

## Community Organization Among Neotropical Nectar-Feeding Birds

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**SYNOPSIS.** Assemblages of neotropical hummingbirds are organized according to parameters of available resources and morphological-behavioral attributes of particular hummingbird species. We distinguish five types of flowers relative to hummingbird foraging, and we define six community roles for hummingbirds in exploitation of various flower types. These roles are: high-reward trapliners, which visit but do not defend nectar-rich flowers with long corollas; territorialists, which defend dense clumps of somewhat shorter flowers; low-reward trapliners, which forage among a variety of dispersed or nectar-poor flowers; territory-parasites of two types (large marauders and small filchers); and generalists, which follow shifting foraging patterns among various resources. Simple communities on islands usually contain one species of low-reward trapliner or generalist and one territorial species, and sometimes support one high-reward trapliner; often these species are sexually dimorphic. More complex mainland communities support varying numbers of species in different roles, depending on the relative importance and constancy of different flower types. High-reward trapliners are particularly important in forest under-stories, while forest canopies and open habitats support large numbers of shorter-billed, mobile birds filling the other five roles. We conclude by pointing out the many parallels that exist with other consumer groups.

### INTRODUCTION

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Terrestrial habitats in the American tropics commonly support several species of birds that feed primarily on nectar. Repeated patterns in the morphology and behavior of coexisting species suggest that certain basic principles are involved in the ecological organization of these assemblages. Investigation of these principles is facilitated by several factors. Nectar production and nutritional value are precisely measurable. Foraging patterns of birds are easily observed and quantified. The coevolution of bill morphology and flower morphology sets certain limits on the patterns of particular species. Since behavioral interactions between birds are also obvious, it is often possible to infer the effect of interference on resource use. The considerable : actability of the bird-flower

system permits detailed comparison with the organizing parameters of other well-studied groups and with predictions from general ecological theory.

We concentrate on neotropical hummingbirds because they are the most intensively studied nectar-feeding birds and apparently the most dependent upon nectar. We summarize published information and previously unpublished data to (a) list the types of food resources distinguished by hummingbirds; (b) discuss the relationships among morphological features of hummingbirds that determine broadly which resource types they exploit; (c) link morphology with behavior and ecology to distinguish the community roles available to different hummingbirds; and (d) assemble food resources and hummingbird roles into natural communities. Finally, we compare the organization of hummingbird assemblages to that of other consumer groups. Although we emphasize the patterns in which hummingbirds exploit nectar, it must be remembered that these derive ultimately from the coevolution between hummingbirds and plants exploiting them as pollen vectors (Stiles, 1978; Feinsinger, unpublished).

We refer from time to time to previously unpublished data obtained by Feinsinger (PF) and Colwell (RKC). Feinsinger gathered data at the following sites and times: Monteverde, a lower montane site in Costa Rica, October, 1971–May, 1973, during studies reported elsewhere (Feinsinger, 1976), and 10 June–13 July, 1975; the northwest quarter of Martinique, West Indies, 27 June–7 July, 1976; Tobago and northern Trinidad, West Indies, 15 July–16 August, 1975, 12 June–26 June, 1976, and during an intensive study (assisted by L. A. Swarm and J. A. Wolfe) 11 January, 1977–2 March, 1978. In addition to studies reported elsewhere (Colwell, 1973), Colwell gathered data at the following sites and times: Chile, various localities, 1 October–25 December, 1973; Más Atierra Island, Juan Fernández Archipelago, 30 November–4 December, 1973; northern Trinidad, 26–31 December, 1973, 28 July–12 August, 1975, 10–25 March, 1976.

#### ATTRIBUTES OF FLOWERS AND ARTHROPODS THAT AFFECT FOOD SELECTION BY HUMMINGBIRDS

##### *Flowers*

*Habitat.* Tropical hummingbirds distinguish between adjacent forested and non-forested habitats (Snow and Snow, 1972; Stiles, 1975; Feinsinger, 1976, 1977), less obviously between mesic and xeric habitats (Wolf, 1970; Feinsinger, 1977). It follows that similar flowers may attract different hummingbirds in different habitats.

*Zone.* Within a habitat, a flower's location affects its roster of visitors. Hummingbirds foraging in different layers of vegetation may encounter different plant species (Snow and Snow, 1972) or distinct subsets of flowers on a single plant (Stiles and Wolf, 1970; Colwell *et al.*, 1974; Feinsinger, 1976; Lyon, 1976). Slow-flying hummingbirds searching through herbs and shrubs encounter many flowers missed by fast, high-flying species (Feinsinger, 1976).

*Dispersion.* Flowers sufficiently dense to sustain a hummingbird for several hours invite foragers adept at defending them against intruders, whereas dispersed flowers, usually far less defensible, generally preclude such interference competition and invite visitation by hummingbirds with more mobile foraging behavior (Linhart, 1973; Feinsinger and Chaplin, 1975; Stiles, 1975, 1978).

*Flower characters.* Flowers that differ in corolla morphology (Snow and Snow, 1972; Colwell, 1973; Hainsworth, 1973; Stiles, 1975; Wolf *et al.*, 1976) or nectar reward (Snow and Snow, 1972; Wolf *et al.*, 1976) attract different hummingbirds.

*Flower types.* In natural communities corolla morphology, nectar reward, and dispersion of flowers are often highly interdependent, leading to the following categories of flowers, which are quite distinct when defined relative to bird foraging:

(1) "Dispersed rich flowers": dispersed flowers with long or curved corollas that exclude most insects and most hummingbirds, offering substantial nectar re-

wards. For example, vines of *Mandevilla hirsuta* (Apocynaceae) on Trinidad produce from one to about eight 41-mm flowers daily, each secreting from 69 to 120  $\mu$ l (98-169 cal) of nectar. Other dispersed rich flowers are produced by shrubs and epiphytes such as *Bomarea* (Amaryllidaceae), *Centropogon* (Lobeliaceae) (Snow and Snow, 1972; Colwell, 1973; Wolf *et al.*, 1976), and by some species of the herb genus *Heliconia* (Musaceae) (Stiles, 1975).

(2) "Clumped rich" flowers: Rarely, and often as a result of human or natural disturbance, rich flowers (as defined above) exist in dense clumps. At some Costa Rican sites, clumped rich flowers of *Heliconia* (Linhart, 1973; Stiles, 1975) or *Centropogon* (Colwell, 1973; Wolf *et al.*, 1976) occur.

(3) "Dispersed moderate" flowers: dispersed flowers with moderately long corollas that exclude many insects but few hummingbirds, offering moderate nectar rewards. For example, the average 18-mm flowers on a shrub of *Hamelia patens* (Rubiaceae) on Trinidad secrete 13.5  $\mu$ l (10.8 cal) of nectar daily (PF). Other plants with dispersed moderate flowers include the herb *Lobelia laxiflora* (Lobeliaceae), the subshrub *Cuphea* sp. (Lythraceae) (Feinsinger, 1976), and the vine *Tropaeolum moritzianum* (Tropaeoliaceae) (Hainsworth and Wolf, 1972; Wolf *et al.*, 1976).

(4) "Clumped moderate" flowers: Moderate flowers often exist in dense clumps, either on individual trees or shrubs such as large individuals of *Hamelia patens*, or as aggregations of vines or herbs such as *Lobelia laxiflora* (Feinsinger, 1976; see Lyon, 1976). Late in the day, however, these clumps may hold so little nectar that operationally they enter the following category.

(5) "Insect flowers": flowers with short corollas and minimal nectar rewards, often adapted for pollination by insects. Many insect flowers, such as *Lantana hispida* (Verbenaceae), and *Acnistus arborescens* (Solanaceae) in Costa Rica (Feinsinger, 1976), *Stachytarpheta jamaicensis* (Verbenaceae) and *Asclepias curassavica* (Asclepiadaceae) on Trinidad (PF), attract

occasional hummingbirds. Moth- and bat-pollinated flowers, which may still hold nectar in early morning (see Wolf, 1970), can be assigned to category 3, 4, or 5.

### Arthropods

*Tactics.* Hummingbirds obtain flying arthropods by hawking, arthropods on foliage by hover-gleaning, or arthropods from corollas by probing flowers (Wagner, 1946; Wolf, 1970; Snow and Snow, 1972; Feinsinger, 1976).

*Zone.* On Trinidad, different hummingbirds tend to hawk for arthropods at different heights above ground, or to glean from different layers of foliage (PF; see Snow and Snow, 1972). These distinctions are not necessarily ecologically significant, since arthropods are apparently not often a crucial and limited food resource for hummingbirds (Feinsinger, 1976; Wolf *et al.*, 1976).

### ATTRIBUTES OF HUMMINGBIRD MORPHOLOGY AFFECTING FOOD SELECTION

#### Bills

Bill morphology, which varies widely among hummingbirds, influences the efficiency with which they forage at each flower species (Wolf *et al.*, 1976) and indeed determines which of the flower types listed above they can exploit at all. Most hermit hummingbirds (subfamily Phaethorninae) and certain other species have long or curved bills that provide access to nectar in rich flowers but hamper exploitation of moderate and insect flowers (Snow and Snow, 1972; Stiles, 1975). At the other extreme, many hummingbirds have quite short, straight bills that facilitate opportunistic use of a great variety of moderate and insect flowers but deny them access to rich flowers (Snow and Snow, 1972; Feinsinger, 1976). But some short-billed hummingbirds are nectar thieves, taking nectar from rich flowers by piercing the base of the corolla (Colwell, 1973; Skutch, 1973; Ingels, 1976).

*Body size*

Body size affects a bird's total energy requirements (Brown *et al.*, 1978) and therefore influences its choice of flower types (Snow and Snow, 1972; Wolf *et al.*, 1976). Where interference competition exists, body size *per se* has been thought to affect a bird's dominance relations with other species, hence its ability to obtain nectar from clumped flowers (Stiles and Wolf, 1970).

*Wing disc loading and the energy required to hover*

Wing disc loading and the energy required to hover have proved to be of great importance in interpreting hummingbird foraging. Wing disc loading is the ratio of body weight to a circle whose diameter is wing span. The energy required to hover per g body weight (required power) varies with wing disc loading and with air density (Feinsinger *et al.*, 1979). Birds with high wing disc loading must expend more energy to hover, particularly at high elevations, but are more adept at high-speed aerial maneuvers than energetically more frugal species with low required power. Where significant disparities in required power exist among shorter-billed hummingbirds, those with high required power exploit clumped flowers, which they can defend with ease, while those with low required power exploit dispersed or insect flowers, which they can do with relative efficiency (Feinsinger and Chaplin, 1975).

*Feet*

Hummingbirds use their feet not only for perching while at rest but also for perching while feeding. Some birds (*e.g.*, *Panterpe insignis*, *Oreotrochilus leucopleurus*, *Sephanoides fernandensis*) seem to perch whenever possible while feeding, even vertically or upside down, and have relatively large, strong feet (Colwell, unpublished). This behavior clearly saves energy, compared to hovering. Many long-tubed flowers, however, are presented so that perching by legitimate visitors is pre-

cluded; on this basis we predicted that the strength of a hummingbird's foot should be inversely related to the length of its bill (see below).

*Relationships among morphological variables*

In a study to be detailed elsewhere, Colwell (unpublished) examined the relationship between body size, bill length, an index of foot size, and weight-specific required power among single individuals or small samples of each of 124 hummingbird species represented in the collection at the Museum of Vertebrate Zoology, Berkeley. For each specimen, required power output (cal/g-sec) was computed from wing chord, body weight, and elevation where collected (See Feinsinger *et al.*, 1979). The foot index was computed as the sum of the standardized normal deviates (based on the sample variance) for the specimen's tarsometatarsus length and chord of hallux claw; this index is well correlated with perching versatility among hummingbirds (Colwell, unpublished). Variates were log-transformed to improve normality, except in the computation of required power output, for which raw variates were used. The data were subjected to partial correlation analysis, which permits statistical control of interrelated variables.

Table 1 suggests a high degree of interrelatedness among variables, the ecological and evolutionary significance of which will be detailed elsewhere (Colwell, unpublished). The positive weight-foot correlation simply means that larger birds need larger feet for perching. The positive weight-bill correlation is interesting in view of the nectar-rich flowers to which long-billed birds have exclusive access. It invites speculation on large body size driving the evolution of beaks to exploit rich resources, or access to rich resources inviting the evolution of larger body size, but the correlation may simply reflect evolutionary constraints on allometry. The less striking positive correlation between weight and required power output might also reflect unknown scaling constraints, since a simple scaled enlargement of any particular bird necessarily has a higher required

TABLE 1. Second-order partial correlation coefficients between each possible pair of the morphological variables computed in a sample of 124 hummingbirds (see text).<sup>a</sup>

	Required power output (cal/g · sec)	Foot index	Bill length
Weight	0.20 <sup>c</sup>	0.75 <sup>b</sup>	0.70 <sup>b</sup>
Required power output		-0.19 <sup>d</sup>	-0.004 <sup>e</sup>
Foot index			-0.48 <sup>b</sup>

<sup>a</sup> In each case, indirect effects of the other two variables are statistically controlled.

<sup>b</sup>  $P < 0.0001$ .

<sup>c</sup>  $P = 0.012$ .

<sup>d</sup>  $P = 0.015$ .

<sup>e</sup>  $P = 0.48$ ; not significant.

power output due to a cubic increase in volume relative to a quadratic increase in wing disc area. This positive statistical relationship between weight and required power output suggests that if the competitive environment favors a higher required power output to achieve behavioral dominance and if the resource base can support it, body weight is likely to increase pleiotropically (see discussion of required power output and body size in Feinsinger *et al.*, 1979). The common notion that larger hummingbirds dominate smaller ones merely because their size is intimidating bears a careful case-by-case re-examination in light of this evidence. As predicted, the correlation between bill length and foot index is negative, suggesting that long-billed hummingbirds have little useful to do with their feet but perch to rest, while some shorter-billed species can perch to feed on moderate or insect flowers, or perch to pierce the base of rich flowers. The weak but significant inverse relationship between foot index and required power output suggests one more distinction between the energy-frugal foraging behavior of low-power output birds, which may further conserve energy by perching while feeding, and the energy-profligate, high-power output forms (the territorialists and high reward trapliners of the next section), who can afford to hover while feeding. Finally, the partial correla-

tion between bill length and required power output is not significant. Whereas many long-billed birds have relatively high required power output, these birds are also quite heavy; controlling the effect of weight removes much of their contribution, and there is a counterbalancing effect of birds with equally high required power output but relatively short bills.

#### COMMUNITY ROLES AVAILABLE TO HUMMINGBIRDS

##### *High-reward trapliners*

Dispersed rich flowers with distinctive morphologies attract hummingbirds with equally distinctive beak morphologies, which follow a repeated foraging circuit (trapline) among successive flowers or clumps (Snow and Snow, 1972; Colwell, 1973; Linhart, 1973; Stiles, 1975). Such high-reward trapliners, which have access to abundant energy, tend to have small feet, large bodies, and moderate to high required power output relative to shorter-billed hummingbird species (see Feinsinger *et al.*, 1979). Most hermit hummingbirds (Phaethorninae), the preëminent high-reward trapliners (see Stiles, 1975), hover-glean foliage or spider-webs for arthropods (Young, 1971; Snow and Snow, 1972). Long-billed, non-hermit genera such as *Helimaster* may occasionally hawk for insects as well as glean foliage (PF).

##### *Territorialists*

Clumped moderate and (sometimes) clumped rich flowers attract medium-sized (ca. 4–5 g), shorter-billed hummingbirds with moderate to high required power output and moderate to large feet, which set up feeding territories and defend them against other hummingbirds of the same or different species (Stiles and Wolf, 1970; Wolf, 1970; Colwell, 1973; Linhart, 1973; Stiles, 1975; Feinsinger, 1976; Lyon, 1976; Wolf *et al.*, 1976). Territorialists usually hawk for flying insects (Snow and Snow, 1972; Feinsinger, 1976).

### Low-reward trapliners

In some communities dispersed-moderate and insect flowers are traplined by small, shorter-billed hummingbirds with low required power output and moderate feet, which are excluded from clumped flowers by territorialists (Wolf, 1970; Feinsinger and Chaplin, 1975; Feinsinger, 1976). The low-reward trapliner with which we are most familiar, *Chlorostilbon canivetii* in Costa Rica, also gleans for foliage arthropods (Feinsinger, 1976).

### Territory-parasites

Some clumped moderate flowers attract hummingbirds acting in one of two distinct roles, in essence parasitizing the resident territorialist. Large birds with moderate-length bills, high required power output and small feet forage with impunity among flowers defended by smaller territorialists, ignoring attempts to displace them. These "marauders" include *Phaeochroa cuvierii* (Stiles and Wolf, 1970) and *Anthracothonax prevostii* (Wolf, 1970) in northwest Costa Rica, occasional *Anthracothonax nigricollis* and *Florisuga mellivora* on Trinidad and Tobago (PF). Small, short-billed hummingbirds that resemble large insects filch from territories, often feeding in zones not heavily used by, or invisible to, the resident territorialists. *Philodice bryantae* in Costa Rica (Feinsinger and Chaplin, 1975), *Atthis heloisa* in Mexico (Lyon, 1976), and *Lophornis ornata* on Trinidad (PF) sometimes act as filchers. Both marauders and filchers regularly hawk for flying insects.

### Generalists

Most communities have available an opportunistic, loosely defined role that includes sporadic visits to dispersed moderate flowers and filching from clumped flowers. When a range of species is present, hummingbirds acting as generalists have short to moderate bills and feet, moderate required power output, and moderate body size relative to other species. Since many generalists switch to low-reward traplining when flower availability and the competitive environment

dictate, they have also been termed "facultative trapliners" (Feinsinger and Chaplin, 1975).

### Are birds shackled to their roles?

Above and in Figure 1 we have characterized the foraging roles that a community's hummingbirds might fill at a particular time. The morphological correlates are summarized qualitatively in Table 2. Assigning more quantitative values to roles is not possible. The availability of roles varies with place and time (see below). In some communities certain available roles are not filled, or are absorbed by generalists. Likewise, in one community each role may be played by different species at different times. Furthermore, while a given bird's morphology must suit it especially for one primary role which it most often plays, with a shift in flower availability or a shift in the spectrum of competitors the same bird might be allowed or forced into alternative roles. For example, *Amazilia tobaci* on Trinidad, commonly territorial, acts as a generalist or even as a low-reward trapliner when birds more suited to these roles (*i.e.*, having a lower required power output) are absent. A consistent low-reward trapliner such as *Chlorostilbon canivetii* (Feinsinger, 1976) may behave territorially at clumped moderate flowers in the absence of species that normally dominate it. Trinidad's *Lophornis ornata*, sometimes a filcher, more often feeds at insect flowers largely ignored by other species (PF). Large birds that often maraud, such as *Anthracothonax nigricollis* on Trinidad (PF),

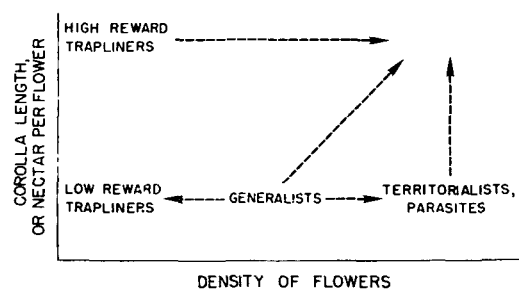


FIG. 1. Community roles of hummingbirds relative to flower dispersion, morphology, and nectar reward.

TABLE 2. *Community roles in relation to morphological characteristics of hummingbird species.*<sup>a</sup>

Role	Size	Required power	Bill <sup>b</sup>	Foot <sup>c</sup>
Low-reward trapliner	Small	Low	Short/medium	Moderate
Filcher	Small	High	Short	Large
Generalist	Medium	Moderate	Short/medium	Moderate
Territorialist	Medium	Moderate/high	Short/medium	Moderate
High-reward trapliner	Large	Moderate/high	Long	Small
Marauder	Large	High	Medium	Small

<sup>a</sup> Values of morphological variables were assigned on the basis of the behavior of well-studied species, in relation to a sample of 124 species taken as representative of morphological patterns in the Trochilidae as a whole (see text).

<sup>b</sup> Unadjusted bill length.

<sup>c</sup> Foot index (see text) adjusted for body weight.

act as territorialists, generalists, high-reward trapliners (their bills are of moderate length), or even flycatchers at other times. Even some birds that normally act as high-reward trapliners become weakly territorial when encountering their flowers in unusually dense clumps (see Wolf *et al.*, 1976).

In the proximal sense, then, what determines a bird's community role at one point in time is its ranking along morphological axes, relative to other bird species present, and the availability of flowers. Nevertheless, most often the ranking will remain more or less consistent, and the bird follows the primary role that its morphology dictates. A principle component analysis of the morphometric data for the 124 species of hummingbirds discussed above (detailed in Colwell, unpublished) shows that species known to follow different typical community roles occupy distinct regions of principal component space. Of course, the dictation of role is not only one-way: In evolutionary terms, surely the office (role) makes the bird, and the role a population most often occupies leads in time to the evolution of morphological and behavioral correlates of that role (see Feinsinger and Chaplin, 1975).

#### COMMUNITY FIDELITY

##### *Principals*

Closely studied communities in the mountains of Costa Rica (Colwell, 1973; Feinsinger, 1976, 1977; Wolf *et al.*, 1976)

and in Trinidad (PF) each maintain year-around populations of one or a few principal species. The foraging of these principals determines the availability of resources to, and hence the foraging patterns of, any immigrant species.

##### *Secondary Species*

As the abundance of flowers of different plant species changes there is a constant turnover of "secondary species" of hummingbirds that immigrate as flowers they can exploit become available and emigrate as those flowers decline to levels too low for efficient foraging (Feinsinger, 1976). While some immigrants are from nearby communities' principal populations, others are chronic migrants, travelling from resource flush to resource flush in annually recurring patterns. Species that typically play roles dependent on clumped moderate flowers are especially migratory, acting as sequential specialists (*sensu* Colwell, 1973) in a series of communities. High-reward trapliners in open habitats must migrate frequently in search of dispersed rich flowers. Finally, many generalists follow opportunistic, highly migratory patterns that take them to two or more geographically disjunct communities each year (Feinsinger, 1976; Wolf *et al.*, 1976). The ecological significance of these fugitive species behaviors, such as the resulting seasonal partitioning of flowers among hummingbirds, is discussed elsewhere (Feinsinger, 1979).

CONVENING HUMMINGBIRD ASSEMBLAGES FROM  
THE COMPONENTS*Islands*

An inquiry into general rules for hummingbird assemblages should begin with islands, which harbor fewer coexisting species than other benign neotropical habitats and in which the basic organizing variables should be most easily discernible (see Morse, 1971; Terborgh, 1973; Diamond, 1975). Although no long-term, in-depth studies of island hummingbirds have yet been concluded, scattered information can be gleaned from several sources (cited below) as well as from the authors' studies on Más Atierra Island (Juan Fernández Archipelago) (RKC) and Tobago (PF). Apparently, communities on isolated islands lack dependent, migratory populations, since moving from resource flush to resource flush would entail migrating from island to island or island to distant mainland (see Lack, 1973, 1976; Feinsinger, 1979). Thus island communities contain principals only, usually two or three species (MacArthur *et al.*, 1972; Lack, 1975). Puercos Island, off the Pacific coast of Panama, supports *Chlorostilbon canivetii*, *Amazilia edward*, and the hermit *Phaethornis anthophilus* (MacArthur *et al.*, 1972). On the mainland, *C. canivetii* is an exemplary low-reward trapliner (Feinsinger, 1976); *Amazilia* is a genus of many territorialists (Stiles and Wolf, 1970; Feinsinger, 1976); and *P. anthophilus*, a moderately large hummingbird with a long, decurved bill, belongs to the genus of quintessential high-reward trapliners (*e.g.*, Stiles, 1975). Thus Puercos evidently supports one low-reward trapliner, one territorialist, and one high-reward trapliner. Coiba Island, much larger, supports in addition the territorialist *Amazilia tzacatl* (see Wolf, 1970; Feinsinger, 1976), but here *A. edward* is rare (MacArthur *et al.*, 1972).

Most lesser Antillean islands support the small *Orthorhyncus cristatus* and the large, longer-beaked *Sericotes holosericeus* (Lack, 1973). On Martinique, *Sericotes* of unknown sex were seen defending territories

at dense moderate flowers on large *Hamelia patens* shrubs, excluding all *Orthorhyncus*; male *Orthorhyncus* acted as generalists or defended peripheral territories at smaller *Hamelia* shrubs, excluding females; female *Orthorhyncus* traplined dispersed *Hamelia* flowers with other dispersed moderate and insect flowers (PF; see also Wolf, 1975; Ingels, 1976). From these observations we predicted wing disc loadings to follow the sequence *Sericotes* > ♂♂ *Orthorhyncus* > ♀♀ *Orthorhyncus*. Table 3, which summarizes data J. Terborgh (personal communication) obtained on Guadeloupe and satellite islets, confirms these predictions.

Many island communities that contain *Sericotes* and *Orthorhyncus* also support a third species, *Eulampis jugularis*, large birds with quite long, sexually dimorphic bills (see Wolf, 1975; Lack, 1976). Both sexes of *Eulampis* are often territorial at rich clumped flowers (Wolf, 1975), but at least females also act as high-reward trapliners at dispersed rich flowers of *Heliconia* spp. and *Centropogon surinamensis* (PF; see Wolf, 1975). In addition to *Sericotes* and *Orthorhyncus*, Grenada supports the high-reward trapliner *Glaucis hirsuta*, although there is some habitat separation (Lack, 1976). The community currently being studied (PF) on Tobago, close to the South American mainland, also supports *Glaucis hirsuta* in addition to *Amazilia tobaci tobaci* (more often a territorialist than a generalist), *Chrysolampis mosquitus* (more often a generalist than a territorialist), occasional *Anthracothorax nigricollis* (marauder and generalist), and, rarely, marauding *Florisuga mellivora*. Few precise data exist on the foraging roles of other Caribbean hummingbirds, but Lack (1973, 1976) suggests that most communities support two species greatly disparate in size, with the larger of the two often having a longer or more decurved bill. The last feature, and the presence of *Heliconia*, *Centropogon*, and other rich-flower plant genera on most Caribbean islands, imply that species-specific, coevolved bird-plant interactions occur. Nevertheless, there is abundant evidence that in many communities the two hummingbird species often meet each



TABLE 3. Weights, wing disc loadings (ratio of weight to a circle whose diameter is wing span), and dominance relations in two species of Lesser Antillean hummingbirds described in text.<sup>a</sup>

	N	Weight (g)	Wing disc loading (g/cm <sup>2</sup> ) <sup>b</sup>	Number of aggressive encounters won against: ♂♂ Ortho.      Unsexed Ortho.      ♀♀ Ortho.
<i>Serriotes holosericeus</i> (♂♂, ♀♀)	7	5.6 18.28 ( $P < .001$ )	0.0330 6.48 ( $P < .001$ )	7      8      3      5
<i>Orthorhynchus cristatus</i> ♂♂	16	2.7 2.98 ( $P < .005$ )	0.0243 1.93 ( $P < .05$ )	0      1      2      5
<i>Orthorhynchus cristatus</i> ♀♀	5	2.3	0.0215	0      0      0      0

<sup>a</sup> Aggressive encounters were tallied in a *Hamelia patens* patch on Martinique; weights and wing disc loadings were obtained from individuals (in the same subspecies) netted on Guadeloupe and its islets by J. Terborgh (personal communication).

<sup>b</sup> Calculated with the formula  $L_{wb} = W/\pi (\ell + 0.404\ell^{0.66})^2$ , where  $W$  is body weight in g and  $\ell$  is wing chord in cm; see Feinsinger *et al.*, 1979.

other at moderate flowers and engage in dominance interactions there (Wolf, 1975; Ingels, 1976; PF).

The most remote islands supporting hummingbirds are the two Juan Fernández Islands, 660 km off the coast of central Chile. Situated in the tropical counter-current, the islands are climatically subtropical. On Más Atierra Island, two species are found: *Sephanoides sephanoides*, indistinguishable from populations along the Chilean coast, and its peculiar endemic congener, *S. fernandensis*. The latter species is remarkably dimorphic, the males weighing about 11 g, the females only 7 g. The smaller *S. sephanoides* is less dimorphic: males weigh about 6 g, females average 4.5 g. A brief field study (Colwell and King, unpublished) showed that male *S. sephanoides* and both sexes of *S. fernandensis* are strongly territorial, while female *S. sephanoides* are low-reward trapliners or generalists. Wing disc loading (or required power output) and an apparently inviolate behavioral dominance hierarchy follow the order of body weights. Both sexes of *S. fernandensis* have very large feet (those of the male are apparently the largest in the Trochilidae) and both sexes consistently perch to feed. All four forms have nearly indistinguishable bill lengths (15-17 mm) and all native hummingbird flowers have very similar, short corollas. Of the seven other species of land birds on Más Atierra, none is an aerial insectivore. Colwell and King (unpublished) speculate that the spectrum of body weights (4.5, 6, 7, and 11 g) reflects size-partitioning of arthropod prey, as commonly occurs among coexisting tyrannid flycatchers (Hespenheide, 1975). Selection for character displacement in body size as a response to arthropod feeding would be intensified by seasonal scarcity of nectar, which apparently characterizes the flora of Más Atierra.

In summary, the instructions for convening a basic hummingbird assemblage are: Given the omnipresent moderate and insect flowers, enter one bird species that can fill low-reward trapliner or generalist roles, one species that can act as a generalist-territorialist. These will combine

to exploit all of the above-named flowers. If rich flowers immigrate along with the birds, after the birds, or evolve along with the birds, allow the larger species (usually the territorialist) to double as high-reward trawler. An alternative: if near the mainland, enter a high-reward trawler as the third species. Finally, if isolation occurs for sufficient time, allow the evolution of sexual dimorphism to fill in unoccupied roles.

#### *Mainland: Forests*

Mainland tropical forests harbor two distinct hummingbird assemblages, understory and canopy (see Snow and Snow, 1972). Although each is considerably more complex than island communities, the basic structure found on islands can be discerned. In the understory, rich dispersed flowers such as those of *Heliconia* spp. dominate the resource base and support numerous high-reward trawlers, especially hermits (Snow and Snow, 1972; Linhart, 1973; Stiles, 1975). Moderate dispersed flowers also exist, attracting generalists. In mature lower montane rain forest at Monteverde, Costa Rica, several species of the plant families Rubiaceae, Gesneriaceae, and Acanthaceae attract the principal generalists *Eupherusa eximia* and female *Lampornis calolaema* (PF; see Feinsinger and Chaplin, 1975). Moderate clumped flowers, which exist primarily in light gaps, attract the same generalists or support territorialists, such as male *L. calolaema* (PF). On riverbanks and in large openings, usually the result of human activity, rich clumped flowers support territorialists (Linhart, 1973; Stiles, 1975). While the phenology of a forest's complete resource base has not been documented, Stiles' (1975) data for *Heliconia* and our observations suggest that total flower numbers vary over the year but not nearly so widely as in open habitats (see below). These fluctuations prompt some shorter-billed principals, such as *Lampornis* and *Eupherusa*, to migrate short distances to adjacent habitats (Feinsinger, 1976), but apparently the absence of dramatic resource flushes discourages highly migra-

tory secondary species. Populations of long-billed birds, whose males may attend year-round leks (e.g., Hilty, 1975), appear to be quite sedentary. Hermits' pronounced insectivory might be one response to what flower shortages do recur, while during flowering peaks considerable nectar in dispersed rich flowers may go unused (PF). The long-term sedentariness of plant and hummingbird populations may ultimately be responsible for the preponderance of rich dispersed flowers, by allowing the continuous evolution of specific relations between those flowers and the high-reward trawlers (see Stiles, 1978).

Potential overlap in resource use, hence competition, among hummingbirds of the forest understory varies with the species. Coexisting hermits (usually two to four species) typically have distinctly shaped bills that equip them for somewhat different sets of dispersed rich flowers (see Stiles, 1975; J. Terborgh, personal communication). Likewise, there is little potential overlap between hermits and shorter-billed species that exploit moderate flowers (Snow and Snow, 1972). Nevertheless, shorter-billed territorialists that defend clumped rich flowers (Linhart, 1973; Stiles, 1975) usurp extensive nectar supplies that would otherwise be available to hermits, which should affect hermit population sizes. Potential overlap among shorter-billed species must also be high at sites like La Selva, Costa Rica, where five such species coexist (Stiles, 1975), although Monteverde forests contain but one or two such species (Feinsinger, 1977). Interference by territorialists at clumped flowers of course decreases the actual (measurable) overlap among shorter-billed species, or between shorter-billed species and hermits, such that when actual foraging patterns are calculated flowers are partitioned quite distinctly among hummingbird species (see Snow and Snow, 1972; Linhart, 1973; Stiles, 1975).

Fewer data have been obtained on hummingbirds of the forest canopy. Flowering trees and epiphytes evidently provide large numbers of dispersed moderate and clumped moderate flowers that attract

many pollinator species (Snow and Snow, 1972). In cloud forest at Monteverde, *Elvira cupreiceps* exploits dispersed moderate flowers of many plant species, while clumped moderate flowers such as the epiphytes *Macleania* spp. and *Cavendishia* spp. (Ericaceae) attract *Panterpe insignis*, an aggressive territorialist that excludes *Elvira* (see also Colwell, 1973; Wolf *et al.*, 1976). A few vines and epiphytes provide dispersed rich flowers that attract high-reward trapliners such as *Helioaster longirostris* on Trinidad (Snow and Snow, 1972), but the abundance and diversity of long-billed birds is considerably less than in the understory. In contrast, many species with relatively short bills converge on flushes of clumped moderate flowers, which fluctuate widely in numbers as different tree or epiphyte species bloom (PF; see Snow and Snow, 1972) and whose lack of specific coevolution with hummingbirds may be dictated by the necessity for large seed crops and short, concentrated flowering peaks (see Janzen 1971b, 1975). Diet overlap among these birds is only temporary, however; canopy communities seem to follow the pattern of maintaining only one or two shorter-billed principals (such as *Elvira* and *Panterpe* at Monteverde), and other birds emigrate in diverse directions when flowers dwindle (PF; see French, 1973; Snow and Snow, 1972). These divergent migration patterns, and pronounced insectivory in large birds such as *Anthrothorax nigricollis* (French, 1973), doubtless alleviate competition for nectar resources. The preponderance of shorter-billed, opportunistic species exploiting moderate flowers resembles the pattern found in open habitats.

#### Mainland: Open habitats

The open tropical habitats whose hummingbirds have been studied originate in disturbances and undergo secondary succession (Feinsinger, 1976; Wolf *et al.*, 1976). Extensive coevolution between particular bird populations and particular plant populations is unlikely; instead, most hummingbirds have relatively short, straight beaks, and most flowers have rela-

tively short, straight corollas. Open habitats on the Cerro de la Muerte support a single principal species, *Panterpe insignis*, which acts as a territorialist or, less often, a generalist (Colwell, 1973; Wolf *et al.*, 1976). Open habitats at Monteverde support two principals, territorial *Amazilia saucerottii* and low-reward traplining *Chlorostilbon canivetii* (Feinsinger, 1976). At both sites dispersed moderate flowers occur consistently throughout the year. Clumped moderate flowers are absent at some times, but extraordinarily abundant at others. At Monteverde, flushes of clumped moderate flowers attract numerous secondary species of territorialists, generalists, and territory-parasites (see Fig. 2), while various moderate dispersed flowers not used by the principals also support secondary species at other times. A similar response occurs on the Cerro de la Muerte but involves fewer species (Wolf *et al.*, 1976), indicating a decrease in hummingbird species diversity at very high elevations (see also Carpenter, 1976; but see Terborgh, 1977; Feinsinger *et al.*, 1979). The diversity of species at montane sites in general probably results from the feasibility of patch-to-patch migration (Feinsinger, 1979).

At successional sites near mature forest, rich clumped flowers also exist. These may support long-billed birds such as *Eugenes fulgens* (Colwell, 1973; Wolf *et al.*, 1976), or they may attract shorter-billed ter-

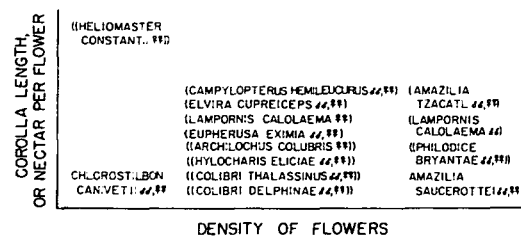


FIG. 2. Hummingbird species and the roles they played in open, successional habitats at Monteverde, Costa Rica (from Feinsinger, 1976). Species without parentheses: Principal species in those habitats. Species in single parentheses: Principal species of nearby communities. Species in double parentheses: Species presumed to be highly migratory. One additional species, and male *Archilochus* and male *Helioaster*, were seen too rarely to be assigned roles.

ritorialists. Since the latter can extract only a fraction of each flower's nectar, however, for them the flowers are operationally "clumped moderate." For example, on Trinidad and Tobago dense clumps of *Heliconia wagneriana* (chord of curved corolla ca. 36 mm) are defended by *Amazilia tobaci* (total culmen length 22-23 mm, straight), which cannot reach the innermost 40-75  $\mu$ l (ca. 61-112 cal) of nectar; each flower secretes but 40-140  $\mu$ l (ca. 61-208 cal) per day (PF and K. A. Jepson, unpublished data). Finally, the few rich dispersed flowers that occur in open habitats support sparse populations of high-reward trapliners such as *Helimaster constantii* at Monteverde or *Helimaster longirostris* on Trinidad, whose 37.5-mm bill (total culmen) suits it for visiting the *Mandevilla hirsuta* flowers described above (PF). In open habitats, high-reward trapliners rarely act as principal species; the abundance of rich flowers drops to zero at some seasons, forcing the birds that exploit them

to emigrate (Feinsinger, 1976). Figure 2 and Table 4 summarize the array of hummingbirds in the Monteverde community studied by Feinsinger (1976).

Thus, flowers in open habitats are partitioned among bird species on the basis of plant species and flower density (Colwell, 1973; Feinsinger, 1976; Wolf *et al.*, 1976). Different foraging heights and flight mannerisms among hummingbirds are partly responsible for this, and also result in the spatial partitioning of clumped moderate flowers among the many species these attract (Feinsinger, 1976). Late in the day, when clumped moderate flowers have lost most of their nectar and come to resemble insect flowers, territorialists abandon them to low-reward trapliners or generalists, effecting temporal partitioning (Feinsinger, 1976). Thus actual resource use by these hummingbirds may overlap relatively little (Feinsinger, 1976; Wolf *et al.*, 1976). Most resource partitioning among the shorter-billed birds is the result of interference

TABLE 4. Attributes of hummingbirds at Monteverde, Costa Rica, diagrammed in Figure 2.

Species, sex <sup>a</sup>	Community fidelity <sup>b</sup>	Role where studied <sup>c</sup>	Culmen from base, mm (N)	Weight, grams	Wing disc loading, g/cm <sup>2</sup>
<i>Amazilia saucerottii</i> ♂♂, ♀♀	P	T	23.2 (119)	4.45 (126)	0.034
<i>Lampornis calolaema</i> ♂♂	(P)	T, M	23.2 (7)	5.60 (7)	0.034
<i>Amazilia tzacatl</i> ♂♂, ♀♀	(P?)	T	25.7 (5)	5.12 (5)	0.035
<i>Philodice bryantae</i> ♂♂	S	F, T	19.6 (5)	3.31 (5)	0.041
<i>Philodice bryantae</i> ♀♀	S	F, T	20.2 (2)	3.42 (5)	0.041
<i>Campylopterus hemileucurus</i> ♂♂	(P)	G <sup>d</sup>	35.6 (14)	11.22 (14)	0.041
<i>Campylopterus hemileucurus</i> ♀♀	(P)	G <sup>e</sup>	38.2 (17)	8.86 (17)	0.038
<i>Elvira cupreiceps</i> ♂♂	(P)	G	18.2 (3)	3.22 (3)	0.030
<i>Elvira cupreiceps</i> ♀♀	(P)	G	19.0 (2)	3.02 (3)	0.031
<i>Lampornis calolaema</i> ♀♀	(P)	G	23.0 (2)	4.23 (2)	0.030
<i>Eupherusa eximia</i> ♂♂	(P)	G	23.0 (43)	4.48 (50)	0.028
<i>Eupherusa eximia</i> ♀♀	(P)	G	22.8 (29)	2.97 (31)	0.029
<i>Archilochus colubris</i> ♀♀	S	G	21.0 (2)	2.93 (2)	0.035
<i>Hylocharis eliciae</i> ♂♂, ♀♀	S	T, G	20.9 (5)	3.59 (6)	0.034
<i>Colibri thalassinus</i> ♂♂, ♀♀	S	G	26.8 (19)	5.24 (24)	0.030
<i>Colibri delphinae</i> ♂♂, ♀♀	S	G	20.0 (1)	7.27 (1)	0.031
<i>Chlorostilbon canivetii</i> ♂♂	P	L	17.5 (6)	2.62 (7)	0.026
<i>Chlorostilbon canivetii</i> ♀♀	P	L	19.0 (12)	2.48 (12)	0.026
<i>Helimaster constantii</i> ♀♀	S	H	41.0 (1)	7.16 (1)	0.035

<sup>a</sup> Where both sexes are indicated for one set of values, sexes were not distinguished.

<sup>b</sup> P = principal species in community studied; (P) = principal in a nearby community; S = presumed to be a highly migratory species.

<sup>c</sup> T = territorialist; M = marauder; F = filcher; G = generalist; L = low-reward trapliner; H = high-reward trapliner.

<sup>d</sup> High-reward trapliner and territorialist in its preferred habitat.

<sup>e</sup> High-reward trapliner in its preferred habitat.

competition, however. Excepting the few high-reward trapliners, potential diets of open-habitat hummingbirds overlap greatly. Thus territorialists, by controlling rich resources, may compete severely with other species and curtail their populations. Contrary to previous interpretation (Feinsinger, 1976), low-reward trapliners may depress territorialist populations in turn, by more efficiently exploiting dispersed moderate flowers that otherwise might support some of the less efficient territorialists (PF). Fluctuations in hummingbird species diversity and numbers, as well as niche parameters, track shifts in the resource base, and few nectar resources in open habitats go to waste (Feinsinger, 1976). In short, the hummingbirds of open tropical habitats may be the premier example of a food-limited animal guild.

#### CONCLUSIONS AND PROSPECTS

##### *Parallels with other nectar-feeding birds*

We have ignored organization among other neotropical nectar-feeding birds simply because the neotropics contain no other distinctive groups of nectar-feeding birds of comparable importance. Although tanagers (Thraupidae), honeycreepers (Coerebidae), and certain other passerine and non-passerine birds consume nectar and even flowers that otherwise might be available to hummingbirds, populations of few non-hummingbirds are more dependent on nectar supplies than on fruit and insects (Snow and Snow, 1971). The few coerebids that are highly nectarivorous, such as flower-piercers *Diglossa* (Lyon and Chadek, 1971; Colwell *et al.*, 1974; Wolf *et al.*, 1976), the orangequit *Euneornis campestris* (Lack, 1976), and the bananaquit *Coereba flaveola* (Snow and Snow, 1971), can be classed operationally with generalist hummingbirds. Although they use many plants also available to hummingbirds, they tend to visit sets of flowers spatially distinct from those most heavily exploited by hummingbirds (PF; see Colwell *et al.*, 1974).

On continents lacking hummingbirds, sets of passerines that feed on nectar are

more tightly organized, apparently around the resource-density parameter that determines much of hummingbird community structure. Large species of African sunbirds (Nectariniidae) defend territories at clumped flowers; while smaller subordinates wander among dispersed or less rewarding flowers (Gill and Wolf, 1975). In Australia, large species of honeyeaters (Meliphagidae) likewise exploit clumped flowers and displace smaller species to scattered flowers (H. A. Ford, unpublished). The onset of such studies on Old World nectar-feeders (*e.g.*, Carpenter, 1978) is encouraging, although continued in-depth study is needed before detailed intercontinental comparisons can be made.

##### *Parallels with insect flower-visitors*

Comparisons between hummingbirds and insects are complicated by (1) many insects' exploitation of pollen along with, or instead of, nectar (Michener, 1974; Gilbert, 1975) and (2) complex social organization among bees, the most numerous flower-visitors (Michener, 1974; Heinrich, 1976a, 1976b). Nevertheless, resource characteristics that organize hummingbirds also affect most insects. For example, many hawkmoths (Cruden, 1970; Cruden *et al.*, 1976; Linhart and Mendenhall, 1977) and butterflies (Gilbert, 1975) act as high-reward trapliners among flowers with which they are highly coevolved. Like their hummingbird counterparts, coexisting butterflies (Schemske, 1976) and bumblebees (Brian, 1957; Heinrich, 1976a) select different flowers based on correspondence between proboscis and flower morphologies. In contrast, many small, social bees occupying open habitats overlap extensively in flower preference; among these, as among shorter-billed hummingbirds, interference competition leads to partitioning of floral resources by flower density (Johnson and Hubbell, 1975).

This suggests that the numerically dominant flower type available to bees, and the dominant community role played by bees, vary with habitat in the fashion de-

scribed for hummingbirds. Indeed, the small, eusocial bees (and certain large, unspecialized solitary bees) with generalized, overlapping food preferences dominate second-growth neotropical habitats and abundantly flowering trees in the forest canopy (Johnson and Hubbell, 1974, 1975; Frankie *et al.*, 1976; Hubbell and Johnson, 1977; A. B. Bolten, personal communication), while specific, highly coevolved relationships between traplining solitary bees and particular plant species are most numerous in those relatively stable habitats where plants do not undergo pronounced flowering bursts, such as forest understory or subcanopy (Dressler, 1968; Dodson *et al.*, 1969; Janzen, 1971a). Community-wide studies in progress (A. B. Bolten, personal communication; G. W. Frankie, personal communication) might reveal additional organizational similarities between nectar-feeding insects and hummingbirds. At present, though, more striking parallels can be found in the literature on consumers having little to do with nectar (see below).

#### *Rules for resource partitioning*

Differences in foraging zone and flight mode, which contribute to the partitioning of flowers among hummingbird species, affect resource partitioning in other birds as well (*e.g.*, Root, 1967; Stallcup, 1968; Morse, 1970; Williamson, 1971; Cody, 1974; Hespenheide, 1975). Coexisting desert lizards also segregate by means of foraging mode (Pianka, 1973). Other lizards consume similar foods at different times of the day (Pianka, 1973) or year (Fuentes, 1976), effecting temporal resource partitioning like that experienced by some hummingbird species. Other comparisons between hummingbirds' resource partitioning and partitioning among other animals are made elsewhere (Feinsinger, 1976; see Schoener, 1974 for a general discussion).

In more general terms, diets of sympatric hummingbirds differ because (1) their beak morphologies equip them for distinct species of flowers or, if beak morphologies are similar, because (2) their interference

abilities or exploitation efficiencies equip them for exploiting different densities of flowers. The first condition occurs commonly not only in other nectar-feeders (*e.g.*, Brian, 1957), but also in many other animal groups (*e.g.*, Heatwole and Davis, 1965; Lack, 1971; Liem and Osse, 1975). The second condition occurs in a wide variety of organisms ranging from starfish (Menge and Menge, 1974) and limpets (Stimson, 1970) to gut parasites (Holmes, 1973) and plants (Sharitz and McCormick, 1973). Colwell and Fuentes (1975) review other examples, while Miller (1967), Morse (1974), and Case and Gilpin (1974) review the general theory.

#### *Assembly rules and community convergence*

Diamond (1975) has proposed the intriguing concept of "assembly rules" that predict the sequence of bird species added to a community expanding from 1, 2, . . .  $N$  species. We have likewise defined "assembly rules" for hummingbirds, starting with the basic pair of territorialist and low-reward trapliner or generalist, adding one high-reward trapliner, then adding various secondary species as flower types and opportunities for migration allow. "Assembly rules" (Diamond, 1975) properly refer not only to the sequence of roles added as species richness increases but also to the precise sequence of species that arrive. Except for the Lesser Antilles, we cannot yet predict species sequences for hummingbirds, partly because many hummingbird species have limited geographic ranges. But the potential for discovering assembly rules among hummingbirds in archipelago-like regions, say the Andes, clearly exists. The hypothesis testing we have attempted here (Table 3) and elsewhere (Feinsinger *et al.*, 1979) is hopefully but a precursor of the type of predictive studies (*e.g.*, Diamond, 1975; Pulliam, 1975) that could be performed on hummingbird communities.

On a broader scale, the relative constancy of community structure (spectrum of roles) from site to site and role-playing by ecological analogues in disparate communities finds many parallels in other con-

sumer groups. Desert rodent communities (Brown, 1975) and lizard communities of Mediterranean climates (Fuentes, 1976) support superficially similar arrays of species filling ecologically equivalent roles even though their species composition varies from site to site. Community convergence also occurs in many insect-eating and seed-eating birds (Cody, 1975). McNab (1971), who defined bat roles based on both foraging habits and morphology, found approximately one principal species of bat per role on Trinidad and elsewhere. Karr and James (1975) discuss morphological and behavioral convergence of birds filling similar roles in different communities. Furthermore, Karr and James (1975) demonstrate correlations among morphological variables with community role over a broad range of bird species and communities. Their approach and results parallel our multivariate analysis of hummingbird morphology and its relation to role. We conclude that hummingbirds, whose ecological and evolutionary relationships with their food resources are so readily obtainable, are capable of illuminating a great many principles of community organization.

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