Avian Community Assembly Rules: The Foliage-Gleaning Guild

James W. Haefner

Curriculum in Ecology – 046A, University of North Carolina, Chapel Hill, N.C. 27514, USA

Summary. The theory of animal community organization has been dominated by general models based on the Lotka-Volterra equations. The predictions of these models are difficult to test in particular situations. Moreover, a great deal of ecological information is incommensurate with the data requirements of these models. A different approach to community organization addresses the "ecosystem assembly problem". This problem is defined to be that of constructing an algorithm which assembles a subset of a species pool in a specified environment.

A model of ecosystem assembly, based on generative grammars as used in theoretical linguistics, is described. It was constructed from and validated with data collected by D.H. Morse on a guild of foliage-gleaning birds inhabiting spruce forests on islands off the coast of Maine. The data were divided into two groups. One group, from the years 1967–1970, was used for model construction; the second group, from 1971–1975, was used to validate the model.

The model has two major components. One component inserts species onto islands according to the microhabitat used by each species and the resources available on each island. A second component deletes those inserted species from islands on which they were not observed to occur during 1967–1970. This component is composed of deletion rules that remove species depending on (a) their sizes and resource requirements, (b) the sizes and resource requirements of other species present in the ecosystem, and (c) the structure of the vegetation on the islands. Model validation was performed by comparing the predicted distributions of species against observed distributions not used in model construction. Model accuracy for the later data (1971–1975) was slightly higher than for the earlier data (1967–1970), approximately 88% and 84%, respectively.

The behavior of the model was investigated with several simulations. These included the effects of the removal of certain deletion rules and the effects of the application of the rules without regard to their order. Other simulations demonstrated the application of the model to the prediction of the effects of habitat manipulation and the removal of particular species from the species pool.

Introduction

The study of animal community organization comprises an enduring set of questions concerning a diverse collection of taxa and a broad range of ecological phenomena. Four extensive approaches addressing these questions can be identified. First, a collection of models has developed which are extensions of the Lotka-Volterra predation and competition equations (e.g. May 1973; Schoener 1976; Roughgarden 1979). By analyzing relatively simple equations this approach seeks to predict the characteristics of populations that coexist under different conditions (e.g. variable environments, different biotic interactions).

In addition to this theoretical approach, three classes of empirical methods have developed. The first of these uses experimental manipulations to elucidate the relative importance of abiotic factors and biotic interactions in determining the coexistence of species (e.g. Connell 1961). The second empirical approach is correlative, relying on the comparison of natural "experiments" to elucidate relationships between community-level measures such as diversity, niche width, niche overlap, and species richness (e.g. Pianka 1974; Willson 1974; Yeaton and Cody 1974; Rabenold 1978). Often using the results of theory, the second empirical approach attempts to test hypotheses of community organization with observational data. The third class of empirical methods is more recent and is also correlative. Unlike the second approach, it has not emphasized the test of general theories or community-level measures. This third approach uses multivariate statistical analysis to elucidate patterns in the spatial distributions of species (Sabo and Whittaker 1979) or in the resource utilization differences among species at different sites (James 1971; Cody 1978).

The purpose of this paper is to describe a model of avian community organization which is most closely related to the second and third approaches. This model attempts to understand animal community organization by addressing what I call the ecosystem assembly problem. A general statement of this problem is: *Construct an algorithm such that, given an arbitrary species pool and an arbitrary collection of environmental factors, the output of the algorithm is a list of species associated with the environment.*

The ecosystem assembly problem is deliberately stated so as to emphasize the need for both generality and particularity in the model. The model must be general by being applicable to any given environment and species pool. It must also, however, produce specific predictions of the spatial distributions of particular species. This does not assume that only one process (e.g. competition) is important in determining community organization. Clearly, many factors, including both biotic and abiotic components, are important, and the theoretical framework must incorporate these. Although there may be many formalisms in which to state an ecosystem assembly algorithm, generative grammars, as described below, can both be generally applicable and produce specific predictions. Because of these properties, the formalism of generative grammars is the framework underlying the model discussed here.

Overview of the Algorithm

Details of an ecosystem assembly grammar have been published elsewhere (Haefner 1977, 1978), and only a brief treatment will be presented here. The first of two major components is a set of procedures that describes the conditions under which assembly occurs. This has two parts: description of the abiotic conditions at a site and description of the species pool available for colonization. The second component is a set of procedures that determines the set of co-occurring species. In other words, the algorithm is a grammar that describes the conditions under which assembly occurs and, given those, the subset of the species pool that is associated with the particular abiotic conditions.

This report treats only the second component, but to understand its form, some knowledge of the first is required. In particular, since the second component manipulates the species pool, the description of species in the pool must be clarified. Each of N species in the pool is described (generated) by a set of rules of the basic form:

(i) $A \rightarrow B + C + \ldots + Z$

(ii) $B \rightarrow a + b + \ldots + z$.

Such rules exemplify the basic form of a generative grammar; they may be read as: "A is composed of B and $C \ldots$ and Z". In any particular grammar, each of the rules must be fully interpreted. One model (Haefner 1977) gives an interpretation which results in each species being decomposed into an hierarchical description of activities and sub-activities (corresponding to the upper case letters). Each activity is further described as having certain resource requirements (corresponding to the lower case letters). For example, such a grammar might contain the rules:

(i)   Reprod $\rightarrow$ Feed + Nestbuild

(ii) Feed $\rightarrow$ $+$(0–3 m)* $+$(3–6 m)* $-$(6–9 m).

(Asterisks indicate the logical "and" relation.) These rules describe a species as performing reproduction with two activities (nest building and feeding) and further, that feeding requires vegetation heights 0–3 and 3–6 m but not 6–9 m. Additional rules would be required to describe nest building requirements.

A collection of rules of this type produces an hierarchical tree for each species which integrates behavior and habitat requirements. Figure 1 shows one example of this hierarchical structure. A crucial aspect of species descriptions used in the statement of assembly rules is behavioral plasticity of resource use (Noon and Able 1978). The current ecosystem assembly

grammar incorporates plasticity by decomposing a species into a set of *species types*. Each species type represents a set of environmental conditions which are required by the species for survival and reproduction. Plasticity is represented as qualitatively different requirements described by alternate species types (e.g. different sets of foraging heights). For example, Fig. 1 shows a species (Black-throated Green Warbler) which comprises two species types (T1 and T2) and therefore exhibits behavioral plasticity.

The following discussion does not emphasize the description of species but rather the determination of a set of co-occurring species. This latter modeling problem is the specification of a collection of rules such that only the "correct" set of species are grouped together in association with a description of the vegetation and a set of environmental features. Two basic types of rules are important to this modeling problem: species insertion rules and species deletion rules. Insertion is modeled as a simple transformation rule (Chomsky 1957) that moves a species description from the species pool to the current ecosystem description. The details are not a concern here, but the criterion for this movement is that the set of resources required by the species is a subset of the set of environmental features in the current ecosystem description (Haefner 1977). Every species type in the pool has an equal opportunity to be inserted.

For the data sets I consider here, this insertion criterion creates communities at most sites with more species than are observed. Consequently, rules are needed to remove some of those species inserted initially based on the total environment (biotic and abiotic) of each species. Such rules are called deletion rules, and a majority of this report describes the form, creation, application, and adequacy of a set of deletion rules applied to some foliage-gleaning avian insectivores. The analysis was performed by examining the available literature for quantitative data on the feeding behavior and spatial distributions of the species of different bird communities. Using these data, a model that assembled communities was constructed; it was subsequently validated with additional data not used during model construction.

Methods

Literature Search

The available literature was searched for appropriate quantitative data from bird communities. Published studies were used if they contained: observations of more than one species studied at more than one site,
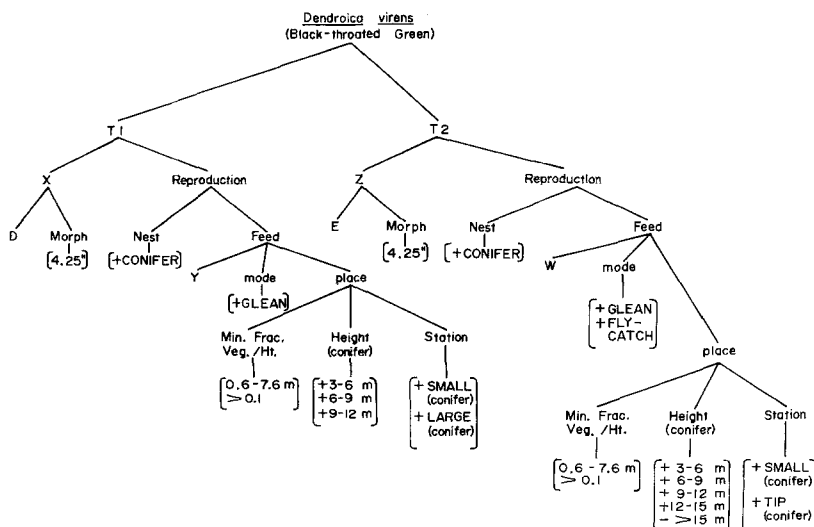

Fig. 1. The hierarchical description of one species (Black-throated Green Warbler) showing the relation of activities to resource requirements. Additional details in text

quantitative data on the behavior and natural history of each species at each site (e.g. feeding station use), and vegetative and abiotic data for each site. Much of the work done on bird communities is not suited for modeling with grammars either because the research did not meet one or more of the above criteria or the published article did not contain sufficient detail.

The selected studies were separated into two groups: one group was used for model construction, and the other was used to test the model. This report considers only a small portion of the total available data on bird communities: those of a foliage-gleaning guild of insectivores studied by Douglass H. Morse. Model construction considered data collected from 1967–1970; testing used the data of 1971–1975.

Model Construction

Morse (1980) reviewed his studies on the spruce-wood warblers that inhabit small islands off the coast of Maine. This 15-year study emphasized foraging ecology, arrival times, and interactions within and between species during the breeding seasons. The Maine islands are small (0.16–3.5 Ha) and the forests on them shorter (12–20 m) than similar mainland forests. The vegetation is predominantly spruce forest with patches of deciduous undergrowth. Other birds, primarily ground-dwelling species, occur on the islands. Because the foliage-gleaning and ground species do not interact significantly, the latter group is not considered further.

The foliage-gleaners are primarily warblers, and are small (3.5–4.75 inches, Robbins et al. 1966), migratory, and have small populations size (1–6 breeding pairs per island, Morse 1967, 1971, 1973). They are intraspecifically territorial, and there is evidence of interspecific territoriality (Morse 1967).

Data from Morse (1967, 1971, 1973) were examined as a basis for insertion and deletion rule construction. From these, I extracted the quantitative data on resource utilization and foraging behavior of each species (male and female combined) on each island. In addition, quantitative data on the vegetation and abiotic conditions of the islands were also compiled from the studies. These data formed the basis for the descriptions of species and deletion rules.

The available data comprise the numbers of seconds of observations of each species at different vegetation heights (e.g. 3–6 m) and feeding stations (e.g. small branches). The categories and intervals are those defined by Morse. The data were transformed to frequencies for each of the major categories (i.e. height and station). The frequency data for each species on each island were compiled and reduced to a discrete form of pluses (+) and minuses (−). A plus means the item (i.e. a particular feeding station or vegetation height) is required; a minus means the item is not required. For example, +TIP indicates that the tips of branches are required for feeding. To create this discrete form, the percentages within each major category (i.e. feeding height and feeding station) were summed, beginning with the most frequently used class of a given category. Pluses were assigned only to the most frequently used classes necessary to account for 80% of the observations. All others were given minuses. This is similar to an expository technique used by MacArthur (1958). The results of this process are shown in Table 1.

The data showed that, when some species occurred on more than one island, habitat requirements varied according to conditions on the island and the local composition of the bird community. Consequently, the data were further manipulated to describe behavioral plasticity. For every island on which a species was observed, the species' discrete representations were collated, and a set of species types were subjectively defined for the species. To do this, I sought a set of species types such that some subset of the species types, when combined, would reproduce the species' resource use pattern on a given island. For example, species type T2 in Fig. 1 reproduces the discrete form of the resource use by the Blackthroated Green Warbler on Indian Island, and T1 describes that species' resource use on Crane Island. A combination of T1 and T2 is required, however, to describe the resource use of the Black-throated Green Warbler on Thief island. Consequently, the observed resource use by a species on an island is described by combinations of the species' plastic behaviors (species types). I interpret species types to represent sets of species activities, each of which alone is sufficient to account for the survival and reproduction of the population. Species types do not represent distinct groups of individuals within a species.

The procedure was repeated for each species. Because Fig. 1 is a bulky representation of the basic information, I have reduced each tree to one or more rows of a table (Table 1). Each row is a condensed description which can be mapped onto the output of a generative grammar (i.e. trees such as Fig. 1).

The available environment on an island was described using techniques similar to those for the species descriptions. Islands were assigned one or more patches to describe ecotones based on quantitative and non-quantitative information in Morse (1967, 1971, 1973, 1977).

Table 1. The ecological distributions of the species pool for the Maine islands. Column 1 is the length of species; column 2 is the requirement for a minimal patch size of 4 Ha; column 3 is the requirement for a minimal average vegetation height of 20 m; column 4 is the requirement that at least 10% of the vegetation occur within the interval 0.6–7.6 m; columns 5–10 are foraging heights; columns 11–15 are foraging stations. A "T" indicates species types of a species.

	Size (Inches)	>4 Ha Min.	≥20 m Ave. Ht.	% veg. 0.6–7.6 >0.1	Conif. 0–3 m	Conif. 3–6 m	Conif. 6–9 m	Conif. 9–12 m	Conif. 12–15 m	Conif. >15 m	Small Conifer	Large Conifer	Tip Conifer	Dead Conifer	Deciduous
Black-throated Green – T1	4-1/4	−	−	+	−	+	+	+	−	−	+	+	−	−	−
Black-throated Green – T2	4-1/4	−	−	+	−	+	+	+	+	+	+	−	+	−	−
Magnolia	4-1/4	−	−	+	−	+	+	+	−	−	+	+	−	+	−
Parula – T1	3-3/4	−	−	+	+	+	+	+	−	−	+	−	−	−	+
Parula – T2	3-3/4	−	−	+	−	+	+	+	−	−	+	−	+	−	−
Parula – T3	3-3/4	−	−	+	−	+	+	+	+	−	+	+	−	−	−
Golden Crowned Kinglet	3-1/2	+	−	+	−	+	+	+	−	−	−	−	+	+	−
Blackburnian	4-1/4	−	+	+	−	−	−	+	+	+	+	+	+	−	−
Redstart – T1	4-1/2	−	−	−	+	+	+	+	−	−	+	−	−	+	−
Redstart – T2	4-1/2	−	−	−	+	+	+	+	−	−	−	−	−	+	+
Yellow-rumped – T1	4-3/4	−	−	+	−	+	+	+	−	−	+	+	−	+	−
Yellow-rumped – T2	4-3/4	−	−	+	+	+	+	−	−	−	+	−	−	−	+
Yellow-rumped – T3	4-3/4	−	−	+	−	+	+	+	−	−	+	−	+	+	−
Yellow	4	−	−	−	+	+	+	−	−	−	+	−	−	+	+

Table 2. Communities of the foliage-gleaning guild on small islands off the coast of Maine. Pluses indicate presence; blanks indicate absence

Species	Islands										
	Crotch	Ram	Crow	Jim's	Crane	Indian	Thief	Franklin	Wreck	Haddock	Hog
Parula *(Parula americana)*	+	+	+	+	+	+	+		+	+	+
Yellow-rumped *(Dendroica coronata)*		+	+	+	+	+	+		+	+	+
Yellow *(Dendroica petechia)*	+				+		+	+	+	+	+
Black-throated Green *(Dendroica virens)*				+	+	+	+				+
Redstart *(Septophaga ruticilla)*					+	+		+	+	+	+
Golden-crowned Kinglet *(Regulus satrapa)*								+			+
Magnolia *(Dendroica magnolia)*											+
Blackburnian *(Dendroica fusca)*											+

An island was assigned two patches if in Morse (1977, his Table 2) "overall area vegetated" exceeded "forest area". Major categories used to describe patches were: vegetation vertical distribution, presence of feeding stations, fraction of vegetation in each of three layers, forest size in a patch, and average forest height. Vegetation vertical distribution, obtained from quantitative data of Morse, was discretized by dividing height into increments of 3 m and assigning a plus to those increments accounting for 80% of the total vegetation volume. All feeding stations in patches of conifer forests were assigned a plus. All other patches (deciduous vegetation) were assigned minuses to indicate the absence of conifer feeding stations.

Following these data reductions, modeling proceeded by implementing the assembly algorithm (Haefner 1977). Model construction used an heuristic procedure. That is, I performed several iterations of creating insertion and deletion rules followed by tests of their effects on species lists against the observed distributions (Morse's 1967–1970 data) before a satisfactory collection of rules was obtained. Both the substance of the rules and their order were manipulated in this model construction process.

Species distributions were predicted by applying the insertion rule and each deletion rule in an established order to every island (see Results for an example). The species predicted for each island are those inserted species which survive all deletion rules. Not every species was inserted on every island. Model success was measured as the number of correct predictions divided by the number of observed presences and absences in the species/island matrix (Table 2). Model construction was terminated when the model's prediction of the observed species/island matrix was at least 80% correct.

Model Evaluation

Following construction, the model was tested against the pooled 1971–1975 distributional data. Since both the island vegetation and species characteristics were assumed not to have changed during this period, the test involved only the comparison of the distributions predicted by the model with the observed distributions for this period. No alterations were made to the model, nor was it necessary to recompute the predicted species distributions.

Additional analysis of the model involved examination of the importance of rule order to the predicted outcome. This was performed by forcing deletion rules to operate simultaneously. Unlike the ordered procedure, each deletion rule was applied to the inserted species, but no species were deleted until all rules had operated. Those species marked for deletion earlier were deleted "simultaneously" after all rules had been applied.

Results

Model Input

Table 2 shows the distributions of species by island for 1967–1970 (Morse 1971). Table 3 gives the vegetation description of each island in the study. A plus indicates that the category at the top of the table was present in the patch of the island. Several islands have patches, and these are indicated by P1, P2, or P3 following the island name. Pluses in height categories indicate that the category was required to account for at least 80% of the vegetation height distribution. Presence or absence of different feeding stations in the conifer trees is also indicated, as is the size and average height of the forests.

Table 1 gives an analogous representation of the habitat requirements of the species types of each species in the species pool. The variables used to describe species are: feeding station (e.g. the tips (TIP) of conifer branches), feeding height (in 3 m increments), minimum average forest height, minimum forest size, and ratio of vegetation volumes in middle to upper height categories [i.e. (% at 0.6–7.6 m)/(% at > 7.6 m)]. Also included in this table is the size of each species (Robbins et al. 1966). Recall that this table is only a succinct form of a hierarchical tree (Fig. 1) that describes these variables as the requirements for certain behaviors or activities (e.g. reproduction).

Deletion Rules

Seven deletion rules were derived from Morse's data. These rules (Appendix) all have the basic form: "Delete T/C", which reads: "delete a species type (T) whenever it is found in the context of C". Differences between rules are due to different species types and environmental descriptions being substituted for T and C. In all rules, T is a set of habitat requirement features for one or more species types (i.e. a subset of Table 1), including a description of size. C is variable across rules; it may contain vegetation or patch information, as well as a description of one or more species types that are in the environment of T. All species types satisfying the description of T which are in an ecosystem fulfilling the conditions of C when the rule is applied are deleted from the ecosystem. Species types are the objects that are deleted; a species has been deleted from an ecosystem only when all of its species types have been deleted.

In addition to the conditions for rule application contained in the variables T and C, there may be auxiliary conditions stated at the end of the rule. These conditions state necessary relationships between variables used in the statement of T and C. If these auxiliary conditions are not fulfilled, the rule does not apply. For example, in Rule 1 the size relations between T and species types in C are important, and these are stated as an auxiliary condition.

Application of Rules to One Island

To illustrate the effect of these rules on species distributions, their application to Crow Island is discussed in detail. Deletion rules are applied in the order described in the Appendix to the species list resulting from the application of the previous rule. Rule 1 applies to the species list that results from insertion. The environment of Crow Island is shown in Table 3, and the

Table 3. The environment of patches and islands off Maine. The P_i associated with some islands refers to distinct patches. Columns 1–2 are quantitative measures of patch size and average patch height, respectively; columns 3–6 indicate presence or absence of available feeding stations; columns 7–16 describe the vegetation distribution of vegetation height; columns 17–20 are measures of the relative distribution of vegetation by height. Asterisks indicate personal estimates not given by Morse

Island	Patch Size (Ha)	Ave. Ht. (m)	TIP (Conif.)	SMALL (Conif.)	LARGE (Conif.)	DEAD (Conif.)	Decid. >3 m	Decid. <3 m	Conif. 0–3 m	Conif. 3–6 m	Conif. 6–9 m	Conif. 9–12 m	Conif. 12–15 m	Conif. 15–18 m	Conif. 18–21 m	Conif. >21 m	Frac. <0.6 m Veg.	Frac. 0.6–7.6 Veg.	Frac. >7.6 m Veg.	Frac. 0.6–7.6/ Frac. >7.6
Crotch	0.16	12	+	+	+	+	+	+	+	+	+	+	−	−	−	−	0.05	0.67	0.29	2.3
Jim's	0.49	14	+	+	+	+	+	+	+	+	+	+	+	−	−	−	0.13	0.44	0.43	1.02
Crane P₁	0.53	14	+	+	+	+	−	+	+	+	+	+	+	−	−	−	0.12	0.25	0.63	0.4
Crane P₂	2.28	1*	−	−	−	−	−	+	+	−	−	−	−	−	−	−	0.9*	0.1*	0.0*	−
Hog P₁	100*	20	+	+	+	+	−	+	+	+	+	+	+	+	+	+	0.04	0.18	0.78	0.23
Hog P₂	25*	16*	−	−	−	−	+	+	+	+	+	+	−	−	−	−	0.15*	0.5*	0.35*	1.43
Hog P₃	10*	1*	−	−	−	−	−	+	−	−	−	−	−	−	−	−	1.0*	0.0*	0.0*	0.0
Thief P₁	1.50	15	+	+	+	+	−	+	+	+	+	+	+	+	−	−	0.06	0.36	0.58	0.62
Thief P₂	0.14	1	−	−	−	−	−	+	+	−	−	−	−	−	−	−	0.9*	0.1*	0.0*	−
Ram	0.39	14	+	+	+	+	+	+	+	+	+	+	+	−	−	−	0.22	0.35	0.43	0.81
Crow P₁	0.35	13	+	+	+	+	+	+	+	+	+	+	−	−	−	−	0.32	0.36	0.32	1.13
Crow P₂	0.25	1*	−	−	−	−	−	+	+	−	−	−	−	−	−	−	0.9*	0.1*	0.0*	−
Indian	0.69	16	+	+	+	+	−	+	+	+	+	+	+	+	+	−	0.12	0.35	0.53	0.66
Franklin P₁	1.77	14	+	+	+	+	−	+	+	+	+	+	−	−	−	−	0.60	0.02	0.38	0.05
Franklin P₂	1.72	1*	−	−	−	−	−	+	+	−	−	−	−	−	−	−	0.9*	0.1*	0.0*	−
Wreck	3.86	14	+	+	+	+	+	+	+	+	+	+	+	+	−	−	0.15	0.52	0.33	1.57
Haddock P₁	1.86	14	+	+	+	+	+	+	+	+	+	+	+	−	−	−	0.04	0.67	0.29	2.3
Haddock P₂	0.71	1*	−	−	−	−	−	+	+	−	−	−	−	−	−	−	0.9*	0.1*	0.0*	−

history of the application of insertion and deletion rules is given in Table 4. The first column shows which species types were inserted and which were not. For example, Tables 1 and 3 show that T2 of the Black-throated Green warbler was not inserted due to its vegetation height requirements (>12 m).

Following insertion, application of Rule 1 is attempted. Since the vegetation conditions specified by Rule 1 (n/m > 1.4) do not hold on Crow Island, it has no effect. The conditions on the context of Rule 2 are fulfilled because Crow Island has two patches (one coniferous forest and one deciduous undergrowth). Since both Parula T1 and Yellow-rumped T2 are members of the ecosystem and are described as [+SMALL* +DECID* − LARGE* −TIP* −DEAD], they are deleted.

Rule 3 does not apply because there are no species in the ecosystem which are [+SMALL* +DECID] and which are sufficiently small to satisfy the rule's context. In other words, there are no species of intermediate size to be deleted which are bounded by a smaller species using [+SMALL* +DECID] and a larger species using [+SMALL]. The species type to be deleted, in this case, might have been Yellow and the larger species type (LBₖ) might have been Yellow-rumped T1, but Rule 2 has removed Parula T1, the only candidate for the smaller species type (LBⱼ). Consequently, Yellow is not deleted.

Identical procedures are used in applying the remaining four rules. Rule 4 also fails for the lack of the proper context. All of Yellow, Yellow-rumped T3, and Redstart T1 and T2 satisfy the species type to be deleted. There exists, however, no sufficiently small species type to fulfill the requirements of LBⱼ. Rule 5 fails to apply because the only candidate for deletion, Parula T1, has been previously removed from the ecosystem. Rule 6 deletes two species types (Black-throated Green T1 and Magnolia) due to Parula T2 (=LBⱼ) and Yellow-rumped T1 (=LBₖ). Rule 7 deletes no species, because the vegetation of Crow Island does not meet the habitat requirements (n/m > 1.4).

Table 4. The history of the operation of the ecosystem assembly grammar as applied to foliage-gleaning guild on Crow Island, Maine. Pluses indicate presences, a minuses indicate absences. The predicted species list is the final column. See text for details

Species	Insert	Rule 1	Rule 2	Rule 3	Rule 4	Rule 5	Rule 6	Rule 7
Black-throated Green – T1	+	+	+	+	+	+	−	−
Black-throated Green – T2	−	−	−	−	−	−	−	−
Magnolia	+	+	+	+	+	+	−	−
Parula – T1	+	+	−	−	−	−	−	−
Parula – T2	+	+	+	+	+	+	+	+
Parula – T3	−	−	−	−	−	−	−	−
Golden-Crowned Kinglet	−	−	−	−	−	−	−	−
Blackburnian	−	−	−	−	−	−	−	−
Redstart – T1	+	+	+	+	+	+	+	+
Redstart – T2	+	+	+	+	+	+	+	+
Yellow Rump – T1	+	+	+	+	+	+	+	+
Yellow Rump – T2	+	+	−	−	−	−	−	−
Yellow Rump – T3	+	+	+	+	+	+	+	+
Yellow	+	+	+	+	+	+	+	+

The species list produced by these rules is those species with a plus in the last column of Table 4. Based on Morse (1971 and unpublished data for 1967–1970), this incorrectly places Yellow and Redstart on Crow Island. The process has been repeated for the other islands in Morse's data and the results are shown in Table 5. Pluses without circles indicate species present in both the data of Morse (1971) and the model output. Circles around pluses are observations of presences by Morse not predicted by the model, and asterisks are predictions of presences 'not reported by Morse (1971). Based on this matrix, the model is 84.1% correct (number of correctly predicted matrix elements, 74, divided by the total number of matrix elements, 88).

Table 5. The species distributions predicted by the grammar for all islands compared to observations during the breeding seasons of 1967–1970. Blanks indicate observed and predicted absence; pluses without circles indicate observed and predicted presence; pluses with circles indicate observed presence not predicted; asterisks indicate predicted presence not observed

Species	Islands										
	Crotch	Ram	Crow	Jim's	Crane	Indian	Thief	Franklin	Wreck	Haddock	Hog
Parula	+	+	+	+	+	+	+		+	+	+
Yellow-rumped	*	+	+	+	+	+	+		+	⊕	+
Yellow	⊕	*		+		+	+		⊕	+	+
Black-throated Green				⊕	⊕	+	+				+
Redstart	*	*	*	*	+	+	*	+	+	+	+
Golden-crowned Kinglet							⊕				+
Magnolia											⊕
Blackburnian											+

Table 6. Comparison of model output and observations made during the breeding seasons of 1971–1975. For notation see Table 5

Species	Islands										
	Crotch	Ram	Crow	Jim's	Crane	Indian	Thief	Franklin	Wreck	Haddock	Hog
Parula	+	+	*	+	+	+	+		+	+	+
Yellow-rumped	*	+	+	+	+	+	+		+	⊕	+
Yellow	⊕	+	⊕	+	⊕	+	+	⊕	+	+	+
Black-throated Green						+	+				+
Redstart	*	*	+	+	+	+	+	+	+	+	+
Golden-crowned Kinglet											+
Magnolia							⊕				⊕
Blackburnian											+

Table 7. Comparison of 1971–1975 observations with a model that does not use Rules 3 and 4 and applies the remaining rules in order. Notation as in Table 5

Species	Islands										
	Crotch	Ram	Crow	Jim's	Crane	Indian	Thief	Franklin	Wreck	Haddock	Hog
Parula	+	+	*	+	+	+	+		+	+	+
Yellow-rumped	*	+	+	+	+	+	+		+	⊕	+
Yellow	*	+	+	+	+	+	+	+	+	+	+
Black-throated Green						+	+				+
Redstart	*	*	+	+	+	+	+	+	+	+	+
Golden-crowned Kinglet											+
Magnolia							⊕				⊕
Blackburnian											+

Model Validation

To test this model, which was derived from data for the period 1967–1970, I compared the model output to distributional data from the period 1971–1975. The results of this comparison are shown in Table 6. Although several additional mistakes were made by the model, several previous mistakes agree with the later data. In the latter category are the correct predictions of presences for Redstart on Crow, Jim's, and Thief Islands and Yellow on Crow Island. Some absences are also correctly predicted for the later data: Black-throated Green is absent on Jim's and Crane Islands, and Golden-crowned Kinglet is absent on Thief Island. Among the mistaken predictions of absences are Yellow on Jim's and Indian Islands, and Magnolia on Thief Island. The only new case of a failure to predict an observed

absence in this later data was the absence of Parula on Crow Island. Because of Parula's small size, none of the deletion rules remove Parula once it has been inserted. This matrix is 87.5% correct. Four of the mistakes involve the unpredicted presence of the Yellow Warbler on four islands. The predicted absences are due to either Deletion Rule 3 or 4, and they can be corrected by removing these rules from the model. When this is done, the results are as shown in Table 7. This matrix is 90.9% correct. For comparison, a model without Rules 3 and 4 correctly predicts 83.0% of the 1967–1970 data.

Discussion

Simulation Results

1. Random Model

Because of the deterministic nature of this model it is of interest to compare the success of the model with the success of a null hypothesis in the form of a random or "neutral" model. To do this, I related the model predictions of presences and absences to the observed presences and absences in 2×2 contingency table. The null hypothesis is that random sampling, assuming the probabilities of selecting correct and mistaken predictions are defined by the marginals of the table, will make as many or more correct predictions than the model. The probability that this null hypothesis is true (Fisher's exact test, Pielou 1977) is very low ($P < 0.001$).

While this result encourages the use of deterministic models, other random models can and should be examined. The design of meaningful null hypotheses is complicated in this case, since the model manipulates species types while accuracy is assessed using species. There is a positive correlation between the number of species types used to represent a species and the number of islands on which it is predicted to occur (e.g. Table 5). This suggests that the above null hypothesis is not appropriate. A more rigorous test would compute the probabilities of obtaining the observed associations of species using a 2^k contingency table (Pielou 1977). Because this is computationally unmanageable, a neutral simulation model, with the probabilities of placing species on islands constrained by the data, could be used. The neutral model used by Connor and Simberloff (1979) constrained these probabilities in several ways (e.g. by the number of islands on which a given species was observed). The choice of these constraints, however, is a subtle issue because they depend on both the alternative, non-neutral, biological hypothesis and on the assumptions that define the statistical population from which the observed sample is drawn. For example, a model neutral with respect to a competition hypothesis may differ from a neutral model of a predation hypothesis. Alternatively, a neutral model of island colonization could assume that the observations are drawn from a population where all species have equal probabilities of colonizing all islands. The evaluation of any neutral model, therefore, must include an assessment of the relevance of the probability constraints to the biological system.

In the assembly grammar, except for the habitat requirements contained in descriptions of species types, no restrictions are placed on the number of islands onto which any species type may be inserted. Nor are explicit restrictions placed on the number of species types that may be inserted onto any given island. The constraints on a neutral process that generates the expected distributions should reflect these assumptions. Further applications of neutral models to test this assembly grammar are in progress.

2. Details of 1971–1975 Comparison

Predictions and comparisons of presence/absence data can be misleading, in that rarity is still presence and not absence. This can result in a misleading assessment of the accuracy of model output when compared with presence or absence matrices (Table 2). Several species have small breeding populations, and the model's predictions of their distributions requires comment.

The model incorrectly predicts the absence of the Magnolia Warbler on Thief Island. This species, however, was represented during 1967–1975 by only one breeding pair (1975). This indicates that the habitat on Thief Island may not be well-suited for Magnolia reproduction. Thus, although the model made a mistake on this island, the result must be considered in light of the low population size.

The deletion rules also predicted that the Yellow-Warbler was absent from Indian Island, where the species had only one breeding pair (in 1974) during 1967–1975. Thus, the model response may be better than indicated by the simple comparison of presence/absence data.

The same cautions must also be noted in those borderline cases where the model was correct. The model correctly predicts the presence of Redstart on both Crow and Jim's Islands. However, this species' breeding population was only one pair during 1971 on Crow Island and 1972 on Jim's Island. Further, the Yellow-rumped, correctly predicted on Wreck Island, was represented by one breeding pair for each of the years 1970 and 1971. In these cases, then, the model response is probably worse than the comparison with qualitative (presence/absence) data indicates.

A second concern is the relative importance of the insertion process compared to the deletion process. If no deletion rules are used, then insertion alone, based only on habitat requirements, is 69.3% accurate for 1967–1970 and 76.1% accurate for 1971–1975. Therefore, some of the correct predictions of the model are due to hypothesized habitat incompatibilities (i.e. the non-insertion of species types). Both the Golden-crowned Kinglet and the Blackburnian Warbler are inserted (and not deleted) on Hog Island only, due to hypothesized habitat requirements (large and high forests, respectively). These hypotheses may be wrong, and the presence of the Kinglet on Thief Island (one breeding pair in each year of 1968–1970) indicates that that island does indeed provide adequate habitat for reproduction. These data were not available during model construction, and this influenced the structure of the model.

3. Autocorrelation

Since the validation data were taken from years following the data used for model construction, it may be that the accuracy of validation is due to autocorrelation in the time series. Small sample sizes and the discrete nature of the data prohibit standard time series analyses, but an indication of autocorrelation can be obtained from several different analyses. First, the species turnover rate for the islands (excluding Hog) is 16.7%/year (Morse 1977). Relative to other island avifaunas, this is a large figure that indicates rapid change. A related method of assessing species constancy is by counting the differences in the observed distribution matrices (Tables 5 and 6) for the two periods. Eleven of 88 elements in the matrices do not match, which represents a degree of similarity of 0.875. Assuming autocorrelation is important, the expected correct percentage can be calculated as follows. Since the model is deterministic and made 73/88 correct designations, $(73) \times (0.875) = 63.875$ is the number of expected correct designations in 1971–1975 due to the similarities of the

two data sets. In addition, if there is an equal chance of the differences between the two data sets being correct or incorrect in 1971–1975, then this contribution to correct designations is $0.5 \times 11 = 5.5$. Now, while $(63.875 + 5.5)/88 = 0.789$ is not statistically different than the predictions (0.875, $P = 0.06$), it is substantially less and supports the interpretation that model validity is not due solely to autocorrelation.

A second approach to the problem is to compute the Spearman rank correlation coefficients between years for every species for which sufficient data exists. If marked autocorrelation exists, the coefficients between all the years 1967–1970 and all the years 1971–1975 should be significantly different from zero. This analysis was performed on the presence/absence data for five species and the number of significant correlations counted. Eighty tests were performed [$5 \times (4 \times 4)$, there is no data for 1973], and 12 were different from 0.0 at the 0.05 level of significance. While this is more than expected by chance, it does not indicate extreme correlation between the two periods. Moreover, since both the Golden-crowned Kinglet and the Magnolia Warbler were present on only one island for which there is complete data, they were not included in the analyses. Their distributions, however, suggest no autocorrelation: the Kinglet was present only in 1967–1970 and Magnolia only in 1971–1975. This analysis has not treated Hog Island due to insufficient dynamic data.

A third approach is to determine model accuracy using smaller time periods which are separated by a period of time. This was performed for the years 1967–1968 and 1974–1975, and model accuracy was 85.2% and 84.1%, respectively. This reduction in validation accuracy may indicate that autocorrelation is a problem, or it may mean that random differences between years is important and sample sizes must be sufficiently large for a deterministic model to be accurate. That model accuracy did not fall when compared with the data of 1967–1968 does not necessarily argue against the latter view. This second view is supported by noting that the accuracy of the insertion rule alone (no deletion rules operating) was 68.2% for 1974–1975 as compared to 76.1% for 1971–1975. This decrease is expected if the bias introduced by subsampling from 1971–1975 is important.

Finally, there is no striking evidence that a biological mechanism for autocorrelation exists. Morse (1971) has argued that each species of the Maine birds constitutes a single gene pool. During 1967–1969 he banded and recorded the individuals of three species breeding on seven of the islands (Morse 1971, his Table 1). For the breeding seasons for which positive identifications were made, there was a potential for 25 instances of an individual returning to the same island. Of these possibilities, Morse observed five actual occurrences of an individual breeding on an island more than once. Of these five, there were no three year runs of an individual on an island and no cases of an individual returning the third year following an absence. Morse does not discuss the incidence of offspring returning to the island of their birth. Thus, although autocorrelation is almost certainly contributing to the accuracy of model validation, there is statistical and biological evidence indicating that it is not the sole determinant.

Rule Order

The order in which the deletion rules are applied influences the response of the model. It is of interest to test the extent to which model response is determined by the order of the deletion rules. Such a test was performed as described in the Methods section.

When all of the original rules are applied simultaneously, the model accuracy for the 1967–1970 data drops to 78.4%. The impact of rule simultaneity is not evenly distributed across all species; its greatest influence is upon the Yellow Warbler and Redstart. When rule order is eliminated, the Yellow Warbler is predicted to be present only on Franklin Island and Redstart absent only on Wreck Island.

A comparison of the results of simultaneous rule application to the 1971–1975 data is approximately the same: 79.6%. Because in that data set the Yellow Warbler occurs on more islands, the effect of rule simultaneity is greater (percent correct for the Yellow Warbler is only 18.2%). Removal of Rules 3 and 4 followed by the simultaneous application of the remaining rules gives better results: 89.8% correct.

One can conclude from these exercises that species of intermediate size are more sensitive to the order in which these deletion rules are applied. These species are deleted depending upon which species are present at the extremes of the size spectrum. Therefore, the importance of rule order depends on the geographical distribution of these sensitive species (such as the Yellow Warbler or Redstart). Correct prediction of widely distributed species will not require complex deletion rules, since they rarely need to be deleted. Thus, these species will not greatly influence the results of other rules in the model. Consequently, if species of intermediate size are widely distributed and the distributions are accurately predicted by a rule-ordered model, then it is likely that the distributions will also be accurately described by a rule-unordered model. An example of this is the simultaneous application of a model without Rules 3 and 4 when compared to the 1971–1975 data (89.8% correct).

Model Application

The model has been exercised, to this point, with the intent of describing the current conditions on the Maine islands. The model can also be applied, however, to different, hypothetical situations. Such applications are important to any general framework of community organization because they state predictions. These predictions may then be used to test the model or, in the case of well-validated models, to aid managerial decisions regarding the effects of habitat manipulations on the species compositions of ecosystems. To illustrate these two applications of ecosystem assembly grammars, two hypothetical situations are examined: (a) alteration of the species pool, and (b) habitat modification on one island.

1. Species Exclusion

In an ecosystem assembly grammar, species can be prevented from colonizing an ecosystem by removing them from the species pool. This may be done either to describe systems beyond the species' geographical range or to simulate the effects of experimental manipulations.

Table 8 shows the predicted species distributions of the Maine islands if the Parula Warbler is removed from the species pool. This simulation used the complete, rule-ordered model. Parula is one of the smallest species in the original species pool and, in previous simulations, was a species in the context of many deletion rules. Without Parula, many rules do not apply and, consequently, fewer species are deleted. The Magnolia, Black-throated Green, and Yellow Warblers are the most sensitive to the absence of Parula. They are present on many more islands when Parula is excluded (compare Table 5). This result suggests an obvious experimental test of the model.

Table 8. Model output when the Parula Warbler is removed from the species pool. Pluses indicate presence; blanks indicate absence

	Islands	Crotch	Ram	Crow	Jim's	Crane	Indian	Thief	Franklin	Wreck	Haddock	Hog
Yellow-rumped		+	+	+	+	+	+					+
Yellow	+	+	+	+	+	+	+	+		+	+	+
Black-throated Green	+	+	+	+	+	+	+			+	+	+
Redstart	+	+	+	+	+	+	+	+		+	+	+
Golden-crowned Kinglet												+
Magnolia	+	+	+	+	+	+	+			+	+	+
Blackburnian												+

2. Habitat Manipulation

A description of the environment at a site is an input to the model. The effects of environmental alteration can be simulated by altering these inputs. This may be done to simulate the effects of anthropogenic environmental degradation, wildlife management practices, or experimental habitat manipulation.

To illustrate this, the description of the environment of Indian Island was altered to represent selective thinning of the forest by cutting all tall trees. For both patches, the forest was described as $-(12\text{--}15\text{ m})^* - (15\text{--}18\text{ m})^* - (18\text{--}21\text{ m})^* - (>21\text{ m})$, with pluses at other heights, and (% vegetation at 0.6–7.6 m)/(% vegetation at >7.6 m)=1.52. The species present on Indian Island after this environmental manipulation are Parula, Redstart, and Yellow-rumped. The Black-throated Green Warbler can no longer exist on the island.

Using a series of such simulations, with the environment described as having different forest heights, one could determine the maximum degree of habitat manipulation which would not cause the deletion of any given species (such as the Black-throated Green Warbler). This could be useful in assessing environmental impacts. As these impacts become more frequent and as the interest in preserving particular communities of organisms (e.g. non-game birds, Balda 1975) grows, the ability to predict the effect of habitat modifications on species distributions becomes more important. These practical concerns compel us to develop theoretical methods that relate directly to the perturbations imposed upon the systems: habitat modifications and alterations of species assemblages. Ecosystem assembly grammars are one method that formalizes detailed, quantitative natural historical information on species and ecosystems and which potentially has the capacity to make the necessary predictions.

Evaluation of Approach

1. Data Requirements

Construction of an ecosystem assembly grammar is based on the comparison of ecosystems from which specific types of data have been collected. Few of the published studies on bird communities, however, can be compared. In addition, economic constraints have caused journal editors to discourage the publication of the detailed, quantitative data upon which an article is based. Formal modeling of any kind requires that detailed, comparable quantitative data be widely distributed. To encourage the continued publication of these data, I indicate below the data essential for the creation of ecosystem assembly grammars.

1. Distributions and densities of species on each of several sites which possess different environmental conditions.

2. Quantitative characterization of the vegetation and abiotic environment at each site.

3. Quantitative data for all species at every site showing the degree to which each resource category is used, as well as any direct behavioral interactions between species that can be documented and quantified.

4. An estimation of the species pool, in the form of a species list, from areas adjacent to the study site.

In general, most of these types of data are routinely collected by astute field biologists (e.g. Emlen 1977). Unfortunately, often these data do not appear in print, or, just as often, not all of the data are comparable between studies. This latter problem could be solved if the specialists in specific taxomic groups agreed that a minimal set of observations be collected using standardized methods. Clearly, studies with different objectives and species will require that different sets of variables be measured. This is inevitable, but if community organization patterns are to emerge from field studies, those studies must be comparable.

2. Assumptions

Two assumptions of the model described here require comment. First, the structure of the model (definition and order of rules) is fixed, and the effects of the rules are deterministic. This determinism is contrary to some recent re-evaluations of island biogeographical data (Connor and Simberloff 1979). One manifestation of the determinism in the present analysis is the pooled data from which the model was constructed and against which it was tested. All data from a set of years were lumped into two sets. This removes the existing stochastic variation and increases the likelihood that a deterministic model will be applicable. To evaluate the importance of randomness, models and test procedures should be developed to incorporate yearly variations.

Ecosystem assembly grammars can incorporate random events with the construction of a model where insertion is random and deletion is deterministic. In such a model, the set of species types inserted on an island would be a random subset of those species types whose habitat requirements are fulfilled by the available environment. Subsequent deletion of species types from this initial list would, in this approach, remain deterministic as in the current model. Because of the importance of the biotic context of the deletion rules, a model with random insertion would undoubtedly predict species distributions different from those in Tables 5 or 6. Model validation would require comparisons of statistical distributions.

A second major assumption of this particular model is that the population sizes of the species are unimportant in determining spatial distributions. This is, of course, a difficult assumption to justify in general. The current model, however, is based on the initial, simple hypothesis that in this case of small, near-shore islands, population sizes are not important in determining the geographical distribution of the species. If abundance controls species distribution, then this model should be easily falsified. Evaluation of the importance of abundance requires assembly grammars that incorporate population densities; formulation of these should be a priority of future work.

3. Limitations

Two limitations of the current approach require discussion. First, the procedures described are correlative and cannot claim to be descriptions of causal relations. The arbitrariness of the correlations that emerge from such a study can be reduced by selecting interesting groups of systems to compare. This is the motivation behind any study of "natural experiments". By analyzing islands with different vegetation structures and different species lists, one hopes to produce correlations that reflect the interrelations of available resources, behavior, and resource partitioning in determining the species composition of the community. Experimental validation of these rules is feasible in principle with both habitat manipulation and selective removal and addition of different species. As simulations show, the predicted results of these experiments can be stated prior to the manipulation.

Although the methods used are correlative, ecological hypotheses have been incorporated. First, the basic model structure of insertion, based on habitat requirements, followed by deletion due to proposed biotic interactions is one implementation of the "individualistic approach" to communities and succession. Second, the deletion rules hypothesize biotic interactions which are contingent upon particular vegetation structure (e.g. Deletion Rule 7). This is believed by some (e.g. Abbott 1980) to be an important aspect of these interactions. Third, size relations between species types are an important element of many of the rules, and this is in concord with modern theory. Thus, although this is not a model of the biological mechanisms that underlie the assembly grammar, the deletion rules, in their specifics, incorporate biological hypotheses.

The second limitation is the subjective nature of the model construction process. This is a feature common to many modeling approaches (e.g. the construction of sets of difference equations) and to that extent does not require defense. Nevertheless, several aspects of the modeling process reported here are analogous to parameter estimation in other approaches, and it is desirable to develop objective techniques for the automatic estimation of model elements. The description of species types is an example, and the use of multivariate techniques such as factor analysis has promise.

4. Advantages

Despite the limitations, I believe this approach has some significant advantages. First, this approach can be a procedure for the detection of pattern in the organization of bird communities that is not obvious from a superficial examination of data. The application of standard multivariate statistical procedures are either purely descriptive (Sabo and Whittaker 1979) or describe patterns in terms of linear combinations of variables that are difficult to interpret ecologically (Niemi and Pfannmuller 1979). Moreover, grammars have a predictive capability not present in most multivariate analyses (but see Cody 1978). A combination of grammars and multivariate techniques could be a powerful tool.

Second, the grammatical approach is general in the sense that alternative, competing hypotheses can be stated in the formalism and their different outcomes compared. For example, the differences between models that do or do not incorporate behavioral plasticity can be examined. Further, this generality allows multiple causes to influence model response. For example, in the current model both biotic interactions and available vegetation influence the ultimate species distributions when both the insertion rule and deletion rules are considered. The importance of the interaction between these two factors has been reviewed (Abbott 1980).

Third, this approach is based on and ultimately validated by comparisons of different ecological communities (e.g. different islands). These comparisons can be performed on systems having different degrees of similarity. They may be performed on systems that have developed on different, but geographically close, islands, as reported here using the Morse data. The com-

parisons may also be performed on other communities with different representatives of the foliage-gleaning guild, e.g. the European titmice. Alternatively, they may be performed on similar biomes on different continents. Extrapolation of the model to other, more distantly related taxa (e.g. *Anolis* lizards) is also feasible, and would constitute an extremely stringent test of the universality of the rules. However unlikely the success of these latter comparisons, they can, nevertheless, be performed and yield insight into the differences in community organization among different taxonomic groups. Model failure in such a test should evoke the desire for new generalizations that subsume the variability, not dismay at the magnitude of the variation.

Conclusions

This report has concerned the analysis of avian community organization using generative grammars. A collection of insertion and deletion rules were derived from published studies and validated with a data set not used during model construction. Several simulations were performed that showed: (a) the accuracy of the model for the 1971–1975 data is improved when Deletion Rules 3 and 4 are removed; (b) the deletion rules can be reasonably accurate when they are applied without order; and (c) changes in species distributions are predicted when habitats and the species pool are altered.

A solution to the ecosystem assembly problem is the fundamental goal of this research. This problem is interesting because it relates directly to the older problem of explaining the distribution and abundance of organisms and to the theory of the niche (Haefner 1980). Moreover, the solution discussed here has explicitly used data on foraging behavior and geographical distributions. These data are often incommensurate with the data requirements and predictions of other theoretical approaches (e.g. the Lotka-Volterra equations, or systems ecology). Although these data often have flaws, as noted above, they can be synthesized by an ecosystem assembly grammar.

However desirable experimental manipulation may be, correlation and comparison of communities will continue to be an important form of analysis. For patterns to emerge from comparisons, the differences between systems must be subsumed by general statements. For comparisons to foster predictions, testable statements about particular systems must be made. Any formalism that exploits these data of comparisons must, therefore, both subsume inter-system variability with general statements and produce specific predictions. One of the attractions of generative grammars is their incorporation of both generality and particularity. Generality is present, for example, because deletion rules are stated without reference to particular species names or geographical places. Particular predictions result from generative grammars as shown in Table 5.

In general, substantive empirical generalizations in science have a limited domain of applicability; while not referring to particular individuals, they are, nevertheless, true of only a finite set of individuals (Nagel 1961). An important challenge, therefore, is to state these generalizations in forms that can be tested, define the class of systems in which the generalizations are true, and then to provide satisfying theoretical explanations of them. As a collection of generalizations, the accuracy and universality of these insertion and deletion rules can only be assessed after their application to other systems. Undoubtedly, refinement of the rules will be necessary, as will definition of the class of systems to which the rules apply. This is to be expected: no simple set of rules such as these will account for all the diversity

of avian community organization that we observe. Other guilds and taxonomic groups will require different rules, but once stated these rules may permit our comparisons and analyses to be made at more abstract and encompassing levels of generality.

Appendix

The seven deletion rules (Figs. 2–8) all have the basic form "Delete T/C". This can be translated as: "delete a species type (T) whenever it occurs in the context C". T and C are variables which possess different values in the rules. The concise statement of T and C requires notation that reflects the fact that species types are hierarchical trees derived from rewrite rules of a generative grammar (Fig. 1, see Haefner 1977). Deletion rules are, in fact, transformational rules which alter the structure of hierarchical trees (Chomsky 1957). Consequently, the hierarchical structure of these trees must be represented by the deletion rule. The most important aspect of tree structure is the relation between the branch points of the tree (activities or categories) and the habitat requirements for successful completion of those activities. This relationship is represented in the deletion rule by labeled brackets (Fig. 2). A bracket enclosing a set of habitat requirements indicates that the set is required for the activity for which the bracket is labeled. Parentheses enclosing requirements indicate that at least one of the items is required by T. Since in general only a part of the hierarchical tree is important to any given rule, those irrelevant parts are denoted by upper case letters (e.g. X). The standard form of transformational rules (e.g. Chomsky 1957) is not used here so as to simplify the presentation. These deletion rules could be stated in the standard form, but no appreciable gain in clarity would be achieved.

Fig. 2. The first deletion rule. See text for definitions of notation and interpretation

Deletion Rule 1

Deletion Rule 1 is shown in Fig. 2. The context of the rule (item C in the general formula) contains restrictions on both the vegetation structure of the island and the bird community. The vegetation restriction states that the ratio of vegetation volume between height classes 0.6 m–7.6 m and >7.6 m must exceed 1.4. This condition restricts the application of Rule 1 to those islands with appropriate vegetation characteristics. The bird species condition of the context of the rule requires the presence of another species with size α_j that uses vegetation heights 3–12 m and forages on feeding stations of small branches and tips of branches (+SMALL, +TIP). The species type to be deleted (item T in the general formula) is any species type which (a) uses either large or dead limbs (+LARGE, +DEAD) or both, (b) uses small branches (+SMALL), (c) does not require deciduous vegetation, and (d) has some size (α_i). The auxiliary conditions specify the vegetation restrictions $(n/m > 1.4)$ and the necessary size ratios between the two species $(\alpha_i/\alpha_j < 1.2)$.

The biological interpretation of this rule is that a species type is deleted from certain patches if (a) it uses certain feeding stations (as stated) and (b) is not sufficiently larger than another species which uses another set of feeding stations (as stated). The rule states that there is overlap between the two species (both require +SMALL and similar height classes). The overlap described, however, is neither total nor sufficient for deletion; the other aspects of resource use and vegetation distribution must also obtain. Therefore, other birds which feed at +SMALL may not be deleted if their total feeding distribution is not that cited in the rule.

$$\text{DELETE: } \left[X + \left[\alpha \right]_{MOR} + \left[Y + \left[\begin{array}{c} +SMALL \\ -DEAD \\ +DECID \end{array} \right]_{STA} \right]_{REPRO} \right]_{LB} \bigg/ \left[V + \left[W + \left[m_i \right]_{AVHT} \right]_{PATCH_i \; PATCH_i} + Z + \left[Q + \left[m_j \right]_{AVHT} \right]_{PATCH_j \; PATCH_j} \right]_{ENV} + R \right]_S$$

where: $m_i / m_j < 0.5$

Fig. 3. The second deletion rule. See text for definitions of notation and interpretation

Deletion Rule 2

The context of the second deletion rule (Fig. 3) does not contain a description of a bird species. Its application depends only on the vegetation patch structure of the site. This kind of rule is necessary because insertion is currently modeled as a "local" process. In other words, insertion occurs on a "patch-by-patch" basis with insertion decisions made for every patch without regard to the global distribution of patches. Rule 2 applies to patch j, and a species type is deleted from that patch if it forages at stations $+SMALL * +DECID *$ $-DEAD$. The context necessary for this deletion is the existence of another patch (i) on the island which has an average height less than $^1/_2$ that of patch j. This is stated as the auxiliary condition for the rule. The rule does not apply on islands with only one patch. The rule does not place constraints on the sizes of the patches, the frequencies of two or more patches on an island, or the locations of the patches relative to each other. These variables may be important to bird distribution, but the present rule is perhaps the simplest way of incorporating global spatial heterogeneity into the model.

The biological interpretation, then, is that an edge species type will be deleted from the interior of a patch (j) if that patch has a distinct edge.

Fig. 4. The third deletion rule. See text for definitions of notation and interpretation

Deletion Rule 3

Deletion Rule 3 (Fig. 4) involves three species. The context for the rule contains two species types which forage at $+SMALL * +DECID$ and $+SMALL$, respectively. The former is smaller than the latter and the ratio of their sizes is at least 1.2. The species type to be deleted requires deciduous vegetation and the smaller part of conifer branches. The auxiliary condition states that, in order for this last species type to be deleted, it must be of intermediate size between two other species present in its environment. The biological interpretation is that, if a sufficiently wide range in sizes exists between birds (ratio greater than 1.2) that forage on small parts of vegetation, then an intermediate size bird must be deleted.

Fig. 5. The fourth deletion rule. See text for definitions of notation and interpretation

Deletion Rule 4

Rule 4 is given in Fig. 5 and is similar in form to Rule 3. The context contains two species, the smaller of which requires $+DECID$ and the larger of which requires $+DEAD$. As with Rule 3, these two species must have a ratio of sizes greater than 1.2. The species type to be deleted requires dead vegetation but not large branches. This species must be intermediate in size between the two species in its environment. The biological interpretation of this rule is that the smaller of two species using dead vegetation is deleted only in the presence of a smaller user of deciduous vegetation.

and $\alpha_i \neq \alpha_j$

Fig. 6. The fifth deletion rule. See text for definitions of notation and interpretation

Deletion Rule 5

Rule 5 (Fig. 6) is a different type of rule needed to show the movement of a species type from a less preferred habitat if other species are absent from the ecosystem. The context states that the system does not contain any other species types of a different size than the deleted species type and which uses the smaller portions of the vegetation, and no dead material. The species type deleted requires small and deciduous, but no dead, vegetation. The auxiliary condition states the necessary size relations. Biologically, this states that, for those members of the foliage-gleaning guild that use small conifer branches, deciduous vegetation is less preferred habitat and is used only if another species is using the tips of coniferous vegetation.

Fig. 7. The sixth deletion rule. See text for definitions of notation and interpretation

Deletion Rule 6

As with Rules 3 and 4, Rule 6 (Fig. 7) describes ecological relations between three species. The context contains two bird species types, both using $+SMALL$, with the larger also requiring $+LARGE$. The species type deleted is intermediate in size between the two species in the context, requires small branches, no deciduous vegetation, and either large branches or dead material. The biological interpretation of this is that, among those members of the guild which require small branches, any species type will be deleted if it: (1) is intermediate in size between two others (one an obligate generalist requiring both $+LARGE$ and $+SMALL$), (2) does not require deciduous vegetation, and (3) requires either dead or large vegetation.

where: $\alpha_i > \alpha_j$ and $n/m > 1.4$

Fig. 8. The seven deletion rule. See text for definitions of notation and interpretation

Deletion Rule 7

Rule 7 (Fig. 8) applies only to those islands that have a vertical vegetation distribution as described in the auxiliary conditions (ratio of intermediate to high vegetation greater than 1.4). In addition, the context for this rule is a species type that uses either the smaller portions of vegetation (small and tip) or uses a wide range of vegetation stations (small and large). The species type deleted by this rule requires identical feeding stations and is larger. The biological interpretation of this is that, on those sites with mainly low vegetation ($n/m > 1.4$), large species that use the stations stated will be deleted in presence of a smaller bird using the same stations.

References

Abbott I (1980) Theories dealing with the ecology of landbirds on islands. Adv Ecol Res 11:329–371

Balda RP (1975) Vegetation structure and breeding bird diversity. In: DR Smith (ed), Proceedings of a symposium on the management of forest and range habitats for nongame birds. USDA Forest Serv Gen Tech Report WO-1, pp 59–80

Chomsky N (1957) Syntactic structures. Mouton Publishers. The Hague

Cody ML (1978) Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. Ecol Monogr 48:351–396

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723

Connor EF, Simberloff D (1979) The assembly of species communities: Chance or competition? Ecology 60:1132–1140

Emlen JT (1977) Land bird communities of Grand Bahama Island: The structure and dynamics of an avifauna. Ornithol Monogr 24:1–129

Haefner JW (1977) Generative grammars that simulate ecological systems. In: GS Innis (ed), New directions in the analysis of ecological systems. Simulation Councils, Inc., La Jolla CA. pp 185–211

Haefner JW (1978) Ecosystem assembly grammars: Generative capacity and empirical adequacy. J theoret Biol 73:293–318

Haefner JW (1980) Two metaphors of the niche. Synthese 43:123–153

James FC (1971) Ordinations of habitat relationships among breeding birds. Wilson Bull 83:215–235

MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619

May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ

Morse DH (1967) Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84:490–502

Morse DH (1971) The foraging of warblers isolated on small islands. Ecology 52:216–228

Morse DH (1973) The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54:346–355

Morse DH (1977) The occupation of small islands by passerine birds. The Condor 79:399–412

Morse DH (1980) Foraging and coexistence of spruce-woods warblers. The Living Bird 18:7–26

Nagel E (1961) The structure of science. Harcourt, Brace, and World, Inc, NY

Niemi GJ, Pfannmuller L (1979) Avian communities: approaches to describing their habitat associations. In: RM DeGraaf and KE Evans (eds), Proceedings of a workshop on the management of northcentral and northeastern forests for nongame birds. USDA For Serv Gen Tech Report NC-51, pp 154–178

Noon BR, Able KP (1978) A comparison of avian community structure in the northern and southern Appalachian Mountains. In: RM DeGraaf (ed), Proceedings of a workshop on the management of southern forests for nongame birds. USDA Forest Serv Gen Tech Report SE-14, pp 98–117

Pianka ER (1974) Niche overlap and diffuse competition. Proc Nat Acad Science (USA) 71:2141–2145

Pielou EC (1977) Mathematical ecology. John Wiley and Sons, NY

Rabenold KN (1978) Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecol Monogr 48:397–424

Robbins CS, Bruun B, Zim HS (1966) Birds of North America. Golden Press NY

Roughgarden J (1979) Theory of population genetics and evolutionary ecology: An introduction. MacMillan Publishing Co., NY

Sabo SR, Whittaker RH (1979) Bird niches in a subalpine forest: An indirect ordination. Proc Natl Acad Sci (USA). 76:1338–1342

Schoener TW (1976) Alternatives to Lotka-Volterra competition: Models of intermediate complexity. Theoret Popul Biol 10:309–333

Willson MF (1974) Avian community organization and habitat structure. Ecology 55:1017–1029

Yeaton RI, Cody ML (1974) Competitive release in island song sparrow populations. Theoret Popul Biol 5:42–58