A DISCRIMINANT FUNCTION ANALYSIS OF ASSEMBLAGES OF FRUIT-EATING BIRDS IN CENTRAL AMERICA

ROBERT E. RICKLEFS

Many species of tropical trees are adapted for seed dispersal by birds. Their fruits share many characteristics that promote the dispersal of seeds: relatively large size, fleshy pulp or aril, often with substantial nutritive value, and conspicuous placement or coloration. These fruits are exploited by a wide variety of birds, including species that are primarily insectivorous, but the assemblage of fruit-eating birds attracted to each type of fruit is usually limited to a small subset of the indigenous species, and the assemblages vary according to the type of tree. In this study, I sought to determine whether assemblages of birds exploiting the fruits of four different species of tropical trees could be distinguished by their morphology and, if so, which morphological attributes were most characteristic for each species of tree. The study is based on a discriminant function analysis using 10 morphological characters obtained from museum specimens. The principal result of this study is that where assemblages differ, they are distinguished primarily by size and shape of locomotory appendages rather than by bill structure. Although I have not attempted to relate morphology to behavior, or to interpret either in relation to the needs of the plant for dispersal, the results of this study suggest that morphological approaches to the study of community structure will benefit from using appropriate multivariate techniques to analyze a broad selection of morphological traits.

MATERIALS AND METHODS

This study is based on published accounts of birds seen feeding on *Miconia trinervia* (Melastomataceae) in Guatemala (Land 1963); *Trichilia cuneata* (Meliaceae) in Costa Rica (Leck 1969); *Cecropia mexicana* (Moraceae) in Panama (Eisenmann 1961); and *Stemmadenia donnell-smithii* (Apocynaceae) in Costa Rica (McDiarmid, Ricklefs, and Foster 1977). *Miconia* bears large clusters of berry-like fruits at the tips of branches. The fruits are about 0.5 cm in diameter and the pulp contains numerous tiny seeds. The tree studied by Land was about 23 m tall, located "on a small ridge in rich forest characterized by palm and ceiba trees" in the Department of Izabal in eastern Guatemala. Observations were made in the early morning between June and August. Leck studied a single *Trichilia* tree, approximately 10 m tall, in disturbed river bottom forest near Cañas, Guanacaste Province, Costa Rica, during mid-July. The dehiscent fruits of *Trichilia* are about 1 cm in diameter, each containing several large, rather soft

seeds with a bright orange-red aril. *Cecropia* is a common tree in disturbed areas of Central America. The fruits are long, finger-like catkins clustered on a peduncle close to the slender trunk of the tree, hanging just below the tree's crown. Birds eat at the tip of the greenish fruiting spike, which Eisenmann (1961) found to be "dry and insipid." Most of Eisenmann's observations were made on Barro Colorado Is., Panama Canal Zone, during August. Exploitation of *Stemmadenia* fruits was observed during April in the area of Leck's study. *Stemmadenia* has large (up to 9 × 7 cm) ovoid fruits with a thick woody husk. Ripe fruits open along their distal margins, exposing numerous small (4 × 8 mm) seeds imbedded in a bright orange-red aril. The fruits, usually paired, are located at the ends of branches; the trees observed by McDiarmid et al. were located at the edge of a pasture and in disturbed river bottom forest.

In each of the studies, a list was compiled of species that consumed the fruit. Leck and McDiarmid et al. provided quantitative data on number of visits by each species of bird during 16 and 17.5 h of observation. Land and Eisenmann simply noted occurrences of feeding over longer periods. In all but Eisenmann's study, the authors also noted species commonly seen in the area but not feeding on the fruit.

To avoid problems inherent in assigning species to ecological categories, comparisons of the feeding assemblages were based upon morphology. This approach owes its origin to the principle that morphology reflects the ecological relationships of the species —the species' niche (e.g., Hespenheide 1973, Ricklefs and O'Rourke 1975, Findley 1976, Karr and James 1976). Systematic morphological differences among assemblages of birds that exploit the fruits of different species of trees would suggest that each tree attracts a non-random ecological subset of birds whose characteristics could be related to the properties of the fruit itself.

To avoid biases resulting from preconceptions about important morphological variables, I chose ten measurements that were both readily available and provided as complete a characterization of morphology as possible. The measurements were total length, body length (total length minus tail minus bill length), wing length, tail length, tarsus, middle toe (including the claw), the length, width, and depth of the culmen, and weight. Measurements were obtained from Ridgway's (1901–1918) compilations and from specimens in the Museum of Vertebrate Zoology at the University of California, Berkeley. When males and females differed by more than 10% in any one measurement, they were treated separately. Eighty-two species were considered in the analysis; the sexes were separated in 10 species, making a total of 92 forms. These were distributed among 22 families: Columbidae (4 species), Cuculidae (1), Psittacidae (3), Trogonidae (3), Momotidae (1), Ramphastidae (4), Picidae (6), Dendrocolaptidae (3), Formicariidae (2), Cotingidae (5), Pipridae (3), Tyrannidae (13), Corvidae (3), Troglodytidae (3), Turdidae (2), Sylviidae (1), Vireonidae (3), Coerebidae (2), Paru-

TABLE 1. Results of discriminant analyses between assemblages of fruit-eating birds.

Comparison	Number of species	F	d.f.	P
Stemmadenia vs.	20	1.09	10,25	>0.25
non-*Stemmadenia*	16			
Miconia vs.	24	2.54	10,41	<0.025
non-*Miconia*	28			
Stemmadenia vs.	20	0.75	10,22	>0.25
Trichilia	13			
Stemmadenia vs.	20	3.16	10,33	<0.01
Cecropia	24			
Stemmadenia vs.	20	2.53	10,33	<0.025
Miconia	24			
Trichilia vs.	13	1.34	10,26	>0.25
Cecropia	24			
Trichilia vs.	13	1.49	10,26	>0.10
Miconia	24			
Cecropia vs.	24	0.35	10,37	>0.75
Miconia	24			

TABLE 2. Coefficients of discriminant functions in comparisons revealing significant differences between assemblages.[1]

	Comparison		
Character	*Miconia* vs. non-*Miconia*	*Stemmadenia* vs. *Miconia*	*Stemmadenia* vs. *Cecropia*
Total length	−0.21	0.81	0.17
Body length	−0.25	0.27	0.43
Wing length	0.46	−0.01	0.14
Tail length	−0.10	−0.18	0.18
Tarsus length	−0.13	0.51	0.34
Toe length	0.11	−0.74	−0.51
Culmen length	−0.05	0.08	0.24
Culmen depth	0.02	−0.07	−0.23
Culmen breadth	−0.04	−0.08	−0.09
Weight	0.11	−0.24	−0.31

[1] Values are coefficients of a linear combination of the 10 log-transformed variables. Hence the coefficients provide a relative measure of the importance of each character in distinguishing the species assemblages. Because the variables were log-transformed, characters with positive coefficients enter the discriminant function as multiplying factors and characters with negative coefficients enter as divisors.

lidae (2), Icteridae (4), Thraupidae (9), Fringillidae (5).

Analyses were based on average values for each measurement calculated for a sample of five or more individuals for each form. Tests for skewness and kurtosis revealed that the distributions of all ten measurements among forms were approximately log-normal. The measurements accordingly were transformed to logarithms (base 10) before analysis. The log transformation is all the more appropriate because linear combinations of logarithmic variables, obtained from regression, principal component, and discriminant function analyses, represent products and ratios of untransformed variables and thus may be interpreted in terms of allometric relationships.

Pairs of assemblages of fruit-eating species were compared by discriminant function analysis (BMD-04M, Health Sciences Computing Facility, UCLA). The resulting discriminant function is that linear combination of variables which maximizes the differences between two groups; more precisely, it maximizes the ratio (F) of the between-group mean squares to the within-group mean squares in a single classification analysis of variance (Sokal and Rohlf 1969, Morrison 1967).

RESULTS

The results of eight discriminant function analyses are presented in Table 1. The only significant morphological differences between assemblages involved the *Miconia*-feeding and non-feeding assemblages, the *Stemmadenia*-feeding and *Miconia*-feeding assemblages, and the *Stemmadenia*-feeding and *Cecropia*-feeding assemblages. Neither the *Trichilia* assemblage nor the *Cecropia* assemblage was compared to indigenous species not feeding on these fruits.

Coefficients of the discriminant functions for the three comparisons with significant differences are presented in Table 2. Species that fed on *Miconia* differed from those that did not primarily by the ratio of wing length to body length (log wing length − log body length), *Miconia* feeders being on the lower end of the scale.

Species that fed on *Stemmadenia* differed from those that fed on *Miconia* by having long toes in relation to total length and tarsus length. *Miconia* attracted many tanagers, finches, and icterids—families typically having small feet and which were not among those feeding on *Stemmadenia*, owing, at least in part, to their general absence from deciduous forest during the dry season. Among the most conspicuous species feeding on *Stemmadenia* were woodpeckers, motmots, flycatchers, and jays. Birds feeding on *Stemmadenia* could be separated from those feeding on *Cecropia* partly by their large ratio of toe to tarsus, as in the *Stemmadenia-Miconia* comparison, but also in being rather heavy-bodied and having a rather deep, but not broad, beak. This discriminant function does not bear any apparent relationship to different feeding methods employed by birds exploiting the two kinds of fruits. Species eating *Cecropia* do, however, have much wider morphological variety than those feeding on *Stemmadenia*, the former group including several families (pigeon, parrot, trogon, toucan, cotinga, icterid, and tanager) not observed feeding on *Stemmadenia*. The first four of these families are undoubtedly prevented from feeding on *Stemmadenia* fruit by their morphology. The narrow slit-like opening of the fruit, which exposes the seeds, is either too small to admit the beaks of birds in these families or the beaks are too short to reach the aril-covered seeds within the fruit.

DISCUSSION

Of the four types of fruits investigated here, *Stemmadenia* attracted the most distinctive set of species, and *Trichilia* the least. The habitat of *Stemmadenia* may partly determine the species attracted to the fruit; its exploiters did not differ morphologically from non-exploiters or from species eating *Trichilia*, another tree in the same area. There can be little doubt, however, that the distinctive fruit of *Stemmadenia* effectively excludes several types of potential exploiters. In addition, the species feeding on *Stemmadenia* might be selected from the central portion of the morphological space defined by all species in the area, and thus could not be distinguished from non-feeders by simple discriminant analysis.

In contrast to species feeding on *Stemmadenia*, those feeding on *Miconia* were clearly derived from that end of the morphological spectrum occupied by species with small wing/body length ratios. Notably absent from the feeding group in Land's list were toucans, most cotingids, and virtually all the small foliage gleaners (several flycatchers and vireos) except the Red-legged Honeycreeper (*Cyanerpes cyaneus*).

I shall not speculate on the significance of these results in terms of either the behavior of the birds that exploit different fruits, the taxonomic differences between assemblages, or the role of species with different morphology as dispersal agents. Fruits differ greatly in appearance and structure, both of which place limits on the variety of their exploiters. It is tempting to view the structure of fruits as an adaptation designed to control the patterns of their dispersal by favoring particular types of dispersal agents over others. This study has shown that fruit structure can exercise subtle influence over the morphology of dispersal agents. We do not yet know enough about the relationship between morphology and behavior to contemplate the significance of these patterns, but the results of this study clearly suggest a worthwhile avenue of research.

Morphology apparently influences the assemblage of species feeding on particular types of fruits but the distinctions between assemblages are subtle and, in several cases, non-intuitive. Although ecologists often think of the characteristics that distinguish species feeding on different types of foods in terms of bill measurements, the discriminant functions identified in this study emphasized the relative lengths of tarsus, toe, wing, and body —with culmen and tail measurements playing decidedly minor roles. Characteristics of the legs and feet, specifically the ratio of tarsus to toe length, appeared to be of primary importance, suggesting that character of perch sites at the fruit as well as the nature of the fruit itself may be responsible for molding the morphology of the feeding assemblage. This result emphasizes the need to examine the total morphology of the species when evaluating eco-morphological relationships.

SUMMARY

Assemblages of birds feeding on four species of fruits in Central America are compared among each other, and to species not feeding on these fruit resources, by a discriminant function analysis based on ten morphological characteristics. Of eight comparisons between feeding assemblages, and of these assemblages with non-feeding birds, three exhibited significant morphological differences. In one case, species feeding on *Miconia* were distinguished from non-feeders primarily by the ratio of wing length to body length. The significant discriminant functions separating the feeding assemblages of *Stemmadenia*, on one hand, and *Miconia* and *Cecropia*, on the other, are based, respectively, on the ratio of tarsus and total length to toe length, and on the ratio of tarsus and body length to toe length. Bill characteristics were unimportant. Although the ecological meaning of the discriminant functions was not elucidated by this study, the results indicate, first, that discriminant function analysis may be applied successfully to problems of community organization and, second, that the functions themselves may reveal non-intuitive relationships that could suggest new approaches to understanding a system. In this study, wing, leg, body lengths, and in particular the ratio of tarsus to toe length, overshadow bill dimensions in the discriminant functions.

ACKNOWLEDGMENTS

LITERATURE CITED

EISENMANN, E. 1961. Favorite foods of neotropical birds: flying termites and *Cecropia* catkins. Auk 78:636–638.

FINDLEY, J. S. 1976. The structure of bat communities. Am. Nat. 110:129–139.

HESPENHEIDE, H. A. 1973. Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4:213–229.

KARR, J. R. AND F. C. JAMES. 1976. Eco-morphological configurations and convergent evolution in species and communities. *In* M. L. Cody and J. M. Diamond [eds.], The ecology of species and communities. Harvard Univ. Press, Cambridge, Mass.

LAND, H. C. 1963. A tropical feeding tree. Wilson Bull. 75:199–200.

LECK, C. F. 1969. Observations of birds exploiting a Central American fruit tree. Wilson Bull. 81:264–269.

MCDIARMID, R. W., R. E. RICKLEFS, AND M. S. FOSTER. Dispersal of *Stemmadenia donnell-smithii* (*Apocynaceae*) by birds. Biotropica 9: 9–25.

MORRISON, D. F. 1967. Multivariate statistical methods. McGraw-Hill, New York.

RICKLEFS, R. E. AND K. O'ROURKE. 1975. Aspect diversity in moths: a temperate-tropical comparison. Evolution 29:313–324.

RIDGWAY, R. 1901–1918. The birds of North and middle America. Bull. U.S. Natl. Mus., No. 50, Pt. 1–11.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.