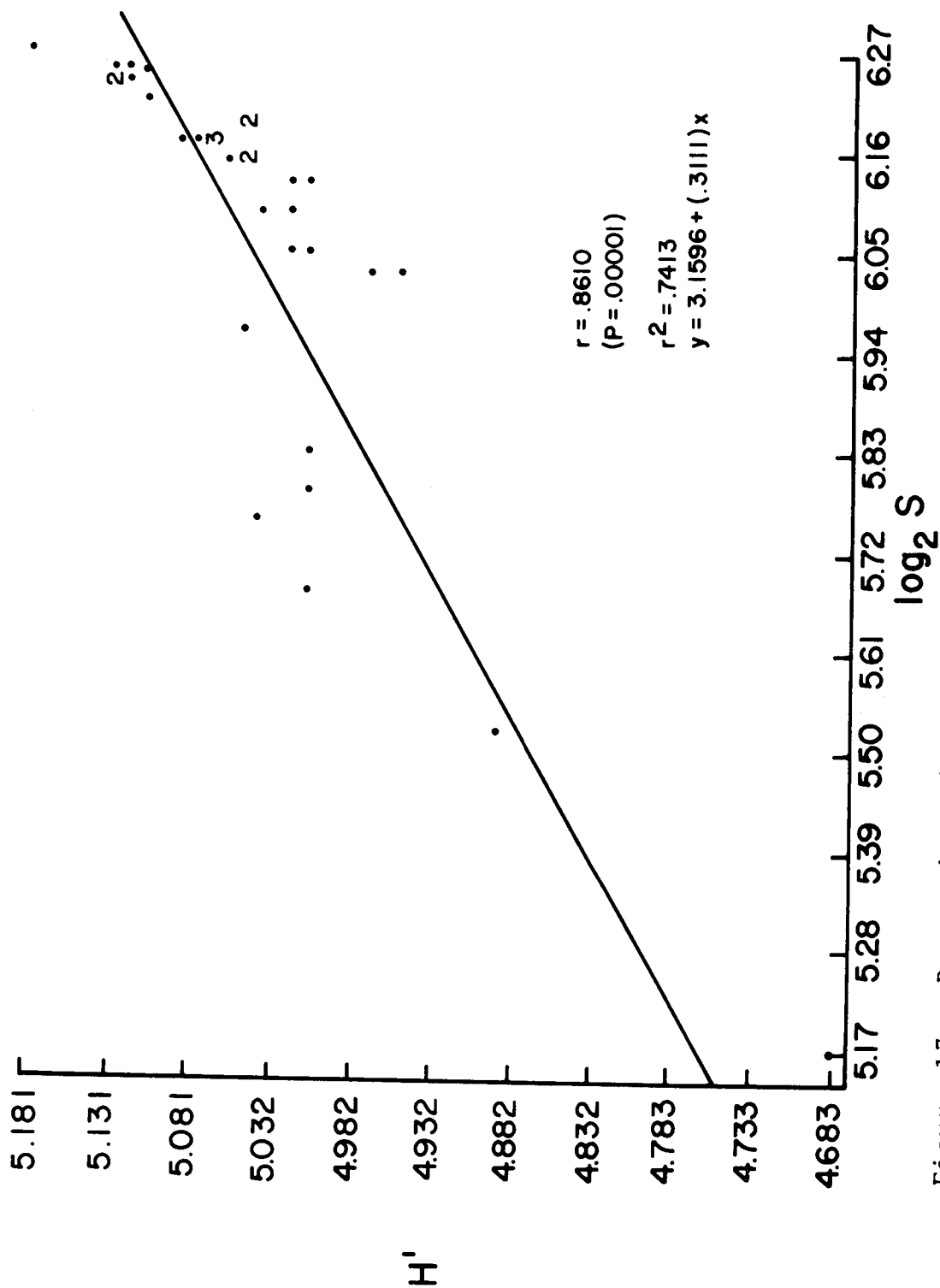


Figure 17. Regression of species diversity (H') against $\log_2$ species richness ($\log_2 S$) for cumulative census data.

of species diversity in studies such as this one, where the change in the diversity components over time (whether measured discretely or cumulatively) is analyzed for a single study area, as it is in studies where the final measured H' and S values from different communities are compared. This disparity in analytic method is important to clarify, for specious conclusions may result from spurious comparisons.

The contrast between the discrete and cumulative data in the relation of diversity to evenness is particularly noteworthy (Table 6, page 59). The relationship is significantly positive in the discrete data ($r = .8766$) and significantly negative in the cumulative data ($r = -.6660$). This shows that for a given series of discrete diversity measurements, the H' trends closely parallel the J' trends which relate to the influence of monospecific flocks discussed above. Regression against J' accounts for about 77% of the variation in H' in the discrete census data (Figure 18). On the other hand, cumulative H' and J' show opposing trends with increasing cumulative sample size (Figures 10, 11, 14, and 15, pages 60, 61, 64, and 65, respectively), as the increase in species diversity is brought about primarily by the addition of rare species, which will always lower the J' value (Hurlbert, 1971). The correlation between cumulative H' and J' is therefore negative, and regression

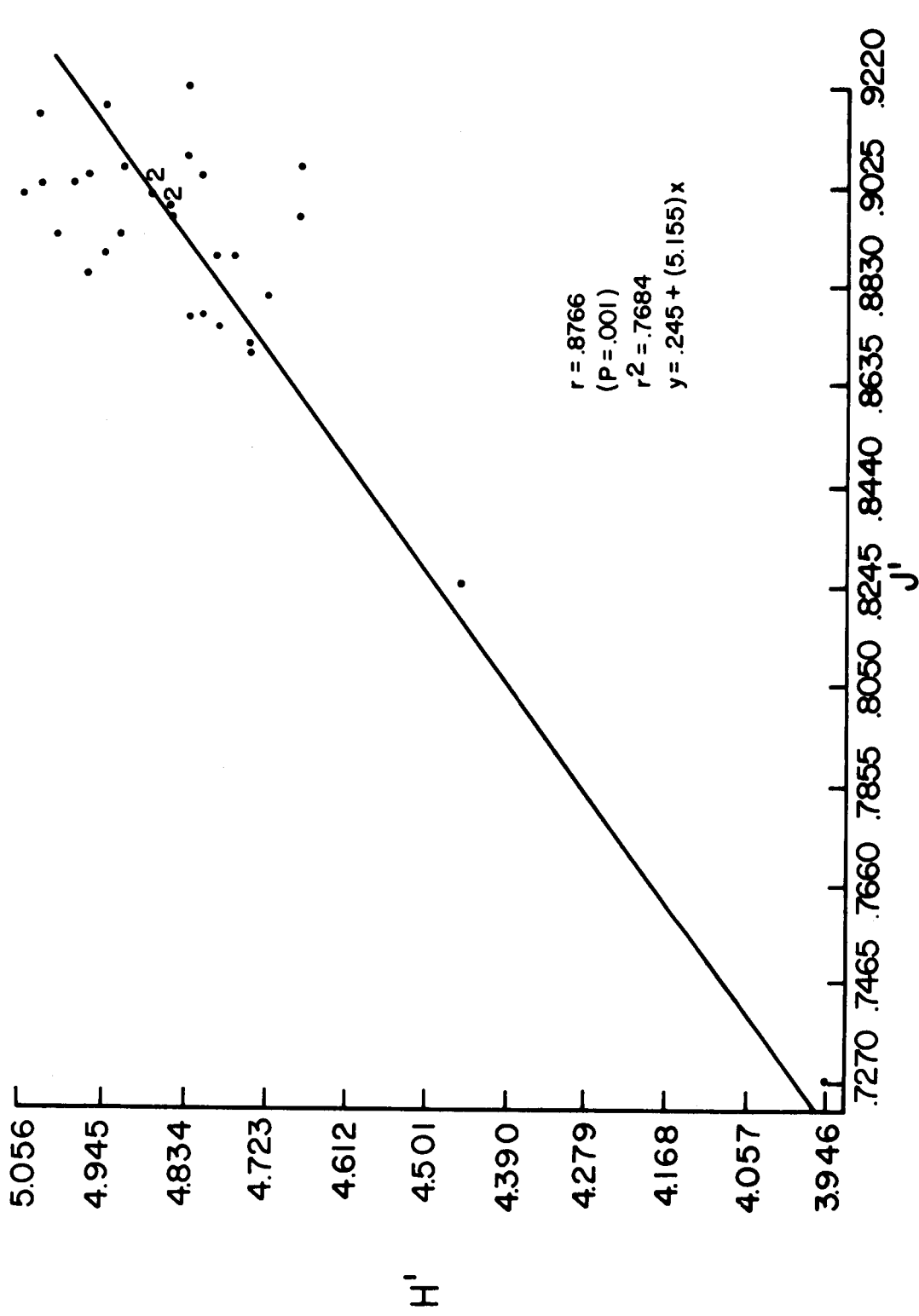


Figure 18. Regression of species diversity (H') against evenness (J') for discrete census data.

against J' accounts for about 44% of the variation in H' (Figure 19). Hence it is predictable that as J' falls with increasing sample size, H' will rise. Again, care must be taken in interpreting such regressions--not all functional relationships observed in nature are cause and effect relationships (Sokal and Rohlf, 1969). In this case, the fact that the data are cumulative and therefore sample size dependent is crucial to proper interpretation. Though both variables are responding to increasing sample size, change in one is predictable from the other.

In the discrete census data there is no significant correlation between species richness and evenness ($P = .327$). Table 6, page 59, indicates, however, that evenness is more strongly correlated (in a negative manner) with species richness in the cumulative data than it is with species diversity or even with study time or sample size, again confirming the expectation that the additional species which raise the S and H' values are rare and therefore depress evenness of the sample. The correlation was even more strongly negative with $\log_2 S$ than with untransformed S ($r = -.9522$ compared to $-.9488$). Regression against $\log_2 S$ accounts for nearly 91% of the variation in J' (Figure 20).

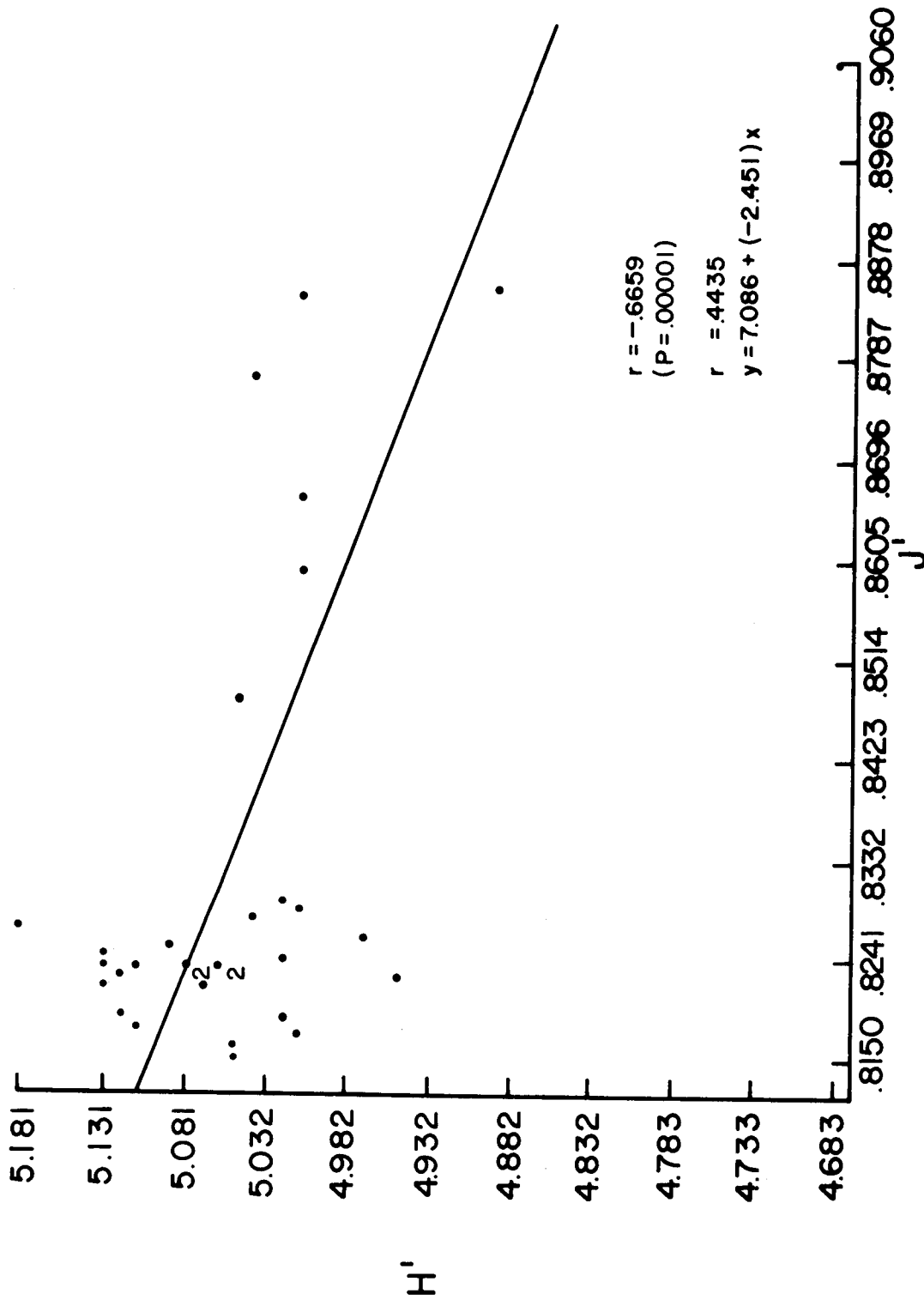


Figure 19. Regression of species diversity (H') against evenness (J') for cumulative census data.

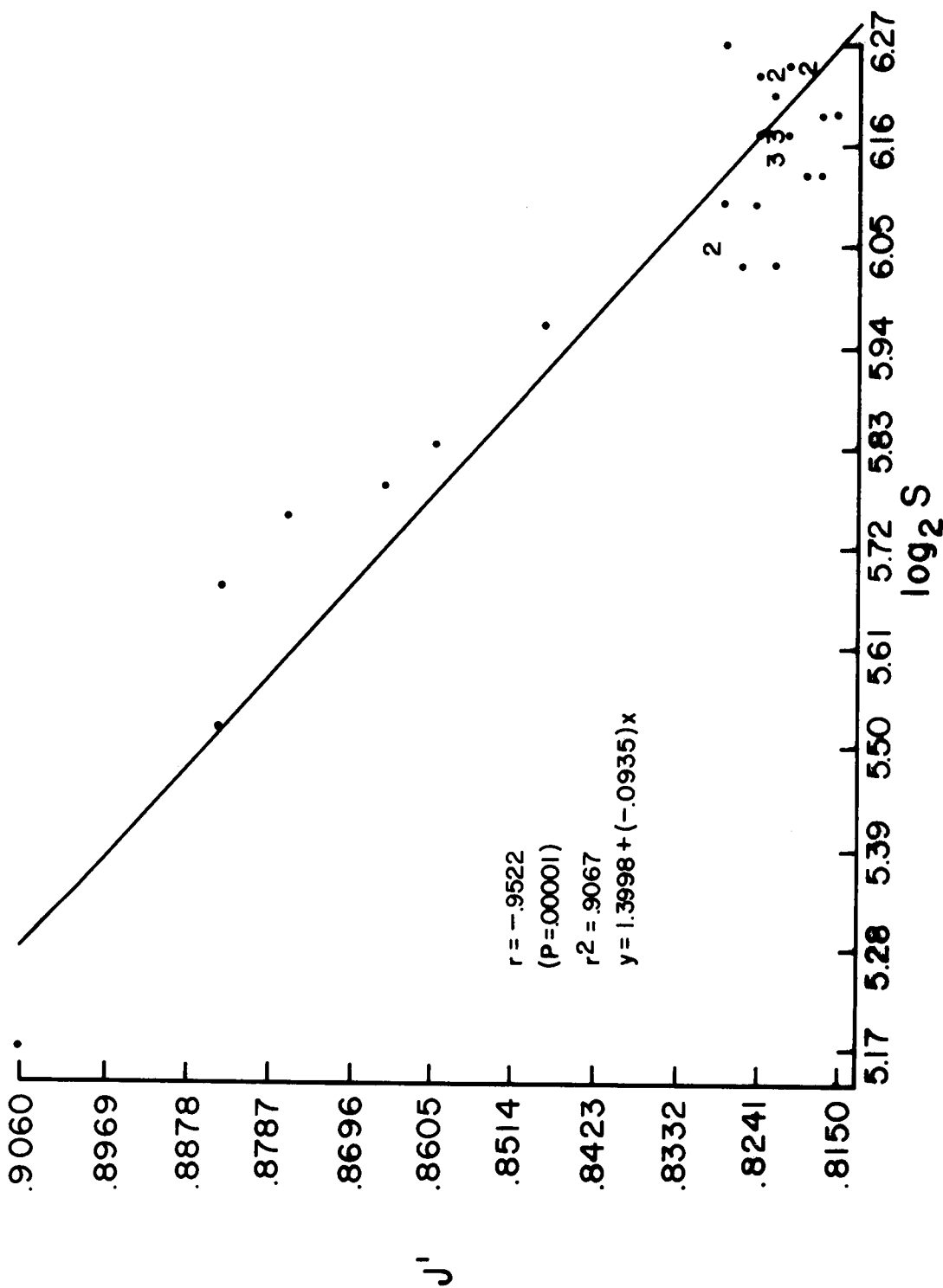


Figure 20. Regression of evenness (J') against $\log_2$ species richness ($\log_2 S$) for cumulative census data.

CHAPTER V

DISCUSSION AND CONCLUSIONS

Measurement of Bird Species Diversity of Sugarcreek Reserve

The measurement of species diversity, as discussed in the introduction to this thesis, has been fraught with controversy and equivocal results concerning the relation of the components of diversity, species richness and evenness, to each other and to the overall informational measure. Additionally, the dependence of the diversity components on sample size has compounded the confusion by invalidating comparisons between communities when sample sizes are unequal (Hurlbert, 1971). It is not the purpose of this study to assess or compare the ultimate utilities of the various diversity measures, nor is it my intention to elucidate the mathematical or ecological relationships of the diversity components to anything whatsoever by the formulation of any generalized or all-encompassing scheme. Rather I seek to provide further empirical evaluation of a method used to measure bird species diversity so that such measurements can be made with confidence of accuracy within the constraints of study time and effort. Underlying this evaluation is the conviction that species diversity is an important, though elusive, element of community structure which demands measurement before decisions of land use

policy may be formulated and implemented.

In this study, diversity components were inter-related under two basic analytic structures. The first, or "discrete" measurement system, started fresh each census with a discrete measurement of the diversity of bird species observed during that daily census. On the average, three three-hour censuses were conducted each week during the 11-week study period and weekly means of these daily measurements of diversity, richness, and evenness, as well as sample size, were calculated for analysis of variance of the components over the study period. The discrete daily values themselves were utilized in correlation and regression analysis to determine the strength and direction of relationships between paired variables. The second analytic structure, based on cumulative values of the diversity components, added the observations from each census to the expanding pool from previous censuses so that the cumulative values for any day were calculated from the total sample of birds observed since the first census of the study. With this system it was possible to test the effects of increasing sample size on each diversity variable, and correlations and regressions between components portray the relationships observed after an 11-week period of increasing sample size.

The necessity of analyzing the data derived from these two analytic structures separately is apparent from

the results of this study: the variables show distinctly different relationships to each other when analyzed cumulatively from when analyzed discretely. Furthermore, both systems are worthwhile approaches to the diversity problem. Whereas the discrete system better illuminates ecological trends over the study period and relationships between diversity components on a single census measurement basis (with 33 repetitions), the cumulative system clearly permits discernment of trends dependent on sample size. In comparing the disparate correlational results of the two methods (Table 6, page 59), it is easy to see how confusion arises in the literature over what is correlated with or a function of what, in what direction, and above all, why. It is, therefore, fundamental to decide which analytic structure, discrete or cumulative, best answers any given question and is legitimately comparable with the results of a given previous study.

In considering the question of whether species diversity and its components vary with time over the season, one must turn to the discrete census data. Essentially, variability in H' , S , or J' is simply the failure of any given bird to be recorded on every census. Absence of a given bird from a census can result from (1) the bird not being present in the study area at the time of the census, or (2) the bird being present but overlooked by the observer (Kricher, 1973). These two effects are not

amenable to precise separation by the observer. The results of this study indicate some temporal variation in the diversity parameters (Figures 2-5, pages 44-47) but the observed variation is not significant when subjected to analysis of variance. The null hypotheses in hypothesis sets I, II, and III, predicting constancy of diversity component values over the summer, are thus supported. Such constancy suggests that species diversity measurements based on appropriate sample sizes should be roughly equivalent for all time segments within the span of this study. Significant positive correlations of H' and S with time reflect the rising trends these variables show for the last seven weeks of the study, but the observed increments apparently result entirely from the addition of vagrant or transient individuals of species not breeding in the study area during the study period. Though interesting in other contexts (they may be potential breeders or important in trophic considerations, for example) most of these non-nesters are probably of negligible ecological importance to the Sugarcreek biotic community. Nonbreeders also affected the results of Kricher's (1973) study when declining bird species diversity over one summer was significant in a New Jersey herbaceous field visited unpredictably by feeding flocks of starlings, grackles, tree swallows, and smaller numbers of other non-nesters.

The general constancy of diversity values over the summer, as found in my study, was also observed by Kricher (1973) for a New Jersey oak forest, and by Adams and Barrett (1976) for two southwestern Ohio beech-maple forests, one virgin and one selectively cut. The latter study, however, found a significant increase in species richness during the first five weeks of censusing, from late April through May, which was attributed to the arrival of breeding residents to the study areas. My study, initiated May 31, by which date all breeding species should have arrived and established territories, had to contend with post-breeding wanderers rather than spring arrivals. The somewhat erratic variation in the evenness component (Figure 3, page 45), ascribed to the sporadic occurrence in censuses of large monospecific flocks, was nevertheless insignificant statistically. As was discussed in the results of this study, such variation in evenness was closely paralleled by variation in species diversity, since discrete H' and J' values were highly correlated ($r = .8766$).

While discretely measured diversity values, as defined here, are certainly useful in observing trends over time, the meaningfulness of between-study comparisons is likely to be obscured by sample size effects. Even the results of studies which use diversity values derived from observations from numerous censuses, and are certainly definable as "cumulative" values, may be of meager

comparative worth if sample sizes are not specified and the effects of rising sample size on the diversity components are not evaluated. The occasional intersection of species richness curves when plotted for different communities against increasing sample size (Hurlbert, 1971) furthermore suggests that comparisons between communities for any of the diversity components are most instructive when the component curves for different communities are plotted and compared as such; comparisons made at a single sample size are biased by the differential increases with sample size exhibited by collections with different species numbers and abundances. In this study the effect of rising sample size was dramatic. The greatest variation occurred in species richness, which showed a rapid rise during the first three to four weeks of the study and then plateaued after four weeks at a sample size of 3000 to 3500. The alternative hypothesis in hypothesis set V, predicting a significant initial increase in cumulative bird species richness with increasing cumulative sample size, is supported by these data. This is concordant with the observation of Hurlbert (1971) that species richness curves will rise rapidly at first and then flatten out, suggesting that comparisons and correlations are only justified at some high, "standardized" sample size. I have determined this optimal sample size for the Sugarcreek summer avifauna as 3030, for reasons discussed in the results, when species

richness was 90.9% of its final value and species diversity was 96.7% of its final value after only 42.4% of the total study hours and 39.8% of the final sample size. Increases in species richness beyond this point as the sample size rose to the final value of 7613 resulted from the addition of transient or vagrant individuals of species thought not to be breeding in the study area. Regression of species richness against the $\log_2$ of sample size (Figure 13, page 63) yielded a predictive linear relationship, with regression accounting for over 98% of the variation in richness. One should not infer from this that species richness will increase indefinitely with sample size in a given community--such an interpretation of the regression equation would most certainly be fallacious. Rather, species richness will increase predictably with sample size up to the ecological limits of the (arbitrarily finite) community in question, as determined by considerations of species packing. As Hurlbert (1971) notes, "a mathematical approach does not oblige a biologist to be modest about his ability to make biological distinctions."

The trend for evenness plotted against sample size was almost precisely antipodal to that of species richness, as cumulative evenness and richness were negatively correlated to an extreme degree ($r = -.9488$). Cumulative evenness fell sharply for the first three weeks of the study and leveled off at a sample size around 2000, largely

attributable to the accumulation of rare species in the sample. This finding supports alternative hypothesis b in hypothesis set VI, with cumulative evenness values declining with increasing cumulative sample size, as predicted by Hurlbert (1971). Again, regression against logtransformed sample size yielded a predictive relationship with regression accounting for 85% of the variation in evenness (Figure 15, page 65).

In contrast to the species richness and evenness trends, there were neither sharp increments nor sharp decrements in cumulative species diversity values with increasing sample size except for a punctuated rise up to the second week of censusing; this is indicated by the SNK multiple range test which grouped only the first week's mean cumulative diversity value apart from those of the 10 succeeding weeks, all of which comprised a single homogeneous subset. After just one three-hour census the H' value was 90.4% of its final value, while species richness at this time was only 46.8% of its final value. The difference between the first week's mean cumulative H' value and the values of the succeeding weeks was significant, however, and the alternative hypothesis in hypothesis set IV is accepted. The relative constancy of the H' value with increasing sample size after the first three censuses can be explained by the countervailing trends displayed by diversity's two components, richness and evenness, which

tended to balance each other with increasing sample size. The cumulative species diversity values show a slow steady rise rather than a decline because diversity is more highly correlated with richness than with evenness in the cumulative data ($r = .8445$ vs. $r = -.6660$). This validates the appropriateness of the Shannon measure over some other diversity measures (Simpson's or McIntosh's, for instance) in which diversity is relatively more highly correlated with evenness (DeJong, 1975) and might hypothetically show declines with increasing sample size as evenness drops, a conceptually distressing phenomenon and perhaps biologically unrealistic. Regression of species diversity against log-transformed sample size accounts for 71% of the variation in diversity. Again, within the constraints of a "real" biological community, the sluggish rise in diversity with increasing sample size would plateau as species richness plateaus. Generally, the results of this study support the contention of those such as Enemar (1959, cited by Karr, 1976) that an observer familiar with the local avifauna of a given temperate forest community can accurately assess species composition and abundances to within 5% of the true community values (which are ultimately unknowable, however, in complex communities) after very few surveys. Using H' as the diversity measure, the 5% level (of final cumulative diversity after 11 weeks of study) was reached in this study after only three censuses in one week (Table 7, page 67).

If, on the other hand, the observer is interested in determining the actual breeding bird composition, species richness, and evenness, rather than the informational diversity value alone, I maintain that quite a few more censuses are required to transcend sample size dependencies and to seek out the more elusive members of the avifauna. With methods tantamount to mine in a similarly sized and structured study site, approximately 42 hours of observation (or a sample size of about 3000) at the appropriate time of the breeding season are required to assume accurate representation of breeding bird species composition and diversity.

The relationships between paired diversity variables differ in strength and, in the case of H' and J' , direction in the two measurement systems utilized in this study. The association between species richness and species diversity is significantly positive in both the discrete and the cumulative data, but the correlation is stronger in the cumulative data ($r = .8445$, compared to $r = .4079$). Both systems of analysis support the alternative hypothesis in hypothesis set VII that increases in species richness are accompanied by increases in species diversity. The prediction of species diversity from species counts alone is, however, much more accurate when sample size is large, as attained with the cumulative system. The relationship between evenness and species diversity is directionally opposite in the two measurement systems. The positive

association ($r = .8766$) in the discrete data supports alternative hypothesis a in hypothesis set VIII, while the negative association ($r = -.6660$) in the cumulative data supports alternative hypothesis b in that set. Such discrepancy is predictable from results of previous studies reported in the literature. The occurrence of large monospecific flocks in particular censuses would expectedly lower both evenness and diversity values for those censuses (Kricher, 1972), while absence of such flocks would result in higher values of both H' and J' . Diversity trends thus parallel evenness trends in the absence of any marked variation in species richness. In the cumulative system, on the other hand, increases in species diversity are brought about by the addition of rare species to the sample with increasing sample size, which will always lower the J' value (Hurlbert, 1971). Finally, the lack of any significant correlation between evenness and richness in the discrete data supports the null hypothesis in hypothesis set IX. The strong negative correlation in the cumulative data ($r = -.9488$) is again related to the addition of rare species to the sample and supports alternative hypothesis b in that set. The characterization of community structure is clearly beset by discrepant relationships among alleged measures of such structure when subjected to different methods of analysis. Investigators must always evaluate

thoughtfully which analytic system best answers a particular question.

Why There Are So Many Kinds of Birds in Sugarcreek Reserve

By all comparisons with similar temperate areas studied, Sugarcreek Reserve is exceedingly diverse in bird species. For example, Karr (1968) found highest diversities in Illinois in a bottomland forest study area. For 100 acres of this forest and a sample size of 489 individuals in 32 species, the calculated H' value using $\log_e$ was 3.315. This sample size is most comparable to my third cumulative census, where a sample size of 537 individuals comprised 51 species and the H' value converted to $\log_e$ calculation was 3.477. My second cumulative census, with a sample size of 336 individuals comprising 46 species, had an H' in $\log_e$ of 3.470, still higher than Karr's value. Remarkably, even my first census with a sample size of 173 individuals included 36 species with an H' in $\log_e$ of 3.246, not much below Karr's highest Illinois diversity measurement. Furthermore, Karr (1968) notes that the bird species diversities reported in his study are higher than those reported by MacArthur and MacArthur (1961) for other locations in the eastern United States, as well as higher than similar measurements from Puerto Rico and all but the mature and young tropical forests in Panama surveyed by MacArthur et al. (1966). Tramer (1969) calculated mean

species diversities for breeding bird populations in nine community types using $\log_2$ as in this study. Unfortunately he did not cite census sample sizes but rather supplied only the number of censuses in each community type from which means were calculated. Lowest diversities were in marshes ($H' = 1.79$, $n = 15$), followed by grasslands ($H' = 1.93$, $n = 38$), shrublands ($H' = 3.14$, $n = 26$), deserts ($H' = 3.25$, $n = 6$), coniferous forests ($H' = 3.53$, $n = 51$), upland deciduous forests ($H' = 3.82$, $n = 62$), mixed forests ($H' = 3.92$, $n = 30$), floodplain deciduous forests ($H' = 4.07$, $n = 18$), and finally tropical woodlands ($H' = 5.23$, $n = 21$). The calculated H' from my initial three-hour census was 4.683, higher than any of Tramer's means except his tropical forest value, which still exceeds my final cumulative H' value of 5.181. In a survey of 17 British woods of 100 ha or larger, Moore and Hooper (1975) found a total of 53 species, and it was not indicated whether all of these were assumed to be breeding. A study conducted by Adams and Barrett (1976) which censused birds in two southwestern Ohio beech-maple forests, one virgin (Hueston Woods) and one selectively cut (Lewis Woods) and the former located within about 50 km of Sugarcreek Reserve, found breeding bird species richness values of 38 and 32, respectively, in contrast to the grand total of 77 species and 61 species assumed to be breeding within Sugarcreek Reserve. The conclusion of these comparisons is that

Sugarcreek Reserve contains a more diverse summer (and/or breeding) avifauna than any corresponding temperate area for which I have found diversities reported in the literature. This high diversity results from three primary factors: (1) high internal habitat heterogeneity and edge effect, (2) the comparatively large size of the study area, and (3) the recent insularization and concomitant supersaturation of the study area as surrounding habitat has become unsuitable for many species.

Of direct concern in this study are the proximate environmental factors influencing bird species diversity on an ecological time scale. There is no attempt to explain the ultimate factors underlying species diversity, such as those determinants which operate on an evolutionary time scale. Theories purporting to explicate or clarify the general phenomenon of species diversity are summarized in the introduction to this thesis. When dealing with bird species diversity in particular, it has generally been considered legitimate to leave the diversity of vegetation structure, which underlies faunal diversity (MacArthur and MacArthur, 1961), essentially unexplained, pushing that problem on to the plant ecologists and general community theoreticians. Nevertheless it has been abundantly documented that the structural characteristics of the vegetation are highly related to the bird species diversity of a given region (MacArthur and MacArthur, 1961; MacArthur

et al., 1962, 1966; MacArthur, 1964; Karr, 1968, 1971, 1975; Cody, 1966; Recher, 1969; Karr and Roth, 1971; Willson, 1974; Roth, 1976, among others). Many of the above studies concluded that the complexity of the vertical distribution of leaves, as measured by foliage height diversity (FHD), was a good predictor of bird species diversity (BSD). As Pearson (1975) points out, however, such conclusions are dependent on the assumption that the community is in an equilibrium or saturated state, such that new species cannot enter the community without excluding species already present. An inability to accurately predict bird species diversity from the foliage profile or other aspects of habitat structure in a given region indicates that the equilibrium assumption may be unjustified; incongruities might be explained by consideration of historical patterns of bird distribution or by competitive interactions among the birds and with other animals (Pearson, 1975). Nevertheless the general positive association of habitat complexity and avian diversity is clear. The number of vertical layers of vegetation alone may account for breeding bird species diversity within relatively homogeneous habitats, but is insufficient to account for diversity within areas that are more "patchy" (MacArthur, 1964). Such patchiness or horizontal variability in the types of profiles in a habitat may be the principal factor determining the variety of birds which breed in a particular area (MacArthur and

MacArthur, 1961; MacArthur et al., 1962; Roth, 1976; Rotenberry, 1978). The abundance of a given species in an area has been shown to be proportional to the number of patches of vegetation whose foliage profile is acceptable to that species, since breeding individuals of a species select sites of a certain vegetational configuration that are more or less unique to that species. The correct structure is ecologically important to birds in providing display perches, shelter and nest sites, and suitable foraging areas (Wiens, 1973) and certain elements of the habitat structure, referred to as the "niche-gestalt" by James (1971), serve to elicit settling by birds in ecologically appropriate environments. Some species, in choosing their nesting habitat, may require profiles of two or more types; a cardinal, for example, may require both woods and open areas rather than some mean profile (MacArthur et al., 1962). It follows that for additional species to be accommodated in an area, there must be either an increase in the number of kinds of patches available, or else more spatial overlap by species in their utilization of available patches (Roth, 1976). Karr and Roth (1971) and especially Willson (1974) have demonstrated that the greatest increase in bird species diversity occurs with the addition of shrub and tree layers to a vegetational series, which provides for the addition of new avian guilds. Despite the plentiful

evidence that habitat heterogeneity, particularly horizontal patchiness, so saliently influences bird species diversity, there is as yet no "efficient, simple, and biologically reasonable heterogeneity index which will predict bird species diversity in both subtle and coarse cases" (Roth, 1976).

Without a good method to evaluate the internal habitat heterogeneity of a study area, comparisons of measured species diversity values from different communities are likely to suffer from a lack of quantification similar in degree to that which plagues diversity comparisons with unequal or unspecified sample sizes. Faced with this dilemma, most studies of bird species diversity have used homogeneity of vegetation structure as a primary criterion in the selection of study areas, in keeping with the assertion of Kendeigh (1944) that "bird censuses should be restricted to single biotic communities." Besides the obvious semantic, theoretical, and empirical difficulties involved in the characterization and delineation of biotic communities, this ostensible homogeneity has never been thoroughly defined as it is, along with heterogeneity, a relative quality. Moreover, although it is imperative to control as many factors as possible in any scientific endeavor, strict adherence to the criterion of homogeneity does not permit evaluation of the horizontal component of habitat diversity. As Karr (1968) notes, it is necessary to

determine what occurs in more complex habitats; that is, those characterized by considerable interdigitation of habitat types. As accounted in the study area description of this thesis, Sugarcreek Reserve constitutes a mosaic of habitat types and seral stages but is nevertheless distinct as an island of more or less natural vegetation in a sea of developed land. This internal heterogeneity, intensified by the relatively large size of the study area (228 ha), is to a profound degree responsible for the exceptionally high bird species diversity of Sugarcreek when compared to other temperate localities.

The application of island biogeographic theory, originally elaborated by Preston (1962) and particularly MacArthur and Wilson (1963, 1967), to land use planning and the design of natural preserves has considerable conservation potential (see review by Diamond and May, 1976). It has been shown that many of the principles which explain species distributions on oceanic islands also apply to isolated continental habitats such as mountain tops (Brown, 1971) and alpine grasslands (Vuilleumier, 1970). In particular, nature reserves may be thought of as habitat islands because they are areas of natural habitat surrounded by expanses of culturally modified land (Terborgh, 1974, 1975, 1976; Wilson and Willis, 1975; Sullivan and Shaffer, 1975; Diamond, 1975, 1976; Diamond and May, 1976; Simberloff and Abele, 1976; Whitcomb et al., 1976; Whitcomb, 1977;

Miller and Harris, 1977; Pickett and Thompson, 1978, among others). Although direct ecological support for island biogeographic theory is sketchy and the extent to which continental habitats are truly insular is often not well documented (Simberloff and Abele, 1976; Miller and Harris, 1977; Simberloff, 1974, 1978), the predictions of island biogeography are often verified for continental habitat islands of differential size and degree of isolation. Forest size, for example, has been found to be a significant predictor of the number of bird species in newly created forest islands in both the United States (Galli et al., 1976; Forman et al., 1976) and Great Britain (Moore and Hooper, 1975). A problem yet to be solved is how to quantify the extent of insularization for a given habitat island. A nature reserve may be contiguous enough with surrounding natural habitat that it represents simply a sample from a larger community and is therefore not a self-contained unit that can be legitimately characterized as insular. As the area around a reserve becomes more developed, however, and hence inhospitable to many species, the reserve becomes isolated and a greater species-area relationship is observed; eventually fewer species may be found in the reserve than in sample areas of equal size (Miller and Harris, 1977). Or, alternately, the species richness may not change much, or may even increase, but species composition will transmute such that "edge" species

are favored while size dependent species which require certain minimum areas for long-term survival will disappear. The latter situation was found in New Jersey by Forman et al. (1976). In this case a forest island of a given size contained more species than did a sample plot of equal size within an extensive forest, but the additional species were birds which primarily inhabit the forest edge, such as the gray catbird, rufous-sided towhee, and common flicker. Birds of the forest interior, such as ovenbirds, black-and-white warblers, black-billed cuckoos, and red-shouldered hawks, were limited to the larger forest islands. In all cases, large forest islands contained more species than did an equal combined area of smaller forest islands.

The above findings fall in line with the predictions of island biogeography, which holds that insular species diversity represents a dynamic balance between the rate of immigration of new species to an island and the rate of extinction of existing species on that island. Islands are continually receiving immigrants due to dispersal from the mainland (or species source) and immigration rate should increase with island area and proximity to the colonization source. The more remote the island, the lower is the immigration rate (Diamond, 1973, 1975). Immigration is proportional to area in the sense that areas of land act as giant "nets," sweeping out larger or smaller fragments

from some large source community (Simberloff, 1978). The larger the net, the more species swept in. Established island populations, on the other hand, risk extinction due to competition and random fluctuations in population size, and smaller islands with smaller populations have commensurately higher extinction rates. As Pickett and Thompson (1978) point out, the components of equilibrium on both oceanic and continental (habitat) islands are the same, but the relative importance of these components differs between the two types of system. Immigration is important in maintaining species equilibrium on oceanic islands with large continental species pools from which colonizers are drawn. But nature reserves as habitat islands either do not or soon will not have such extensive species source areas. Other reserves, often small and limited in number and widely spaced, must perform this function. Immigration will therefore taper off considerably as reserves become increasingly isolated and extinction will become the dominant population process affecting equilibrium. Moreover, the immigrants which do succeed in colonizing habitat islands will most likely be those widespread "weedy" species which do not need reserves for their survival (Terborgh, 1976; Pickett and Thompson, 1978). Those species that require continuous habitat or specialized habitat types are not likely to disperse to sites where they have become extinct, especially in the tropics

(Terborgh, 1974) but also perhaps for neotropical migrant birds which nest in temperate forest interiors, such as many warblers and vireos (Whitcomb et al., 1976; Whitcomb, 1977; Whitcomb et al., 1979). It is thus clear that the destabilizing effect of habitat insularization can lead to regional extirpations of species complexes.

Miller and Harris (1977) contend that it is unnecessary to invoke the theory of island biogeography (MacArthur and Wilson, 1967) to explain trends of species reduction in isolated habitats and reserves. Instead, the empirical relation between the number of species and the size of an area may suffice to quantify species numbers in insular habitats at equilibrium. This species-area relation is a crucial element of biogeographic theory but is useful in itself, without theoretical underpinning. The phenomenological equation is: $S = cA^z$, where S is the number of species on an island, c is a proportionality constant for a given species group in a given archipelago, A is the island area, and z , typically assuming a value in the range 0.18 - .35, is a constant representing the degree of relation between species number and the size of the area (Preston, 1962; MacArthur and Wilson, 1963, 1967; Diamond, 1975; Diamond and May, 1976; Miller and Harris, 1977). Thus the number of species on an island is usually found to increase with island area in a double logarithmic relation. A general rule of thumb, corresponding to a z value of 0.30, is that

a tenfold increase in island area means a twofold increase in the number of species (Diamond, 1975). This empirical relation has been generally validated for a variety of taxonomic groups, both plant and animal, on both oceanic and continental islands. Theoretical explanations for the area effect include the biogeographic dynamic equilibrium between immigration rates and extinction rates mentioned above, the correlation between area and the variety of available habitats, each habitat adding species to the total (Lack, 1973), and the correlation of area and the number of "hot spots," or sites of locally high resource production which may constitute only a small fraction of the territory or home range of a species but are important hedges against extinction (Diamond, 1975, 1976). Furthermore, species with seasonally or spatially patchy food sources must integrate resources over large areas (Diamond, 1976).

The pertinence of the species-area relation to conservation practice is obvious: except in certain special cases, nature reserves should be as large as possible since large reserves will have larger populations and therefore lower extinction rates (Diamond, 1975, 1976; Wilson and Willis, 1975; Diamond and May, 1976; Simberloff, 1978). Pickett and Thompson (1978) have advanced a convincing argument that the design of nature reserves should be based on analysis of "minimum dynamic area, the

smallest area with a natural disturbance regime, which maintains internal recolonization sources, and hence minimizes extinction." The minimum dynamic area, determined by knowledge of disturbance-generated patch size, frequency, and longevity, and the mobilities of the affected species, should be defined by the most extinction-prone taxon. Determination of such minimum dynamic areas, however, will be arduous due to the complexities of patch dynamics and the unpredictability of many disturbance agents. Furthermore direct determination of the appropriate area is probably possible only in large systems which are at equilibrium with respect to their normal disturbance regimes. Thus such analysis may be worthwhile for land use planning in relatively unspoiled areas, such as park planning in Alaska, but is not immediately applicable to the management of small nature reserves in areas as intensively modified as southwestern Ohio, where all existing reserves are probably smaller than the appropriate minimum dynamic areas.

Consideration of the species-area relation, as discussed above, has led most observers to favor one large reserve over two or more smaller reserves of equivalent total area in any given case. Simberloff and Abele (1976), however, have shown that this conclusion may be incorrect under certain conditions. For instance, catastrophes such as fire or epidemic diseases could cause extinction if all conserved lands were united in one large reserve; a system

of scattered parks would clearly be less susceptible to such disaster. Also, several smaller reserves in an inhomogeneous region could each preserve unique combinations of habitats and species. It is possible as well that each small reserve might save a different member of a set of mutually exclusive competitors. Although the above arguments have considerable validity, Diamond (1976), Diamond and May (1976), Terborgh (1976), and Whitcomb et al. (1976) have argued that the other reasons offered by Simberloff and Abele (1976) for the preference of small reserves, under certain conditions, are either irrelevant or biologically unrealistic. For example, although fugitive species or edge species should profit most from parks with high perimeter-to-area ratios, these species will often survive well in the absence of any refuges. Conversely, the species most in need of protection, those with minimum area requirements, will be unable to survive in a system of small refuges. "The question is not which refuge system contains more species, but which contains more species that would be doomed to extinction in the absence of refuges" (Diamond, 1976). Evidence for size dependence in birds, where certain species are found only on islands or in reserves above some lower size limit, has been provided by Diamond (1973, 1975), Galli et al. (1976), Forman et al. (1976), Whitcomb et al. (1976), Whitcomb (1977), and Whitcomb et al. (1979). In some cases,

confinement to the interiors of relatively large forests might arise from psychological factors of habitat selection which restrict the utilization of the marginal areas of forest fragments and islands, as may be the case with ovenbirds (MacClintock et al., 1977). Many investigators now agree that in order to maintain regional species diversity, top priority should be placed on protecting large forests rather than protecting an equal area of small forests. Forman et al. (1976) have demonstrated that in the New Jersey piedmont the most valuable forests would be larger than 40 ha. In Britain, Moore and Hooper (1975) suggest that nature reserves should be 100 ha or more in order to maintain bird species diversity. Finally, Whitcomb (1977) contends that "thousands of contiguous acres may be required to assure the long-term survival of the forest-interior bird species." A second land use priority should be the preservation of numerous small forests, for reasons mentioned above and because such tracts may be important as stepping-stones or rest stops for species dispersal between larger forests (Forman et al., 1976).

Species-area relations suggest that if a large area of natural habitat is destroyed with a small portion retained as a nature reserve, the reserve will initially contain more species than appropriate for its area at equilibrium. Such temporary diversity on newly formed

islands is known as "supersaturation" (Diamond, 1973). Species will go extinct until the new equilibrium number is reached. The "relaxation rate" for a given island is the rate at which its species number drops to the new equilibrium value appropriate for an island of that area. The oft-cited natural experiment to assess such relaxation rates as a function of a reserve's area is the consideration of land-bridge islands, land areas which have been separated from continents to which they were formerly contiguous, such as by rising post-Pleistocene sea levels about 10,000 years ago. Such islands are assumed to have initially contained a species complement equivalent to that of an equal-sized segment of the continent to which they were attached. In the last 10,000 years, however, species numbers have slowly relaxed towards the equilibrium value corresponding to each island's area. Evidence of such declining diversity on land-bridge islands has been provided by Diamond (1973) for New Guinea and Terborgh (1974) for the West Indies and Central America. Both investigators have discovered that significant declines in species numbers can take place over a period of decades in the smallest islands, which are comparable in size to many nature reserves on continents. Willis (1974) has documented the decline in the number of bird species following the insularization of what is now Barro Colorado Island in Panama, an island created by the formation of

Gatún Lake with the construction of the Panama Canal. The 10% decline in species richness conforms with that predicted by Terborgh (1974) for an island of that area and degree of isolation. Although vegetational changes are doubtlessly responsible for part of the species loss (Simberloff, 1978), the extinction of many of the species is clearly an island effect (Terborgh, 1974, 1976; Wilson and Willis, 1975).

Although the degree of insularization of Sugarcreek Reserve, as with most other continental habitat islands discussed in the literature, has not been quantified, the reserve clearly is isolated at least from the standpoint of those species which are ecologically confined to the forest interior. Furthermore, surrounding habitat is becoming increasingly inhospitable as farmland gives way to subdivision and dispersal corridors are severed. Sugarcreek is therefore presently supersaturated with bird species and is not in equilibrium either in the biogeographic sense or the successional sense. Unless land areas around the reserve are acquired and permitted to remain as or to grow back to forest, we can expect large-scale extirpations of many species in the coming decades, not just of birds but of any taxa which are shown to exhibit minimum area dependence, high site tenacity (Adamus and Clough, 1978), low dispersive tendency, or other qualities which promote vulnerability to disruption.

Maintaining Diversity in Sugarcreek Reserve and the Surrounding Region

One reason for maintaining organic diversity, for maintaining some semblance of a natural environment, is to prevent the shift to human activities, distractions, and recreations that we must otherwise make to keep from being bored to death. This shift is self-accelerating and self-reinforcing for two reasons: first because the diversions are so unsatisfactory that they lead to even greater boredom, and second because these attempts to provide ourselves with diversions from real life in the natural world result inevitably in less diversity. So the natural environment and our activities within it become poorer and poorer, while our human world becomes more destructive as well as unfulfilling and meaningless (Kozlovsky, 1974).

Diversity is a complex ecological concept of considerable theoretical interest because of its relation to such holistic environmental qualities as ecosystem stability. Although theory is equivocal as to the diversity-stability relation, the weight of evidence suggests that "diverse systems appear to be more resilient and to have a greater capacity for self-restoration following damage than do naturally simpler ones" (Dearden, 1978). In any case, systems impoverished by man, such as in modern agriculture, are certainly less stable or resilient than are natural ecosystems. Stability aside, the science of conservation is very much concerned with diversity, striving in particular "to preserve viable populations of as many as possible of the species that inhabited the pristine landscape" (Terborgh, 1976). Of course, in probabilistic

fashion, all species are ultimately doomed to extinction. The goal of conservation is not to stop the natural process of evolution, but rather to abate the accelerated pace of species loss that is associated with human dominance of the biosphere. In today's world, it can be assumed that the creative process of speciation is hardly keeping up with species extinction. The best that conservationists could conceivably do would be to "state which ecological conditions minimize the rate of ultimately certain extinction" (Simberloff, 1978). Accordingly, ecological evaluation is quite properly concerned with the maintenance of organic diversity. In many individual cases, however, high diversity per se should not be the primary criterion of conservation strategy. Rather than treating all species as equal in a given locality under consideration, concern should be preferentially directed towards those species and habitats most threatened by human activities (Diamond, 1976). It is evident that different species have very different minimum area requirements for survival, in accordance with the theoretical explanations for the area effect discussed in the preceding section. Analysis of the pattern of species loss from land-bridge islands indicates a phenomenon of "ecological truncation" (Wilson and Willis, 1975), wherein the first species to expire are those high on the trophic pyramid as well as the larger or more

specialized members of feeding guilds. Forman et al. (1976) report that the bird species with the highest minimum area requirements are carnivorous, primarily insect-feeders and vertebrate-feeders. It is consistent with ecological theory that these carnivorous species are the rarest in natural communities because they subsist on a smaller energy base and require more extensive foraging ranges than do herbivores, and in being rarer they are generally the most extinction-prone. Rarer species should thus be given higher priority than common ones in ecological evaluation, other factors being equal (Adamus and Clough, 1978). Whitcomb et al. (1976) and Whitcomb (1977) have concluded that many of the neotropical migrant species that were once dominant in the eastern forest interior tend to disappear from fragmented forests, especially ground-nesting species such as the ovenbird and black-and-white warbler. Island biogeographic theory predicts high species turnover rates on small isolated islands. Terborgh (1976) and Whitcomb et al. (1976) have shown that the combined processes of relaxation and turnover in forest fragments results in a community composed almost entirely of widespread, ecologically generalized "weedy" species, generally those species common to edge habitats and early successional stages and therefore quite capable of long-term survival around farms and suburbs and not in any need of protection at present.

Whitcomb et al. (1976) and Whitcomb (1977) point out that in extensive forest tracts in eastern North America, 92% of the breeding avifauna is composed of neotropical migrants. In fragmented forests, many of the neotropical migrant species disappear and the avifauna of such tracts comes to be dominated by species that are either permanent residents or short distance migrants. In Sugarcreek Reserve, only 25 (41%) of the 61 breeding species are neotropical migrants (Appendix A, LM = long distance migrants). Permanent residents and short-distance migrants, particularly those which are edge species, have apparently benefited from the insularization process. Whitcomb et al. (1976) and Whitcomb (1977) also cite evidence that, in areas where forest has been reduced to isolated woodlots (most certainly the case for southwestern Ohio), avian brood parasites (brown-headed cowbirds), nest predators (small mammals, grackles, jays, and crows), and nonnative nest-hole competitors (starlings) are usually abundant in the surrounding agricultural and urban environments and often invade small forest tracts. The combined impact of these opportunistic species is probably a major force in the avifaunal changes that accompany forest fragmentation and isolation. In this context it is ominous that the above-named opportunists are highly abundant in Sugarcreek Reserve. In terms of relative abundance in the summer avifauna (Table 1, page 39), grackles rank first,

starlings rank seventh, cowbirds rank tenth, crows rank seventeenth, and blue jays rank twenty-ninth out of 77 observed species. Also, only two of the ten most abundant species are neotropical migrants and these, the blue-gray gnatcatcher and indigo bunting, utilize edge habitat extensively. Human disturbance in the form of trampling may also have a severe effect on the neotropical migrants, many of which nest on or near the ground. Whitcomb (1977) and Whitcomb et al. (1979) furthermore note that many of the life history strategies of neotropical migrants are inauspicious in their competition with permanent resident and short distance migrant species in man-altered habitats. Among these characteristics are specialized insectivorous feeding habits, which are not as successful as generalized foraging strategies in such altered habitats, and which moreover demand long-distance migration, resulting in an energy and time deficit for reproduction. Neotropical migrants may also encounter difficulty in recolonizing archipelagos of forest tracts every year following a long-distance migratory flight (Whitcomb et al., 1979). Finally, permanent residents have perhaps more time available for the territorial exploration necessary for successful dispersal. Whatever the factors which may be involved, the rarer neotropical migrant breeding birds of Sugarcreek Reserve, which include many of the forest interior warblers and vireos of great esthetic value to

birdwatchers, have locally at least a very precarious future. A poignant example offered by Whitcomb et al. (1976) is of an isolated forest plot in Rock Creek Park in the District of Columbia, where the percentage of neotropical migrant breeders declined from 87% in 1948 to 35% in 1974. It appears that Sugarcreek Reserve is well on its way to such a low point.

As island biogeography indicates, not only the size of the reserve is crucial, but so also is its isolation from species sources. It has been suggested (Willis, 1974; Diamond, 1975) that linking devices, such as forested corridors or stepping-stones of small forest tracts, might allow for species or gene flow between reserves and hence balance the effects of insularization. It is important to understand that the power of flight does not guarantee birds high dispersal ability (Diamond, 1975; Terborgh, 1975). Some birds, notably the permanent residents of tropical forests, may have insuperable psychological barriers to crossing water gaps or even a few kilometers of unsuitable habitat. Even for migratory birds, site tenacity may dictate that members of a given population return to breed in a certain locality year after year (Adamus and Clough, 1978). If the breeding area becomes inhospitable or population densities are high, individuals will perhaps disperse to nearby favorable habitats if suitable dispersal corridors are

present. By such dispersal, local extirpations can be balanced by incoming colonizers of the same or similar species, and overall species richness may remain high and composition essentially unaltered. MacClintock et al. (1977) offer explicit evidence of the importance of forest corridors in maintaining species numbers in fragmented forests. In their study a small forest tract connected by a corridor to a nearby extensive forest system was characterized by a typical forest-interior avifauna, in contrast to the depauperate condition of similar but isolated forest fragments. In this regard, the destruction (or at least vast reduction) of the small forest corridor along Sugar Creek to the west of the reserve as development began in 1978, effectively isolating the reserve from any continuous forest, is an egregious example of poor land use planning. The Open Space Committee of the Miami Valley Regional Planning Commission in 1971 studied the Sugarcreek area and recommended that "open space corridors, rather than isolated chunks of open space, be maintained." It can be assumed that "open space" in this sense means natural or forested areas. The committee furthermore recommended that public ownership would best protect these corridors and that "development proposals should be modified, where necessary, so that land can be dedicated for park purposes within these corridors" (MVRPC, 1971). It appears that the present planners have

not heeded this worthy advice. In addition to the ruination of the last remaining continuous forest extension to the west of the reserve, "for-sale" signs are appearing regularly on farmland and small woodlots throughout the area, including the fields just south of Conference Road, the southern boundary of the reserve. In evaluating the effects of insularization on the biota of natural reserves, planners must keep in mind that the process of faunal deterioration is, for all practical purposes, irreversible (Whitcomb et al., 1976).

It is recommended here that continuing surveys be made of the faunal and floral composition and diversity of Sugarcreek Reserve and other isolated forest islands under the jurisdiction of the Dayton-Montgomery County Park District so that the effects of insularization as well as visitor disturbance can be identified and hopefully minimized. Such a conscientious long-term planning scheme, if properly managed, would serve as an invaluable model for other park systems to emulate, in addition to generating the empirical data so needed by the developing sciences of applied biogeography and nature reserve design. Confounding the application of island biogeographic theory to land use planning in the case of Sugarcreek, however, is the fact that Sugarcreek is not in successional equilibrium. As mentioned previously in this discussion, the high internal spatial heterogeneity and high species

diversity of Sugarcreek results in large part from the variety of habitat patches of varying successional age. Since plant succession is accompanied by successional changes in avifaunal composition and diversity (Johnston and Odum, 1956; Shugart and James, 1973), the various successional patches in Sugarcreek Reserve each contain characteristic bird communities, and edge species predominate in the all-abundant edges, or interfaces between patches. At any one stage in succession, high diversity may be observed as a result of the presence of many species, some just becoming established, some at their population peaks, and others in decline (Reed, 1978). As Sugarcreek succeeds towards vegetational climax, the variety of habitats relevant to the distribution of birds will decline, as should bird species richness and diversity. Finally, as all woodland in the reserve approaches climax, there should again be a decline in diversity, as predicted by Margalef (1958) and actually found by Karr (1968) in his study of avian succession in Illinois. So even without island effects we should expect to see a decline in bird species in Sugarcreek Reserve over the coming decades. It may be difficult to separate successional effects from insularization effects when examining species diversity trends in forthcoming years, but clues to such separation can be found in analysis of species composition trends. Although both succession and

insularization may lead to declines in species diversity, with succession the edge and early successional species will show declines, while the late successional species will be most adversely affected by insularization.

It appears that the Dayton-Montgomery County Park District has sought to maintain high species diversity through the provision and maintenance of high habitat diversity in their management of Sugarcreek and other reserves. I argue here that this policy is not conducive to the preservation of long-term regional diversity by protection of the most vulnerable species assemblages. The question of consequence is: Do we want to maximize species diversity per se by providing for a rich, heterogeneous assortment of successional habitats, which is the situation we find now resulting incidentally from the land use history patterns, or do we want to preserve particular collections of species which were relatively abundant before human disruption of the habitat but are now declining and faced with regional extirpation? The latter alternative is certainly the most conducive to the maintenance of long-term regional diversity, for the species of undisturbed forests (e.g., the neotropical migrant birds mentioned above) are those most likely to show area dependence and vulnerability to extinction in fragmented habitats. The species of successional habitats can generally get along fine in the man-altered landscape. Therefore "the most

prudent preservation strategies are those that insulate sensitive species from the effects of human disturbance" (Whitcomb et al., 1976). In the case of Sugarcreek Reserve, the prudent strategy would be to allow the vegetation to return to mature forest, thereby increasing the forest island size and hence the population sizes of the vulnerable forest-interior species, while permitting all facets of the natural disturbance regime to operate, which should be sufficient to provide for the habitat heterogeneity required by the indigenous flora and fauna. By all means, human impacts should be kept to a minimum, as stressed by Whitcomb et al. (1979).

Viewed in this light, the past management of Sugarcreek Reserve has been inappropriate and indeed destructive to sensitive species. In particular, the cutting of a wide swath through the bottomland forest around 1971-72 for the installation of a sewer line was an inexcusable land use error. Whitcomb et al. (1976) have reported that when artificial swaths are cut through forests, severe destabilization of the faunal community can occur. In such cases the overall bird species richness may be increased, but only at the expense of the forest-interior species. Furthermore, the creation of such long strips of edge habitat favors colonization by the avian brood parasites, nest predators, and nonnative nest-hole competitors, discussed previously, which this study has shown to be

now exceedingly abundant in Sugarcreek Reserve. Gates and Gysel (1978) have reported that although the creation of narrow forest edges attracts a variety and abundance of open-nesting passerines, these edges may be "ecological traps." Although edges contain the relevant structural cues of the mixed habitat in which such species evolved, birds nesting near man-made habitat discontinuities have smaller clutches and are subject to higher rates of predation and cowbird parasitism. The recent widening of the trails and expansion of the trail system in Sugarcreek similarly creates artificial edge and has the additional pernicious effect of making areas of the reserve more accessible to visitors and thus to adverse human impact, as did the undue enlargement of the parking lot several years ago. The placement of large stepping-stones across the creek was likewise improper, particularly since this perturbation was executed by bulldozer during the avian nesting period. It is hoped that in the future planners will realize that the fundamental purpose of setting aside reserves such as Sugarcreek, which are called "nature reserves," not "recreation areas," is to protect and preserve the indigenous regional biota.

Although birds have been the direct focus of this study, the guidelines for management which arise from such ecological and biogeographic considerations are generally appropriate for other taxa as well. Concerning minimum

area requirements, for example, such requirements for birds, which occupy a variety of trophic levels and are of moderate size, are neither unrepresentatively large nor small (Whitcomb, 1977); but forest tracts that are sufficiently large to preserve populations of some organisms (e.g., most forest understory plant species) may be grossly inadequate as reservoirs for even the smaller forest-interior bird species (Whitcomb et al., 1979). The general responses of avian species diversity and composition to disturbance, relatively easy to discern empirically, moreover suggests that breeding birds are an excellent "indicator taxon" in the identification and evaluation of human impacts on total ecosystems (Adams and Barrett, 1976).

In conclusion, the following observations and recommendations from this study of bird species composition and diversity are especially pertinent:

1. Species diversity variables show distinctly different trends and relationships to one another when analyzed cumulatively from when analyzed discretely. Though both approaches are worthwhile, the cumulative approach combined with close scrutiny of sample size effects is more heuristic and likely to generate predictive relationships.

2. Approximately 42 hours of observation, or a sample size of about 3000, are necessary to assume accurate

representation of breeding bird species diversity and composition in a study area of this size and general structure.

3. Sugarcreek Reserve, with 61 species assumed to be breeding, contains a more diverse avifauna than comparable temperate areas for which diversities have been reported in the literature.

4. High bird species diversity in Sugarcreek Reserve results from high internal habitat heterogeneity and edge effects, the comparatively large size of the study area, and the recent insularization and concomitant supersaturation of the reserve as surrounding habitat has become unsuitable for many species.

5. Future management of Sugarcreek should emphasize preservation of extinction-prone species assemblages rather than high diversity per se. Such policy is most conducive to the long-term maintenance of regional diversity.

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APPENDICES

APPENDIX A

Table 8. Summary of individual species census data.

Species	Status*	Cumulative No. Individuals after (x) Weeks Study Time							Relative Abundance (%)	Importance Value
		2	4	6	8	10	11	12 (total)		
Great Blue Heron (<i>Ardea herodias</i>)	SM						1		0.013 (60t)	3.043 (67t)
Green Heron (<i>Butorides virescens</i>)	SM or LM	1	3	4	7	14	15		0.197 (48)	27.469 (49)
Mallard (<i>Anas platyrhynchos</i>)	PR	6	7	8	20	20	20		0.263 (43)	15.414 (57)
Wood Duck (<i>Aix sponsa</i>)	SM	3	3	3	3	3	3		0.039 (58t)	6.099 (64t)
Turkey Vulture (<i>Cathartes aura</i>)	SM	2	2	2	2	2	2		0.026 (59t)	6.086 (65t)
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	PR	1	2	3	3	4	4		0.053 (57t)	12.174 (62t)
American Kestrel (<i>Falco sparverius</i>)	PR					1	1		0.013 (60t)	3.043 (67t)
Bobwhite (<i>Colinus virginianus</i>)	PR	5	5	6	7	9	9		0.118 (52)	24.360 (51)
Ring-necked Pheasant (<i>Phasianus colchicus</i>)	PR	7	9	12	17	18	19		0.249 (44)	48.733 (42)
Killdeer (<i>Charadrius vociferus</i>)	PR or SM		1	3	6	9	10		0.131 (51)	18.312 (54)
American Woodcock (<i>Philohela minor</i>)	SM	1	1	2	2	3	3		0.039 (58t)	9.129 (63t)
Spotted Sandpiper (<i>Actitis macularia</i>)	LM				1	2	3		0.039 (58t)	9.129 (63t)

Table 8 (Continued)

Species	Status*	Cumulative No. Individuals after (x) Weeks Study Time						Relative Abundance (%)	Importance Value
		2	4	6	8	10	11(total)		
Rock Dove (<u>Columba livia</u>)	PR	10	42	42	45	59	89	1.169 (27)	28.441 (48)
Mourning Dove (<u>Zenaidura macroura</u>)	PR or SM	5	10	14	23	33	37	0.486 (35)	61.092 (41)
Yellow-billed Cuckoo (<u>Coccyzus americanus</u>)	IM	16	34	49	68	87	93	1.222 (26)	101.222 (16)
Black-billed Cuckoo (<u>Coccyzus erythrophthalmus</u>)	IM	2	9	14	19	25	27	0.355 (40t)	70.051 (36)
Great Horned Owl (<u>Bubo virginianus</u>)	PR	1	1	1	1	1	1	0.031 (60t)	3.043 (67t)
Barred Owl (<u>Strix varia</u>)	PR		2	3	3	3	3	0.039 (58t)	6.099 (64t)
Chimney Swift (<u>Chaetura pelagica</u>)	IM	29	44	57	81	116	129	1.694 (19)	98.663 (18)
Ruby-throated Hummingbird (<u>Archilochus colubris</u>)	IM	2	2	2	5	6	7	0.092 (54t)	18.273 (55t)
Belted Kingfisher (<u>Megasceryle alcyon</u>)	PR	5	13	18	23	29	31	0.407 (38)	64.043 (38)
Common Flicker (<u>Colaptes auratus</u>)	PR or SM	16	25	39	58	84	99	1.300 (25)	98.269 (19)
Pileated Woodpecker (<u>Dryocopus pileatus</u>)	PR	7	10	13	14	16	17	0.223 (46)	42.647 (44)
Red-bellied Woodpecker (<u>Centurus carolinus</u>)	PR	12	24	34	42	55	58	0.762 (31)	91.671 (27)
Red-headed Woodpecker (<u>Melanerpes erythrocephalus</u>)	PR or SM		1	1	2	4	5	0.066 (56t)	15.217 (58)

Table 8 (Continued)

Species	Status*	Cumulative No. Individuals after (x) Weeks Study Time							Relative Abundance (%)	Importance Value
		2	4	6	8	10	12	II (total)		
Hairy Woodpecker (<u>Dendrocopos villosus</u>)	PR	1	1	1	1	3	4		0.053 (57t)	12.174 (62t)
Downy Woodpecker (<u>Dendrocopos pubescens</u>)	PR	14	30	54	91	122	128		1.681 (20)	95.620 (21)
Eastern Kingbird (<u>Tyrannus tyrannus</u>)	LM					7	8		0.105 (53t)	12.226 (60)
Great Crested Flycatcher (<u>Myiarchus crinitus</u>)	LM	6	10	12	17	25	27		0.355 (40t)	63.991 (40)
Acadian Flycatcher (<u>Empidonax virescens</u>)	LM	59	105	140	193	235	249		3.271 (13)	103.271 (10)
Willow Flycatcher (<u>Empidonax traillii</u>)	LM	16	29	36	51	61	62		0.841 (30)	85.662 (29)
Eastern Wood Pewee (<u>Contopus virens</u>)	LM	24	43	58	77	98	103		1.353 (24)	101.333 (15)
Tree Swallow (<u>Iridoprocne bicolor</u>)	LM		2	2	2	2	2		0.026 (59t)	3.056 (66)
Rough-winged Swallow (<u>Stelgidopteryx ruficollis</u>)	LM	6	13	21	26	34	39		0.512 (33)	45.966 (43)
Barn Swallow (<u>Hirundo rustica</u>)	LM	2	6	7	11	19	22		0.289 (41)	30.592 (47)
Purple Martin (<u>Progne subis</u>)	LM					9	16		0.210 (47t)	12.331 (59t)
Blue Jay (<u>Cyanocitta cristata</u>)	PR	17	28	33	47	61	65		0.859 (29)	91.763 (26)
Common Crow (<u>Corvus brachyrhynchos</u>)	PR	35	76	103	135	158	173		2.272 (17)	99.241 (17)

Table 8 (Continued)

Species	Status*	Cumulative No. Individuals after (x)						Relative Abundance (%)	Importance Value
		2	4	6	8	10	11(total)		
Carolina Chickadee (<u>Parus carolinensis</u>)	PR	67	142	225	336	415	447	5.872 (3)	105.872 (3)
Tufted Titmouse (<u>Parus bicolor</u>)	PR	36	71	95	135	178	185	2.430 (16)	102.430 (13)
White-breasted Nuthatch (<u>Sitta carolinensis</u>)	PR	5	9	14	21	29	30	0.394 (39t)	73.121 (34)
House Wren (<u>Troglodytes aedon</u>)	SM or LM	31	53	67	85	108	113	1.484 (22)	95.423 (23)
Mockingbird (<u>Mimus polyglottos</u>)	PR	1	1	2	3	3	3	0.039 (58t)	9.129 (63t)
Gray Catbird (<u>Dumetella carolinensis</u>)	SM	6	10	19	21	34	38	0.499 (34t)	67.165 (37t)
Brown Thrasher (<u>Toxostoma rufum</u>)	SM	12	22	36	54	67	68	0.893 (28)	73.620 (31)
American Robin (<u>Turdus migratorius</u>)	PR or SM	25	46	75	163	244	264	3.468 (11)	97.407 (20)
Wood Thrush (<u>Hylocichla mustelina</u>)	LM	6	12	17	24	33	36	0.473 (36t)	70.169 (35)
Blue-gray Gnatcatcher (<u>Polioptila caerulea</u>)	LM or SM	101	180	262	317	363	385	5.507 (6)	105.057 (6)
Cedar Waxwing (<u>Bombycilla garrulus</u>)	PR	1	1	2	2	4	16	0.210 (47t)	12.331 (59t)
Starling (<u>Sturnus vulgaris</u>)	PR	192	242	263	294	338	351	4.611 (7)	92.489 (25)
White-eyed Vireo (<u>Vireo griseus</u>)	SM	13	24	33	42	54	57	0.749 (32)	82.567 (30)
Yellow-throated Vireo (<u>Vireo flavifrons</u>)	LM	8	16	20	23	28	30	0.394 (39t)	64.030 (39)

Table 8 (Continued)

Species	Status*	Cumulative No. Individuals after (x)						Relative Abundance (%)	Importance Value
		2	4	6	8	10	11(total)		
Red-eyed Vireo (<u>Vireo olivaceus</u>)	LM	58	94	141	198	241	251	3.297 (12)	103.297 (9)
Warbling Vireo (<u>Vireo gilvus</u>)	LM	1	1	2	8	12	13	0.171 (49)	36.534 (45)
Black-and-white Warbler (<u>Mniotilta varia</u>)	LM		4	4	7	9	11	0.144 (50)	27.416 (50)
Blue-winged Warbler (<u>Vermivora pinus</u>)	LM	1	6	7	7	7	7	0.092 (54t)	18.273 (55t)
Yellow Warbler (<u>Dendroica petechia</u>)	LM	12	15	15	24	35	38	0.499 (34t)	67.165 (37t)
Cerulean Warbler (<u>Dendroica cerulea</u>)	LM	45	69	96	111	120	122	1.603 (21)	95.542 (22)
Yellow-throated Warbler (<u>Dendroica dominica</u>)	LM	9	14	20	33	34	34	0.447 (37)	73.174 (33)
Ovenbird (<u>Seiurus aurocapillus</u>)	LM	3	4	8	8	8	8	0.105 (53t)	21.317 (52)
Kentucky Warbler (<u>Oporornis formosus</u>)	LM	4	15	22	28	34	36	0.473 (36t)	73.200 (32)
Common Yellowthroat (<u>Geothlypis trichas</u>)	SM	33	64	96	137	185	200	2.627 (15)	102.627 (12)
Yellow-breasted Chat (<u>Icteria virens</u>)	LM	33	52	77	99	111	112	1.471 (23)	95.410 (24)
American Redstart (<u>Setophaga ruticilla</u>)	LM	9	15	19	19	20	21	0.276 (42)	33.609 (46)
House Sparrow (<u>Passer domesticus</u>)	PR	3	7	7	13	18	18	0.236 (45)	18.417 (53)
Eastern Meadowlark (<u>Sturnella magna</u>)	PR	1	2	4	4	5	5	0.066 (56t)	12.187 (61)

Table 8 (Continued)

Species	Status*	Cumulative No. Individuals after (x)						Relative Abundance (%)	Importance Value
		2	4	6	8	10	11(total)		
Red-winged Blackbird (<u>Agelaius phoeniceus</u>)	SM or PR	96	167	234	344	416	432	5.675 (4)	105.675 (4)
Northern Oriole (<u>Icterus galbula</u>)	LM	1	3	4	5	6	6	0.079 (55)	18.260 (56)
Common Grackle (<u>Quiscalus quiscula</u>)	SM or PR	134	293	390	482	516	533	7.001 (1)	107.001 (1)
Brown-headed Cowbird (<u>Molothrus ater</u>)	SM	98	160	205	267	285	285	3.744 (10)	91.622 (28)
Scarlet Tanager (<u>Piranga olivacea</u>)	LM			2	2	2	2	0.026 (59t)	6.086 (65t)
Cardinal (<u>Richmondia cardinalis</u>)	PR	99	169	243	325	421	448	5.885 (2)	105.885 (2)
Indigo Bunting (<u>Passerina cyanea</u>)	LM	97	155	205	254	308	329	4.322 (8)	104.322 (7)
American Goldfinch (<u>Spinus tristis</u>)	PR or SM	65	127	202	288	366	397	5.215 (5)	105.215 (5)
Rufous-sided Towhee (<u>Pipilo erythrophthalmus</u>)	PR or SM	47	84	116	162	211	231	3.034 (14)	103.034 (11)
Field Sparrow (<u>Spizella pusilla</u>)	PR or SM	50	89	135	212	293	315	4.138 (9)	104.138 (8)
Song Sparrow (<u>Melospiza melodia</u>)	PR or SM	30	60	81	108	137	152	1.997 (18)	101.997 (14)
Total		1743	3030	4272	5641	6998	7613	100.0	

*See text for explanation (p. 36).

APPENDIX B

Table 9. Species observed May 10-11, 1978 (spring migration).*

Species
Green Heron (<u>Butorides virescens</u>)
Mallard Duck (<u>Anas platyrhynchos</u>)
Red-tailed Hawk (<u>Buteo jamaicensis</u>)
Ring-necked Pheasant (<u>Phasianus colchicus</u>)
Spotted Sandpiper (<u>Actitis macularia</u>)
Solitary Sandpiper (<u>Tringa solitaria</u>)
Yellow-billed Cuckoo (<u>Coccyzus americanus</u>)
Whip-poor-will (<u>Caprimulgus vociferus</u>)
Chimney Swift (<u>Chaetura pelagica</u>)
Ruby-throated Hummingbird (<u>Archilochus colubris</u>)
Common Flicker (<u>Colaptes auratus</u>)
Pileated Woodpecker (<u>Dryocopos pileatus</u>)
Red-bellied Woodpecker (<u>Centurus carolinus</u>)
Hairy Woodpecker (<u>Dendrocopos villosus</u>)
Downy Woodpecker (<u>Dendrocopos pubescens</u>)
Great Crested Flycatcher (<u>Myiarchus crinitus</u>)
Olive-sided Flycatcher (<u>Nuttallornis borealis</u>)
Acadian Flycatcher (<u>Empidonax virescens</u>)
Least Flycatcher (<u>Empidonax minimus</u>)
Eastern Wood Pewee (<u>Contopus virens</u>)
Rough-winged Swallow (<u>Stelgidopteryx ruficollis</u>)
Blue Jay (<u>Cyanocitta cristata</u>)
Common Crow (<u>Corvus brachyrhynchos</u>)
Carolina Chickadee (<u>Parus carolinensis</u>)
Tufted Titmouse (<u>Parus bicolor</u>)
White-breasted Nuthatch (<u>Sitta carolinensis</u>)
House Wren (<u>Troglodytes aedon</u>)
Mockingbird (<u>Mimus polyglottos</u>)
Catbird (<u>Dumetella carolinensis</u>)
Brown Thrasher (<u>Toxostoma rufum</u>)
Robin (<u>Turdus migratorius</u>)
Wood Thrush (<u>Hylocichla mustelina</u>)
Veery (<u>Hylocichla fuscescens</u>)
Ruby-crowned Kinglet (<u>Regulus calendula</u>)
Blue-gray Gnatcatcher (<u>Polioptila caerulea</u>)
Starling (<u>Sturnus vulgaris</u>)
White-eyed Vireo (<u>Vireo griseus</u>)
Red-eyed Vireo (<u>Vireo olivaceus</u>)
Yellow-throated Vireo (<u>Vireo flavifrons</u>)

Table 9 (Continued)

Species
Warbling Vireo (<u>Vireo gilvus</u>)
Solitary Vireo (<u>Vireo solitarius</u>)
Black-and-white Warbler (<u>Mniotilta varia</u>)
Worm-eating Warbler (<u>Helmitheros vermivorus</u>)
Tennessee Warbler (<u>Vermivora peregrina</u>)
Nashville Warbler (<u>Vermivora ruficapilla</u>)
Parula Warbler (<u>Parula americana</u>)
Yellow Warbler (<u>Dendroica petechia</u>)
Magnolia Warbler (<u>Dendroica magnolia</u>)
Yellow-rumped Warbler (<u>Dendroica coronata</u>)
Black-throated Green Warbler (<u>Dendroica virens</u>)
Cerulean Warbler (<u>Dendroica cerulea</u>)
Yellow-throated Warbler (<u>Dendroica dominica</u>)
Blackburnian Warbler (<u>Dendroica fusca</u>)
Chestnut-sided Warbler (<u>Dendroica pensylvanica</u>)
Bay-breasted Warbler (<u>Dendroica castanea</u>)
Prairie Warbler (<u>Dendroica discolor</u>)
Ovenbird (<u>Seiurus aurocapillus</u>)
Yellowthroat (<u>Geothlypis trichas</u>)
Yellow-breasted Chat (<u>Icteria virens</u>)
Kentucky Warbler (<u>Oporornis formosus</u>)
Hooded Warbler (<u>Wilsonia citrina</u>)
Canada Warbler (<u>Wilsonia canadensis</u>)
American Redstart (<u>Setophaga ruticilla</u>)
Bobolink (<u>Dolichonyx oryzivorus</u>)
Eastern Meadowlark (<u>Sturnella magna</u>)
Red-winged Blackbird (<u>Agelaius phoeniceus</u>)
Common Grackle (<u>Quiscalus quiscula</u>)
Brown-headed Cowbird (<u>Molothrus ater</u>)
Orchard Oriole (<u>Icterus spurius</u>)
Scarlet Tanager (<u>Piranga olivacea</u>)
Summer Tanager (<u>Piranga rubra</u>)
Cardinal (<u>Richmondia cardinalis</u>)
Rose-breasted Grosbeak (<u>Pheucticus ludovicianus</u>)
Indigo Bunting (<u>Passerina cyanea</u>)
American Goldfinch (<u>Spinus tristis</u>)
Rufous-sided Towhee (<u>Pipilo erythrophthalmus</u>)
Field Sparrow (<u>Spizella pusilla</u>)
White-crowned Sparrow (<u>Zonotrichia leucophrys</u>)
White-throated Sparrow (<u>Zonotrichia albicollis</u>)
Song Sparrow (<u>Melospiza melodia</u>)

Table 9 (Continued)

*	<u>May 10</u>	<u>May 11</u>	<u>Mean</u>
S	65	61	63
J'	.902	.920	.911
H'	5.432	5.457	5.445

VITA

Reed Frederick Noss was born in Dayton, Ohio on June 23, 1952. He was raised in the Dayton area and graduated from Centerville High School in June, 1970. After attending Ohio Wesleyan University for two years, during which time he was primarily interested in music, art, and philosophy, Mr. Noss went on to the University of Dayton, where he received his B.S. in Education in April 1975 with teaching fields in Biology and Health and special emphasis in Environmental Education. He then spent one year as a naturalist at the Glen Helen Outdoor Education Center of Antioch College before coming to The University of Tennessee, Knoxville, to study ecology. At The University of Tennessee, Knoxville, Mr. Noss studied herpetological ecology and spent several months in Nicaragua working in land use planning and censusing the birds of a Caribbean coastal area before returning to study the avifauna of Sugarcreek Reserve, near his boyhood home, for his Master of Science degree. After receiving his Master of Science, the author plans to further pursue his interests in vertebrate ecology and the preservation of natural areas.