Competition and community structure: A null model analysis of the hummingbird assemblage on the slope of Volcan de Colima, Mexico

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The hummingbird assemblage on the slope of Volcan de Colima, Mexico, comprises 21 species. The observed species packing along the culmen length dimension was compared with those derived from a simple non-interactive null model. When applied in the four main altitudinal zones (species numbers range from 9 to 11), the null model analysis suggests that the most abundant species in the communities are more similar in culmen lengths than expected. This agrees with the finding that most of the resource flowers are also clustered within a narrow range of corolla tube depths. On the other hand, when the community was divided into guilds, it was observed that all-year residents tend to be more divergent than predicted by the null model, while migrants do show morphological clustering. Also, hummingbirds defending feeding territories were observed to converge in their morphology, while trapliners, feeding on scattered resources, diverged in their culmen lengths more than predicted by the null model. It is concluded that morphology-based null models are not very effective in detecting interspecific competition affecting species coexistence.

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Introduction

Competition takes place when two or more species exploit the same resources and these are in short supply, and/or the species prevent each other from using such resources, even if they are not in short supply (Birch 1957). But how much does competition — exploitation and interference — affect species composition in species assemblages?

In this paper I shall analyse community organization in a group of tropical nectarivorous hummingbirds (Des Granges 1977, 1978, Des Granges & Grant 1979). It has frequently been reported that competition exists among hummingbirds (Feinsinger 1976, 1978, Feinsinger & Colwell 1978, Kodric-Brown & Brown 1978, Gill 1978, Montgomerie 1979, Montgomerie & Gass 1981) and the results of field experiments support this conclusion (Pimm 1978). Species packing in hummingbird assemblages can best be analysed on the culmen length dimension, as culmen length reflects the ability of hummingbirds to probe nectar from the corollas of different flowering plants. Furthermore, there is a growing body of observational evidence that body size determines the outcome of interspecific interference, large specimens frequently being the winners (Feinsinger 1976, Wolf 1978, Des Granges 1978).

A simple null model will be applied to examine whether interspecific competition is manifested as greater differences in culmen length among coexisting hummingbirds than can be expected on the basis of random draws from the appropriate species pool. As there is a large body of evidence for competition in hummingbirds, it is particularly interesting to examine whether the resolution of a simple null model is sufficient to reveal the presence of competition in assemblages of these birds.

Material and methods

The data analysed here were presented by Des Granges (1977, 1978, Des Granges & Grant 1979). He observed the flower visits of 21 hummingbird species for 8 months in four altitudinal zones on the slope of Volcan de Colima, Mexico (Table 1); not all the species were found in all the zones. As the culmen lengths of the species are known (Table 1), we can ask whether the data indicate that the assembly of hummingbird species is affected by interspecific competition for nectar resources. The original data are reported for altitudinal zones and I therefore prefer to keep the hummingbird assemblages observed in the zones as the basis for my community analyses.

In the following I will make two analyses. First, I will examine the culmen length spacings observed among the species in the four altitudinal zones. The species are arranged in descending order of abundance (Table 1). The average culmen length difference observed among the *k* ($k = 2,3,\ldots, S-2$) most abundant species is calculated as

$$D = \sum_{i}^{k-1} \sum_{j=i+1}^{k} C_i - C_j / [0.5k(k-1)] \qquad \text{(Ranta 1984)},$$

where C_i and C_j refer to the culmen lengths of species *i* and *j*. Next, all possible *k*-species combinations are taken out of the total set of *S* species. The average spacings between all species pairs in the possible *k*-species groups are computed in order to calculate the expected spacings, and the standard deviation of the mean is also calculated. Dividing the difference between observed and expected values by the standard deviation, we obtain a standarized *z* score, which tells how many standard deviation units the observed average difference among the *k* species lies to the right (positive *z* values, divergence of the species in accordance with the competition hypothesis) or to the left (negative values, morphological clustering of the species) of the mean of all possible spacings.

Secondly, the species are classified into different ecological groups (Table 1). Residents are present in the habitat all the year round, having a high status in interspecific interactions. Residents form the core of the guild the additional species depending on the seasonal availability of food. Most resident species prefer to feed on tubular flowers, aggressively preventing other hummingbirds from feeding. Some subordinate species feed mostly on cup-shaped flowers. Tropical wanderers are trapliners and they are sequential generalists, feeding on tubular and cup-shaped flowers that cannot be exploited by the residents. Migrants are small birds and thus tend to be subordinate to residents and wanderers. Migrants are territorial and use abundant, and/or sporadically available flowers, mostly cup-shaped, that are not used by the residents or wanderers. Territorial species exploit clusters of flowers and trapliners feed on scattered flowers (Des Granges 1978: 229–231). I therefore asked whether spacing by culmen lengths among the *k* resident species (or wanderers, or migrants, or territorials, or trapliners) is greater than the average spacing expected among any *k* species drawn randomly from the *S* species.

The first analysis is considered necessary as it is claimed by Wiens (1982) that abundance of species should be incorporated into the numerical methods estimating observed vs. expected spacings among coexisting species. In the second analysis the migratory and foraging strategies of the species are contrasted with the morphology predictions of the null model. In both analyses the expectations were calculated on the basis of all *k* species combinations drawn from the total of *S* species available in the given altitudinal zone.

Results

In Fig. 1 the *z* scores obtained are plotted against an increasing number of species (*k*) ranked by their abundance. It is evident that the most abundant species in the four zones on the slope of Volcan de Colima tend to be more similar in their culmen lengths than is expected on the basis of the null model. In view of the competition arguments (Des Granges 1977, 1978, Des Granges & Grant 1979), the results seem unexpected. Some interesting patterns emerged, however, when the observed and expected culmen length spacings were calculated for different migratory and foraging strategies (Table 2): Most of the culmen length spacings that accord with the competition hypothesis are in the ecological groups of trapliners and residents, while in migrating and territorial hummingbirds all the observed spacings are smaller than the expected values. However, less than half of the differences (8/20) are statistically significant or indicative (Table 2).

Des Granges (1977, 1978, Des Granges & Grant 1979) suggests, on the basis of field observations, that the organization of the hummingbird community at Volcan de Colima is maintained by interspecific competition. In contrast, my abundance-based analysis of culmen length spacings suggests no competition among the most abundant species (Fig. 1). Rather, those species are morphologically closer to each other than can be expected from the null model. The conflicting results may be explained in various ways. Either interspecific competition is not manifested as morphological differentiation among coexisting hummingbird species, or my null model does not reveal interspecific competition.

Table 1. Ecological status and abundance rank of the 21 hummingbird species in the four main zones on the slope of Volcan de Colima, Mexico. R = resident, W = wanderer, M = migrant, Te = territorial, Tr = trapliner. Species abundances are given as the ranking, in descending order, for each of the four habitats; they are based on the pooled observations of the five census periods as reported by Des Granges (1978; table 3, culmen lengths are taken from his table 2).

	Exposed Culmen mm	Arid Thorn Forest			Riparian Gallery Forest			Arid Pine-Oak Forest			Humid Pine-Oak Forest		
Atthis heloisa	12.2	–	–	–	–	–	–	W	Tr	7	–	–	–
Tilmatura dupontii	12.9	–	–	–	W	Tr	6	–	–	–	–	–	–
Chlorostibolon cavivetii	14.2	W	Tr	8	R	Tr	2	–	–	–	–	–	–
Stellula calliope	14.9	–	–	–	–	–	–	M	Te	5	M	Te	6
Selasophorus rufus	16.8	M	Te	5	–	–	–	M	Tr	9	M	Te	4
Hylochoris leucotis	16.9	–	–	–	–	–	–	R	Te	1	R	Te	2
Selasophorus platycercus	18.0	W	Te	7	W	Te	9	W	Te	2	W	Te	1
S. sasin	19.1	–	–	–	–	–	–	M	Tr	11	W	Te	8
Colibri thalassinus	19.1	–	–	–	–	–	–	–	–	–	W	Tr	3
Amazia beryllina	19.3	W	Te	10	W	Te	5	R	Te	3	W	Tr	9
Calothorax lucifer	20.3	W	Te	2	–	–	–	W	Tr	10	–	–	–
Cynanthus latirostris	20.4	R	Te	1	W	Tr	4	–	–	–	–	–	–
Lampornis amethystinus	21.1	–	–	–	–	–	–	W	Tr	4	W	Tr	7
Amazilia rutila	21.3	W	Tr	9	R	Te	1	–	–	–	–	–	–
A. violoceps	22.3	W	Tr	4	W	Tr	8	–	–	–	–	–	–
Lampornis clemenciae	24.5	–	–	–	–	–	–	W	Tr	8	–	–	–
Eugene fulgens	26.1	–	–	–	–	–	–	R	Tr	6	R	Tr	5
Heliomaster constantii	34.2	R	Tr	3	W	Tr	10	–	–	–	–	–	–
Phaeothornis superciliosus	39.3	–	–	–	W	Tr	7	–	–	–	–	–	–
Archilochus colubris	16.4	M	Te	6	M	Te	3	–	–	–	–	–	–
A. alexandri	19.6												

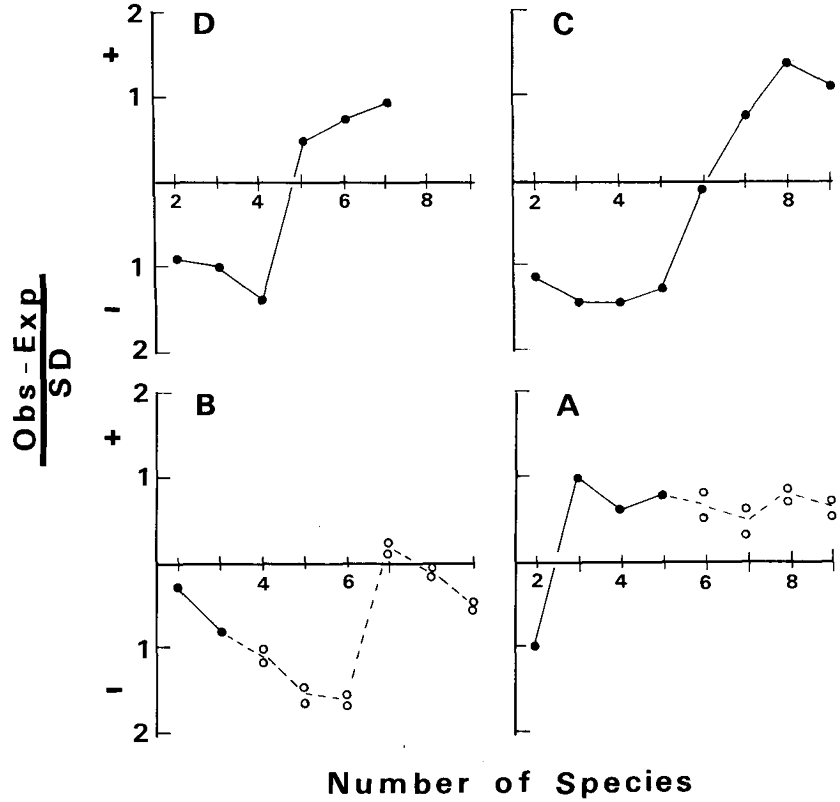

Fig. 1. Culmen length spacings among hummingbird species in the four altitudinal zones (A-D, see Tables 1 and 2) on the slope of Volcan de Colima, Mexico (the zones are arranged from the top (D) to the base (A) of the slope). The culmen length spacings (negative values indicate closer spacing than expected, positive values wider than expected spacings) are given as a standarized *z* score (= (OBS–EXP)/SD, see p. 79) and plotted against increasing number of species (*k*), ranked in order of descending abundance. In the lowest habitats the end of the *z* graphs (broken line, open dots) is uncertain as the two *Archilochus* species are pooled in the field observations (Table 1, and Des Granges 1978).

Discussion

In analyses of morphological spacing (= species packing, size ratios, character displacement) with null models, the availability of the resources is not usually taken into account (Harvey et al. 1983). The single exception is the analyses made by Pulliam (1983). The fact that abundant hummingbird species tend to have similar culmen lengths suggests that most of the resources (in terms of corolla tube depths) are also clustered within a narrow range (Fig. 7 in Des Granges 1978 supports this conclusion). It is possible to quantify the availability of nectar for hummingbirds in tropical flowers of differing corolla tube depths, and as the energy demands of different-sized hummingbirds can be estimated fairly accurately (Hainsworth 1978, Feinsinger et al. 1979, Gass & Montgomerie 1981), more realistic null models can be constructed with algorithms incorporating these variables.

A community of tropical hummingbirds may be divided into guilds, here distinguished by differing migratory strategies. Migrants arriving when resources are becoming abundant show a tendency to morphological clustering, while residents (at least in the Arid Thorn Forest and Humid Pine-Oak Forest) are morphologically divergent in accordance with the theory of competition. The other options, associated with the dominance status of a hummingbird, are to have a territory and defend its resources, or to be subordinate and utilize scattered resources. It is interesting that territorial hummingbird species do not differ in culmen lengths (in fact they are more similar than expected by random draws), while trapliners do. Thus, interference competition does not seem to have led to morphological differences among coexisting territorial species. The morphological closeness of territorial species is understandable, if resource flowers rich in nectar occur in clusters having a patchy distribution, and if they are indiscriminately occupied by any of the territorial species. On the other hand, exploitative competition among trapliners leads to greater differences in their culmen lengths than would be expected.

Recently, much effort has been devoted to discovering whether data on species distributions can prove that interspecific competition operates in structuring animal communities. Difficulties arise in interpreting the role of competition, for real communities cannot always be distinguished from non-interactive null communities (Simberloff 1978, Connor & Simberloff 1978, 1979, Strong et al. 1979, Strong 1980). Some

Table 2. Observed and expected culmen length spacings among hummingbird species in different ecological groups on the slope of Volcan de Colima, Mexico. Habitats, abbreviated as A = Arid Thorn Forest (*S* = 11) B = Riparian Gallery Forest (*S* = 11), C = Arid Pine–Oak Forest (*S* = 11), D = Humid Pine–Oak Forest (*S* = 9), *z* score, n = number of *k* species combinations out of the total of *S* species observed at each habitat, *P* = statistical significance. The cases in which the observed spacings accord with the theory of competition are indicated with >.

Habitat	*k*	OBS		EXP	*z*	n	*P*
Residents							
A	2	13.8	>	5.2	1.691	55	0.045
B	2	7.1		8.6	−0.203	55	0.420
C	3	6.1	>	4.7	0.670	165	0.251
D	2	9.2	>	3.5	1.974	36	0.024
Migrants							
A	3	2.1		5.2	−0.783	165	0.217
B	2	3.2		8.6	−0.718	55	0.236
C	3	2.8		4.7	−0.875	165	0.191
D	2	1.9		3.5	−0.569	36	0.285
Wanderers							
A	6	3.4		5.2	−0.817	462	0.207
B	7	10.9	>	8.6	0.987	330	0.162
C	5	5.5	>	4.7	0.638	462	0.262
D	5	2.1		3.5	−1.084	127	0.139
Territorials							
A	7	2.0		5.2	−1.818	330	0.035
B	5	2.3		8.6	−1.879	462	0.030
C	4	2.4		4.7	−1.389	330	0.082
D	6	1.9		3.5	−1.617	84	0.053
Trapliners							
A	4	10.2	>	5.2	1.583	330	0.057
B	6	12.9	>	8.6	1.529	462	0.063
C	7	5.6	>	4.7	1.051	330	0.147
D	3	4.5	>	3.5	0.489	84	0.312

authors (Grant & Abbott 1980, Hendrickson 1981, Alatalo 1982, Diamond & Gilpin 1982, Gilpin & Diamond 1982) suggest that null models are insufficient for the purpose (guild structure neglected, effects of competition incorporated into the constraints of the models, inefficient Monte Carlo simulations applied, autecological details ignored, and so forth).

The present results demonstrate that even in an ecologically coherent group of species, such as hummingbirds, null models like mine may favour noncompetitive explanations, if guild structure (migratory and foraging strategies) is not taken into account. Furthermore, neglect of the frequency distribution of the available resources will most probably lead to observations which show that abundant species are clustered by their morphological characters. Thus, the data sets used by several authors for null models are in many cases too incomplete for really efficient tests. Fuller field data would allow a better estimate of the role of competition than has been possible up to now.

One further example will suffice to stress my point. In a recent paper on the assembly of temperate North American hummingbird communities, Brown & Bowers (1985) applied a set of well-designed null models and found that the coexisting species are convergent: similar in bill length, body weight and wing length. Yet, in the North American literature, dealing with detailed observations of the ecological behaviour of the hummingbirds, few, if any, doubts are expressed that these species do in fact compete (Feinsinger 1976, 1978, Lyon et al. 1977, Feinsinger & Colwell 1978, Kodric-Brown & Brown 1978, Gill 1978, Montgomerie 1979, Montgomerie & Gass 1981), and the results of field experiments support the generally held view (Pimm 1978, Gill & Wolf 1979, Pimm et al. 1985).

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Selostus: **Kolibriyhteisön rakenteesta Meksikossa**

Meksikossa Volcan de Colima -vuoren rinteillä tutkittu kolibriyhteisö koostui 21 lajista. Tutkimuksen tarkoituksena oli selvittää ilmeneekö lajien välinen kilpailu suurempina nokanpituuseroina kuin satunnaisuuden perusteella voisi olettaa. Analyysin mukaan runsaimpien lajien nokanpituudet olivat odotettua samankaltaisempia. Tämä sopii hyvin siihen, että suurin osa ravintokohteina käytetyistä kukista sijoittuu teriön pituudeltaan varsin lähelle toisiaan. Kun yhteisö jaettiin kiltoihin, havaittiin, että paikkalintujen nokanpituudet vaihtelivat enemmän kuin nollahypoteesi ennusti. Sen sijaan muuttavien lajien nokanpituudet muodostivat tiiviin ryhmän. Ravintoreviirejä puolustavat lajit olivat morfologialtaan samankaltaisia, kun taas hajallaan olevia resursseja käyttävät lajit erosivat nokanpituudeltaan enemmän kuin nollahypoteesi ennusti. Kirjoittaja toteaakin, että morfologiaan perustuvat nollahypoteesit eivät ole erityisen tehokkaita paljastamaan lajien välisen kilpailun vaikutuksia yhteisön rakenteeseen.

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