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Vertical Stratification of Hummingbird Pollinated Plants in Relation to Corolla Length

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Abstract

For members of feeding guilds to co-exist in the same community, species must partition niches to avoid competition. In Tropical Lower Montane Wet Forest, hummingbirds are an important and numerous pollinators, suggesting a large number of niche partitioning mechanisms. Hummingbirds are often tightly co-evolved with the plants they pollinate, having bill lengths corresponding to the length of the flower they pollinate. It is proposed in this study that there is a relationship between heights of hummingbird pollinated plant and length of flower corolla. It is hypothesized that short corolla flowers will exist in some strata and long corolla flowers in other strata. This would indicate vertical microhabitat partitioning of hummingbird resources. This study measured vertical height and flower corolla length of 18 hummingbird pollinated plant species in the Monteverde Cloud Forest Preserve (MVCFP) and Biological Station forest in Costa Rica, covering ~ 40, 000m². Simple linear and polynomial regressions of plant height and corolla length showed no significant correlation. This suggests that vertical microhabitat partitioning is not affecting hummingbird-pollinated plants and that other mechanisms for niche partitioning in hummingbirds, such as differences in foraging behavior, account for the ability to co-exist. This study also examined flowering phenology of hummingbird-pollinated plants in the MVCFP. The number of flowers in bloom on each species was recorded for the 28th of October and 7th and 15th of November in ~16, 000m² area. This data was compared to October and November flowering phenology data from 1981-2 (Linhart et al. 1987).

Resumen

Las especies que son miembros de los mismos gremios que coexisten en la misma comunidad deben repartir esos nichos para evitar competencia. En el bosque nuboso tropical, hay muchos colibríes que actúan como polinizadores importantes y por eso es posible que haya muchas formas de dividir los nichos. En muchos casos, los colibríes presentan una relación coevolutiva específica con las plantas que polinizan, teniendo longitudes de pico que corresponden a la longitud de la flor que polinizan. Este estudio propone que hay una relación entre la altura de las plantas polinizadas por colibríes y la longitud de las corolas de las flores. Se propuso la hipótesis de que las flores con corolas cortas se encontrarían a ciertas alturas y las de corolas largas a otras alturas. Esto indicaría que los colibríes dividen los recursos del hábitat en niveles verticales. Este estudio midió la altura vertical y la longitud de la corola en 18 plantas polinizadas por colibríes en la reserva del bosque nuboso de Monteverde y el bosque de la estación biológica en Costa Rica; el estudio cubrió unos 40,000m². Las regresiones lineales y polinomiales no mostraron diferencias significativas entre las dos variables. Es posible que la relación entre colibríes y sus recursos de néctar sea más general de lo que se había asumido en la hipótesis y haya otras razones para las divisiones de nichos en colibríes, como diferencias en el comportamiento de forrajeo. Este estudio también midió la fenología de plantas polinizadas por colibríes en la reserva del bosque nuboso de Monteverde. En cada especie de

planta, el número de flores abiertas registradas el 28 de octubre, el 7 y el 15 de noviembre en un área de unos 16, 000m². Estos datos se compararon a datos similares de fenología de floración en octubre y noviembre de 1981 y 1982 (Linhart et al. 1987).

Introduction

Tropical forests are characterized by high levels of structural complexity and stratification. This stratification extends vertically, dividing the forest into strata often categorized as understory, sub-canopy and canopy (Richards 1996). Plants in different vertical strata are adapted to cope with the differing abiotic and biotic conditions (Bawa 1990). In flowering plants these adaptations include differences in types of flowering structures, flowering phenology and pollination mechanisms. Flowers are thus adapted morphologically to maximize pollination success. Consumers of pollination rewards such as nectar adapt to exploit these resources most effectively (Bawa 1990). Some pollinators use a generalist foraging strategy, while others have evolved more specific relationships with a certain plant (Murray et al. 2000). Thus, in cases of co-evolution, it has been suggested that plants and their pollinators reciprocally influence abundances in certain vertical strata (Bawa 1990).

In tropical montane cloud forests of Monteverde, Costa Rica, different pollinator guilds do in fact specialize in different strata (Murray et al. 2000). In these forests hummingbirds are relied upon as pollinators because colder temperatures limit insect and bats activity. In fact, hummingbirds make up the largest group of pollinators in tropical montane cloud forests (Linhart et al. 1987, Stiles and Skutch 1989). Hummingbirds are known pollinators in the understory and sub-canopy as well as on certain epiphytic species in the canopy (Murray et al. 2000). Generally, a more diverse set of resources will beget a more diverse set of resources exploiters (Gaston 2000). The large number of hummingbird dependent plants, and thus nectar resources, in cloud forests allows for a large number of hummingbird species to reside in the community (Stiles and Skutch 1989). Because of their high species richness in the cloud forest, it is likely that hummingbirds have evolved many ways to partition niches to avoid interspecific competition, including vertical habitat partitioning. In fact, it has been proposed that hummingbirds reciprocally interacting with their source of nectar have co-evolved so that different plants will be limited to certain strata to minimize competition (Hilty 1994).

Hummingbird morphology, behavior and population ecology are influenced by their source of nectar. For example, floral tube length and shape are often closely linked to bill length and curvature of their hummingbird pollinator, conferring a tightly coevolved relationship (Hilty 1994, Stiles and Skutch 1989). Bill length can usually be categorized as short or long while flower corolla length can also be divided into short and long categories (Linhart et al. 1987). According to Busby (2000) the cloud forests of Monteverde, Costa Rica contain two ecologically separate groups of hummingbird-pollinated plants with their corresponding pollinators. There are plants that have short to medium corollas and are pollinated by several species of short-billed hummingbird, and plants that have long corollas and are pollinated by hummers with a corresponding long bill shape. Complementary data suggests that there are characteristic hummingbird-pollinated species that inhabit the under-story, sub-canopy and canopy

(Stiles 1978). Yet, within these large spatial categories, vertical partitioning in microhabitats, or smaller strata, has not been shown (Haber 2000).

In Monteverde, studies have been conducted comparing the effects of vertical height on hummingbird species visitation to a nectar source (Czerniski 2001, Feely 1997, Grossman and Trachy 2000, Winchell 2000). These studies placed feeders at different heights in the canopy and measured numbers of visitations by hummingbirds with different lengths of bills. Results show no clear pattern, but suggest stratification at some levels. For example, Winchell (2000) showed that some species of hummer only forage in the under-story and others only in the canopy. Feely (1997) showed a preference of one species for the canopy.

These studies suggest vertical partitioning of habitats, yet, do not provide concrete evidence for vertical stratification. Further study in vertical habitat partitioning of hummingbird-pollinated plants is needed. It is expected that if hummingbirds were co-evolved with a certain plant or set of plants, one would find plants at vertical heights that have heights corresponding with the niches of their pollinators. Yet it has not been shown concretely whether plants pollinated by short billed hummingbirds only grow within specific strata and long billed in others, consequently dividing the forest into vertical microhabitats. Thus, this study measured corolla length of hummingbird pollinated flowers and compared it to the height of the plant in the tropical montane cloud forests of Costa Rica. It was hypothesized that there would be a correlation between these two factors, supporting the idea of microhabitat partitioning of hummingbirds in a vertical spatial gradient. The species used in this study were only those in bloom in October and November, and thus flowering phenology impacted the results. Consequently, this study also includes a measure of flowering phenology.

Methods and Materials

Study Site

This study was carried out in Tropical Lower Montane Wet Forest behind the Monteverde Biological Station and at the Monteverde Cloud Forest Preserve (MVCFP) of Monteverde, Puntarenas, Costa Rica.

Methods

Overall, ~ 11,000m² in the Biological Station forest and ~ 31, 000m² in the MVCFP was censused. The trails in the reserve censused were Sendero Nuboso, Pantanoso, Chomogo, Roble, George Powell and Wilford Guindon. Data were collected for three weeks in late October and early November 2004. Heights off the ground and corolla length were measured for every hummingbird-pollinated plant in bloom that was within two meters of the trail edge. This was done with a measuring tape and calipers. Corolla length was defined as the length of the corolla tube that was enclosed entirely. Sections with flaps that exposed the inner flower were excluded. These data were recorded for a total of 24 hummingbird pollinated flower species. However, only 18 were analyzed in this study due to insufficient data for the other species. The sub-canopy and canopy species were identified with binoculars. Height was estimated

using a proportional methodology comparing a known height to an unknown height. Corolla length was measured from flowers found below the canopy plant.

Phenology

Flowering phenology data were recorded for ~16,000m² in the MVCFP on the 28th of October, the 7th of November and the 15th of November. For each day, the species and number of open flowers were recorded. The average of the data from the 7th and the 15th of November were taken to come up with a single value for November. These data were graphically compared to monthly flowering phenology data taken in 1981 and 1982 in transects within the same area (Linhart et al. 1987, Zuchowski pers. comm.) In the earlier study, they covered 16, 470m². Their study, unlike this study, included specific areas that encompassed tree-fall gaps and larger disturbed area as well as primary forest. Since 1981 – 1982 the habitat composition has fluctuated in terms of amount and size of gaps and disturbed areas and thus the data were not compared statistically. The species included in my study were all species studied by Linhart et al (1987).

Results

Eighteen species of hummingbird-pollinated plants were studied, seven species with short corollas (< 3.0cm) and 11 with long corollas (> 3.0cm) as defined by Linhart et al. (1987) due to the differential usage of plant species adapted for hummingbird pollination. Species from five families were found (Acanthaceae, Campanulaceae, Gesneriaceae, Malvaceae and Orchidaceae as well as one unidentified species (See Table 1). Simple linear regressions showed no significant correlation between average corolla length and average vertical height (Fig. 1). A polynomial regression, to test whether certain corolla lengths favored more than one height, showed a more promising trend but was still not statistically significant.

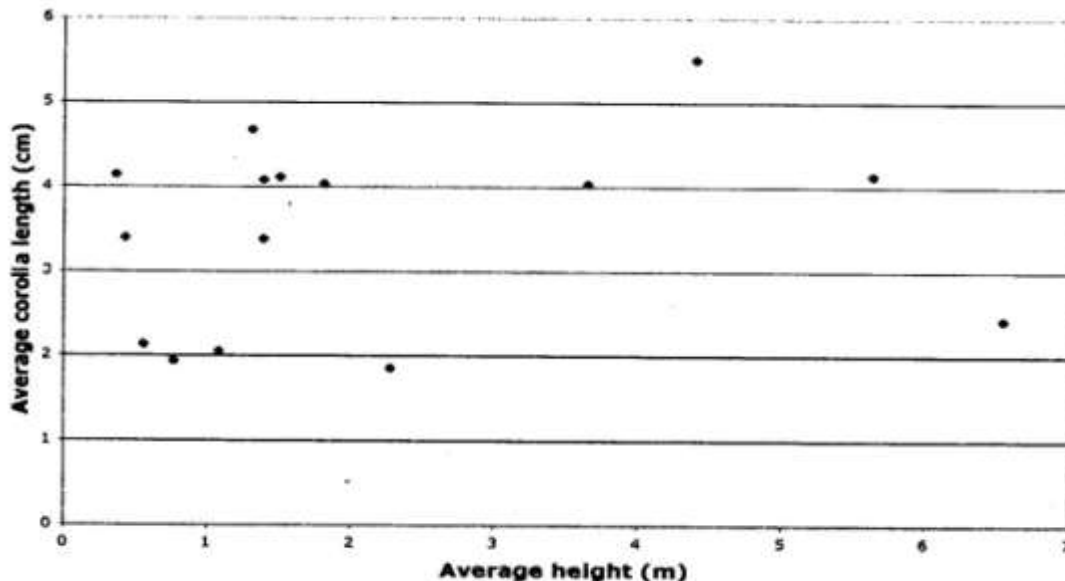


Figure 1. Regression of average corolla length of hummingbird pollinated plants and average height above ground showing no statistically significant trend when analyzed

either linearly or polynomially. Data were taken in montane cloud forest, Monteverde, Costa Rica during October and November 2004.

TABLE 1. Mean corolla length, mean vertical height, corolla sample size = (N_c), height sample size = (N_h) and height range of hummingbird pollinated plants found in montane cloud forest Monteverde, Costa Rica. Mean values are ± 1 SD. Eighteen species were found having a range in height from 0.3 – 14.0 m and corolla length range of 1.4 – 5.5 cm.

Species	Family	Corolla N_c (cm)	Ht (m)	N_h	Ht Range (m)	
<i>Dicliptera iopus</i>	Acanthaceae	1.9 \pm .64	11	.76 \pm .47	6	0.3-1.5
<i>Habracanthus blepharorachis</i>	Acanthaceae	2.1 \pm .12	20	1.1 \pm .45	19	0.3-2.1
<i>Justicia aurea</i>	Acanthaceae	3.4 \pm .30	20	1.4 \pm .81	10	0.6-3.1
<i>Poikilacanthus macranthus</i>	Acanthaceae	4.1 \pm .20	20	1.4 \pm .69	9	0.5-2.1
<i>Razisea spicata</i>	Acanthaceae	4.7 \pm .32	20	1.3 \pm .44	37	0.3-2.5
<i>Alloplectus tetragonus</i>	Gesneriaceae	4.1 \pm .21	20	1.5 \pm .50	15	0.6-2.2
<i>Besleria formosa</i>	Gesneriaceae	1.9 \pm .21	20	2.1 \pm 1.1	16	0.5-5.0
<i>Besleria princeps</i>	Gesneriaceae	2.1 \pm .19	20	0.5 \pm .18	24	0.3-1.0
<i>Columnnea microcalyx</i>	Gesneriaceae	2.4 \pm .52	20	6.5 \pm 3.0	32	1.6-14.0
<i>Columnnea lepidocaula</i>	Gesneriaceae	4.1 \pm .14	11	6.8 \pm 4.1	6	0.8-12.0
<i>Drymonia conchocalyx</i>	Gesneriaceae	5.5 \pm .31	7	4.4 \pm 1.4	8	2.5-6.0
<i>Drymonia rubra</i>	Gesneriaceae	4.0 \pm .24	20	3.6 \pm 2.1	18	1.5-8.0
<i>Burmeistera tenuifolia</i>	Campanulaceae	1.4 \pm .12	8	0.6 \pm .29	3	0.3-1.0
<i>Burmeistera</i> sp.	Campanulaceae	1.8 \pm .19	6	1.8 \pm .15	3	1.5-1.8
<i>Centropogon solanifolius</i>	Campanulaceae	4.7 \pm .30	6	.51 \pm .23	13	0.3-0.8
<i>Malvaviscus palmanus</i>	Malvaceae	4.0 \pm .56	20	1.8 \pm 1.1	3	0.5-4.0
<i>Coccineorchis bracteosa</i>	Orchidaceae	3.4 \pm .34	17	.43 \pm .13	4	0.3-0.6
sp. 1		4.1 \pm .17	5	.36 \pm .05	5	0.3-0.4

All 18 species were found to occur below four meters in height. Two flowers with short corollas (*Besleria formosa* and *Columnnea microcalyx*) and three with long corollas (*Columnnea lepidocaula*, *Drymonia rubra* and *Drymonia conchocalyx*) occurred from four to seven m. One short (*C. microcalyx*) and two long (*C. Lepidocaula* and *D. rubra*) occurred from seven to ten m and two species, one short (*C. microcalyx*) and one long (*C. lepidocaula*) occurred at over ten m in height (Fig.2).

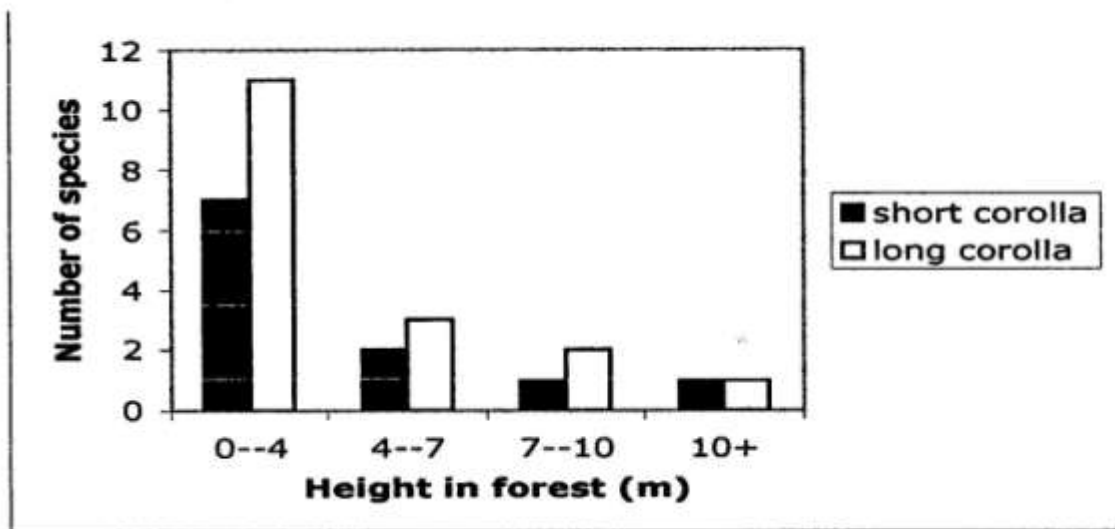
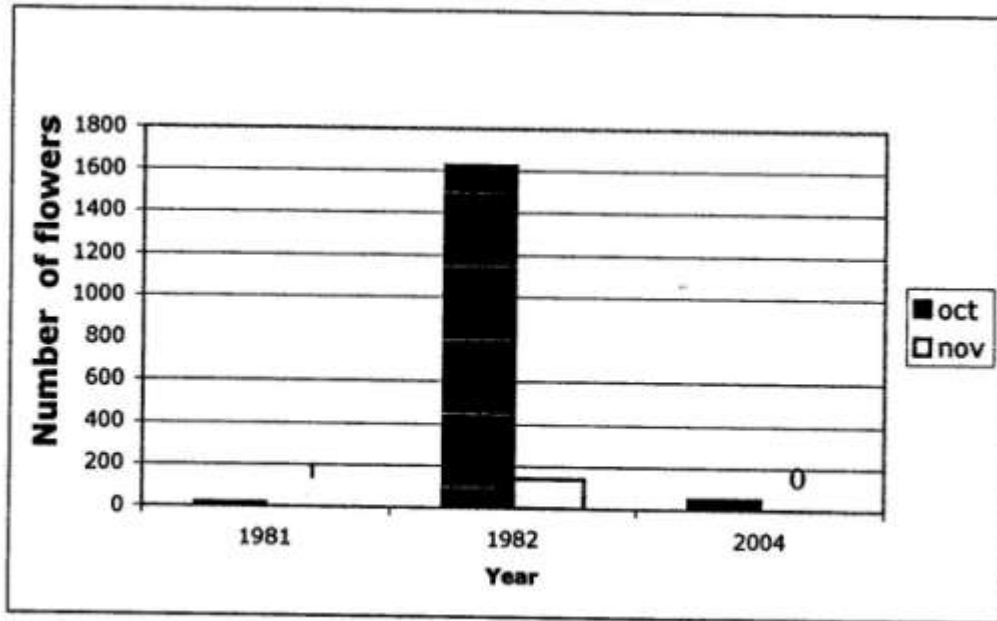


Fig 2. Number of hummingbird pollinated plants occurring at different vertical heights and their corolla length in a tropical cloud forest, Monteverde, Costa Rica. Note prevalence of understory, long corolla species. Short corolla < 3.0cm, long corolla > 3.0cm (Linhart et al 1987). Chi squared test showed that frequency of occurrence of certain corolla lengths in a certain strata was random.

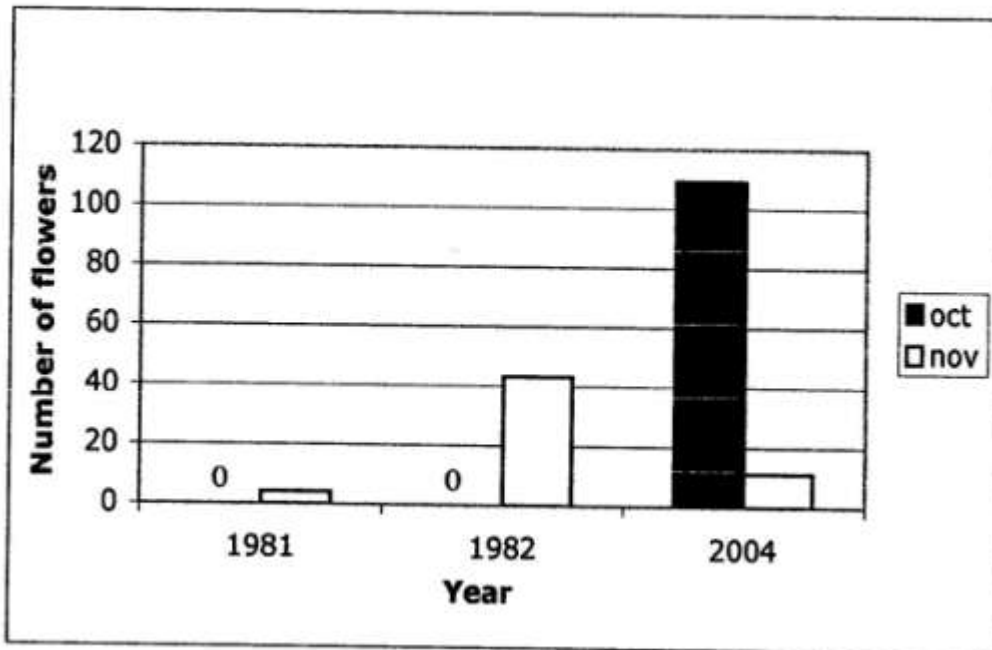
Phenology Results

Phenology results from 2004 compared with the 1981 and 1982 results for the same area in the MVCFP showed changes in monthly abundance for certain species. *Columnnea microcalyx* (short corolla, Gesneriaceae) showed similar flower abundance in 1981 and 2004, but a much higher abundance in October 1982 (Fig. 3A). *Besleria formosa* (short corolla, Gesneriaceae) showed greater numbers in October 2004 compared with October 1981 and 1982 (Fig 3 B). *Justicia aurea* (long corolla, Acanthaceae) was recorded at much lower numbers in 2004 than in either 1981 or 1982 (Fig. 3 C). *Poikilacanthus macranthus* (long corolla, Acanthaceae) was recorded in both 1981, 1982 but was nonexistent in my survey (Fig 3. D). For complete phenology data see Appendix 1.

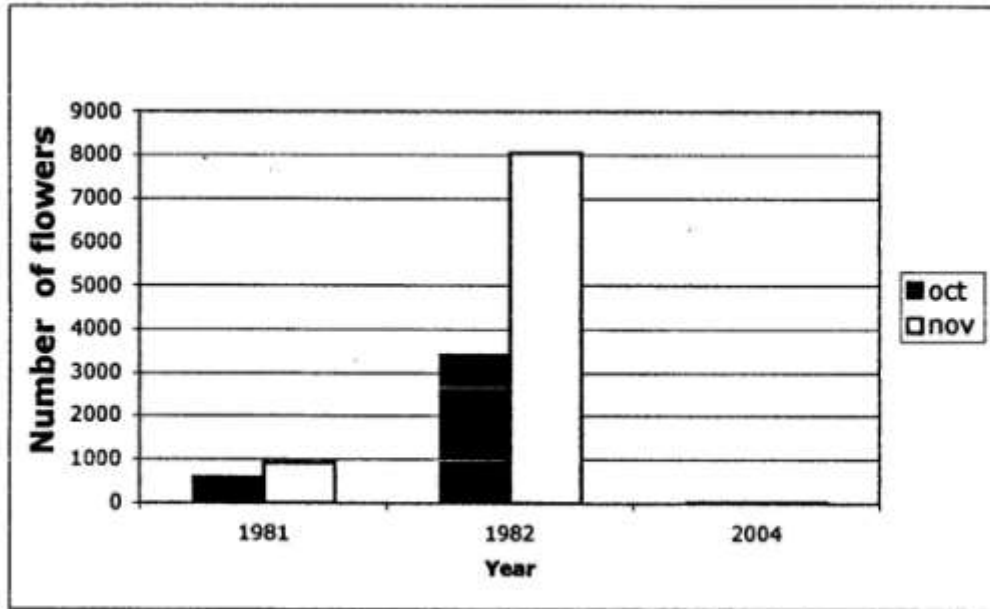
A)



B)



C)



D)

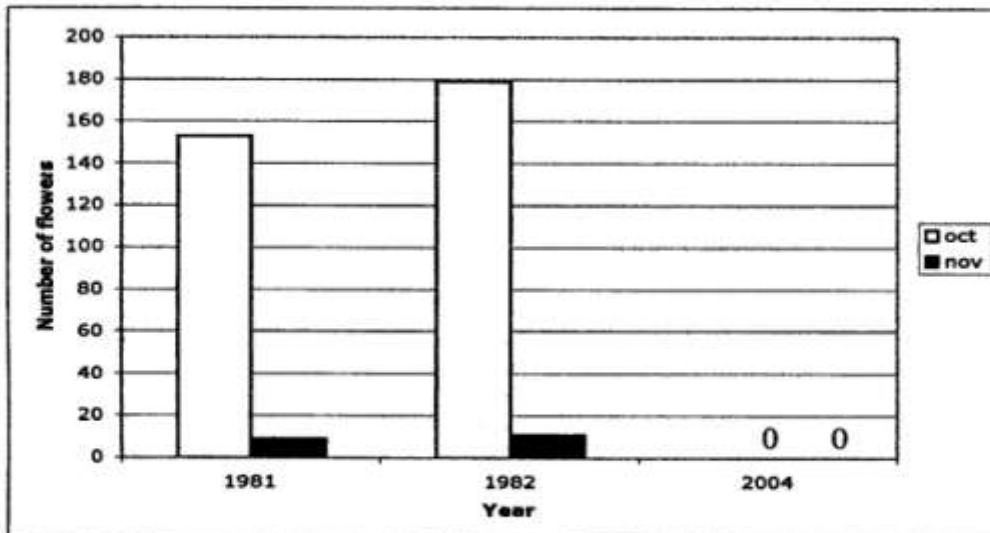


Fig. 3 Number of each species in bloom in October and November 1981, 1982 and 2004 in 8000 meters of the MVCFP. A) *Columnnea microcalyx* B) *Besleria formosa* C) *Justicia aurea* D) *Poikilacanthus macranthus*.

Discussion

The results of this study showed that hummingbird-pollinated plants in the Monteverde cloud forest have a wide range of corolla lengths distributed randomly throughout the vertical strata of the forest. Corolla length was not correlated positively or negatively with vertical height of plant in the forest although there was a trend suggesting a hump shaped distribution, which could become more apparent with a complete census of species in the canopy, especially those in the family Ericaceae.

The 18 species of hummingbird pollinated flowers (range of height = 0.3 – 14m, ranges in average corolla length = 1.4 – 5.5 cm) showed no significant correlation in a linear or polynomial analysis. This indicates that with the eighteen species used in this study there is not significant linear vertical stratification with respect to corolla length. A polynomial regression, which would suggest dominance of certain corolla lengths at more than one specific strata also had no significance. Still, the polynomial regression suggests that a hump shaped distribution may be revealed with a yearlong census of species at all heights. Without the inclusion of more data, the slight hump is explained by the occurrence of most species, both those with short and long corollas, in the under-story and sub-canopy, with one short corolla species in the canopy bringing the curve down at high heights. If more canopy species were sampled, this regression could change.

Half of all Monteverde hummingbird pollinated species are epiphytic, many of these in the canopy (Haber 2000). Yet, the only canopy species that were measured in this study were two species of *Columnea*. Busby (2000) found that seven species of canopy Ericaceae in the Monteverde cloud forest have short corollas and are visited by three species of short-billed hummingbird and one species has a long corolla and is visited by two species of long-billed hummingbird. None of the Ericaceous canopy species were found in high enough abundance to be included, or else were not in flower. Results with Ericad species included could have shown significant polynomial regression values. For example, if canopy Ericad species had been added to the data it may have shown a greater correlation for short corollas in the canopy than is currently represented, resulting in a more hump shaped curve of average height versus corolla length. This would make sense as out of five species of hummingbird in the Monteverde cloud forest utilize resources in the canopy; four are short billed and feed on ericads (Stiles and Skutch 1989).

It does not appear that vertical partitioning is an important part of hummingbird competition avoidance in Monteverde cloud forests. In past studies, Czerniski (1998), Grossman and Trachy (2000) and Feely (1997) found trends of vertical stratification for a few individual species of hummingbirds, but no significant value for stratification on a community level. The overall lack of a major trend in stratification within this study data also supports Feinsinger et al (1976) who found that Monteverde's hummingbird-pollinated plants are not as species specific as hummingbird-pollinated plants in other tropical forests. This implies that flowers were found to attract many different species of hummingbirds, indicating a prevalence of more easily accessible flowers, either in length or by piercing.

What other mechanisms are allowing so many species of hummingbirds to coexist in the same community? The answer may be found in different hummingbird foraging behaviors. There are at least nine species of hummingbird in the study area

(Fogden 1993). Four have long beaks (> 2.8cm) and five have short beaks (Stiles and Skutch 1989). Of these species, three are territorial; guarding a specialized resource and at least one is a long billed trapliner, visiting scattered flowers with high nectar content in the forest under-story. At least two short billed are nectar stealers from long-corolla flowers. All but two of the species have been observed to frequent resources in more than one broad strata (understory, sub canopy and canopy) (Stiles and Skutch 1989). The non-specificity of the hummingbird-flower relationships in this particular forest and diverse feeding strategies that fluctuate due to what is in bloom all help to minimize competition and negate the partitioning of vertical height into specific flower corolla lengths (Hilty 1994). The lack of stratification suggests that hummingbirds in Monteverde cloud forests have relatively broad feeding niches on the whole and will cross vertical strata to find nectar sources. Future studies should address the amount of nectar robbery that occurs in the MVCFP. If a majority of hummingbirds use generalist or nectar robbery strategies to survive, there would again be less need for vertical stratification.

Phenology

The phenology data were not comparable statistically to the 1981-2 data because of various unknowns in aspects of the 1981-2 methodology used by Linhart et al (1987). Still, the trends in the four species highlighted are intriguing. It is known that 1982 was an El Niño year. El Niño years can interrupt or shift normal phenological patterns (Haber 2000). For example, increased rainfall can lead to two flowering peaks per year in species that normally only have one peak (Stiles 1978). This year (2004) was more similar to 1982 flower numbers for some species (*B. formosa*, November 1981), more similar to 1981 for other species (*C. microcalyx*) and not comparable to either of these years in other cases (*B. formosa* October 1981 and 1982, *J. aurea*, *P. macranthus*). Some of these differences can be explained through changes in habitat composition of the MVCFP since the time of the first survey. For example, this survey encompassed less gap and disturbed area than their study. Many species, such as *J. aurea*, bloom more commonly in light gaps (Feinsinger et al. 1988).

Still, other results are complex and not easily explainable. Flowering phenology is influenced by changes in insolation, moisture, temperature, light availability and even competition for pollinators (Linhart et al. 1987, Stiles 1978). It has been proposed that global climate trends are changing the level of cloud formation in Monteverde, increasing the number of consecutive dry days during the dry season, thereby affecting amount of moisture and average temperature (Pounds et al. 1999). This warming trend has a measured increase during El Niño years and has significantly affected various taxa in the Monteverde cloud forest. Comprehensive flowering phenological studies in plants could be the next step in analyzing these changes. The complexity of results from this month- long study provides justification for completion of a yearlong phenological study in the MVCFP to compare to the 1980's. Even without the issue of climate change, phenology is important in any study dealing with community composition of hummingbird-pollinated plants, and is relevant to assessing stratification of vegetation in cloud forests.

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Appendix

Appendix 1. October and November 2004 flowering phenology data for all areas sampled (MVCFP: Sendero Nuboso and Pantenoso, 10/28, 11/7, 11/15, Sendero Chomogo and Roble 11/1, Biological Station: Sendero Principal and Upper Loop trail 11/3), Monteverde Costa Rica.

Species	Family	MVCFP	MVCFP	MVCFP	Est. Biol.	MVCFP
		10/28/2004	11/7/2004	11/15/2004	11/3/2004	11/1/2004
Dicliptera lopus	Acanthaceae	8	5	9	1	6
Hebracanthus blepharorachis	Acanthaceae	63	15	32	124	34
Justicia aruea	Acanthaceae	29	8	21	35	0
Poikilacanthus macranthus	Acanthaceae	0	0	0	22	0
Razisea spicata	Acanthaceae	136	110	221	0	90
Costus wilsonii	Costaceae	2	2	1	0	0
Alloplectus tetragonus	Gesneriaceae	56	30	43	14	1
Besleria formosa	Gesneriaceae	109	20	3	17	50
Besleria princeps	Gesneriaceae	0	0	0	308	0
Columnnea microcalyx	Gesneriaceae	52	3	0	154	71
Columnnea magnifica	Gesneriaceae	0	0	0	2	0
Columnnea lepidocaula	Gesneriaceae	4	3	2	0	8
Drymonia conchocalyx	Gesneriaceae	37	5	4	2	0
Drymonia rubra	Gesneriaceae	27	30	53	18	15
Burmeistera tenuifolia	Campanulaceae	0	0	0	7	0
Burmeistera sp.	Campanulaceae	0	5	0	0	0
Centropogon solanifolius	Campanulaceae	0	2	2	7	2
Malvaviscus palmanus	Malvaceae	11	6	13	35	3
Psychotria elata	Rubiaceae	1	1	0	0	0
Hillia sp.	Rubiaceae	2	0	0	0	0
Symplocos sp.	Symplocaceae	96	16	0	0	0
Coccineorachis bracteosa	Orchidaceae	10	15	8	0	0
sp 2		4	12	25	0	2