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Butterfly Proboscis Length and Pollen Load

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ABSTRACT

Pollination mutualisms between plants and pollinators facilitate increases in genetic variability for plants while providing rewards for pollinators. Specialization of pollinators on specific plants has occurred to maximize benefits of these pollination mutualisms. With this specialization, pollination syndromes have evolved that increase a flower's chance of eliciting visitation of a specific pollinator. For example, "butterfly flowers" have evolved bright colors, short to medium corollas, and strong scents that tend to attract butterflies. However, some of these flowers have evolved long corollas to specialize on long proboscis butterflies. The purpose of this study was to examine the effect of corolla length on degree of pollen specificity in butterfly pollinated flowers. This was completed by observing proboscis length of butterflies and the corolla lengths of flowers visited. A total of 54 butterflies of 29 different species were collected from a fragmented Lower Montane Moist Forest in Cañitas, Costa Rica. Following removal and measurement, proboscises were observed under a microscope for pollen grains of 24 different species of flowering plants. Proboscises of lengths less than 10 mm were defined as short proboscises. Butterflies with proboscises greater than 17 mm were defined as long proboscis butterflies. Butterflies with long proboscises had a greater pollen species richness, often times twice that of small proboscis butterflies. Pollen from long corolla and short corolla flowers was found on all lengths of proboscises. Pollen loads on proboscises suggest that pollination by butterflies is not specific in this community. This non-specificity of butterflies on flowers has ecological and evolutionary effects on community composition and stability.

RESUMEN

Los mutualismos de la polinización entre las plantas y los polinizadores facilitan la variabilidad genética creciente para las plantas mientras que proporcionan recompensas para los polinizadores. La especialización de los polinizadores en plantas específicas ha ocurrido para maximizar las ventajas de estos mutualismos de polinización. Con esta especialización, los síndromes de la polinización han evolucionado para aumentar las posibilidades de la flor de ser visita por un polinizador específico. Por ejemplo, las "flores de mariposa" han desarrollado colores rojos brillantes, corolas de tamaños cortos a medianos y olores fuertes que tienden a atraer mariposas. Sin embargo, algunas de estas flores han desarrollado corolas largas para especializarse en mariposas con probóscides largas. El propósito de este estudio fue examinar el efecto de la longitud de la corola en el grado de especificidad del polen en flores polinizadas por mariposas. Esto fue logrado por medio de la observacion de la longitud de las probóscides de mariposas y las longitudes de la corola de las flores que visitaron. Un total de 54 mariposas de 29 especies diferentes fue colectado de un bosque húmedo montano fragmentado en Cañitas, Costa Rica. Después de ser removidas y medidas, bajo un microscopio para indentificar los granos de polen de 24 especies diferentes de plantas florecientes.Las probóscides con longitudes de menos de 10 mm fueron categorisadas como probóscides cortas. Las mariposas con probóscides de más de 17 mm fueron clasificadas como mariposas con proboscides largas. Las mariposas con las probóscides largas tenían una mayor riqueza de especies de polen, a menudo el doble de las mariposas con probóscides pequeñas. Se contró polen tanto de flores de corola larga como de corola corta todas las longitudes de probóscides. Las cargas de polen en las probóscides sugieren que la polinización por las mariposas no es específica en esta comunidad. Esta falta de especialización de las mariposas a ciertas flores tiene efectos ecológicos y evolutivos en la composición y la estabilidad de la comunidad.

INTRODUCTION

Mutualisms between animal pollinators and plants facilitate plant outcrossing while rewarding pollinators (Proctor et al. 1996). During feeding, pollen grains stick to pollinators allowing their transportation to conspecific plants thus increasing genetic variability (Price 1984). In exchange for pollen transportation, animal pollinators often receive a nectar reward. Specialization of pollinators on specific plants is common, resulting in maximization of potential benefits of the mutualism (Pellmyr 2002). With these specific pollinators, plants have greater chances of moving pollen to conspecific stamens. As a result of this specificity, pollination syndromes have evolved in which morphological characteristics of flowers arise in attempt to elicit specific pollinators (Proctor et al. 1996). For example, “butterfly flowers” typically have bright colors, strong scents and nectar sources that are highly accessible through slender corolla tubes (Proctor et al. 1996). Some of these flowers have evolved long corollas to increase visitation of long tongued or long proboscis butterflies. Although flower visitation may occur by short proboscis butterflies, they are not able to obtain nectar from these long corolla flowers.

Coevolving morphological features of both flowers and butterflies aim to increase pollination specificity (Feinsinger 1983). Butterflies with longer proboscises are presumed to be specialized on longer corolla flowers (Proctor et al. 1996). These flowers should have high visitation by long proboscis butterflies due to consistent nectar reward and decreased competition from short proboscis butterflies for resources. Long proboscis butterflies can also obtain nectar and pollinate short corolla flowers, in turn decreasing pollination specificity.

If specialization is prevalent in communities, a majority of pollen load on long proboscis butterflies should be from long corolla flowers. Butterflies with short proboscises can only access nectar from small corolla flowers (May 1992) thus their proboscis is expected to only have small corolla pollen. In both cases, pollination efficiency of plants should increase and butterflies should exhibit increased effective foraging. On the other hand, if long proboscis butterflies are opportunistic feeders and forage on a wide range of corolla lengths, specialization is not taking place.

The purpose of my study was to examine the effects of corolla length on degree of pollen specificity of butterflies. Proboscises with lengths less than 10 mm were defined as short proboscises. Butterflies with proboscises greater than 17 mm were defined as long proboscis butterflies. It was hypothesized that as length of proboscis increases, butterflies would feed more opportunistically on a wider array of corolla lengths, conferring a higher richness of pollen found on proboscises. With these increases in proboscis length, specificity is expected to decrease.

MATERIALS AND METHODS

Data collection took place in the town of Cañitas, Costa Rica from October 25th to November 15th. The study site consisted of pasture bordered by fragmented Lower Montane Moist Forest (Hayes and Laval 1989). This property is owned by Doña Engracia Arguedas. Fifty-four total individuals of 29 different species of butterflies were collected using a butterfly net. All butterflies were identified to species (DeVries 1987).

Proboscises were removed from butterflies with tweezers and placed on a piece of rolled Scotch tape. Using a metal probe, proboscises were extended to full length on the tape. The tape was then placed on a microscope slide and length of the proboscis was measured. Pollen located on these proboscises was observed with a Carl Zeiss compound light microscope at 400X. Using a self-compiled pollen database of 24 flowering plants within 300 m^2 of the study site, pollen on proboscises was identified to plant species. Corolla lengths of these specific flowering plants were measured to examine the relationship between proboscis length of butterflies and corolla lengths of visited flowers (Table 1). Pollen of the 24 species was easily distinguishable. Unknown pollen species found of proboscises were only included in pollen richness counts on proboscises.

RESULTS

Twelve *Anartia fatima,* four *Heliconius clysonmus,* three *Paplio polyxines,* three *Siproeta epaphus epaphus* and three *Pieriballia mandela noctipennis* were collected. Of the 24 remaining butterfly species, one to two individuals were collected (Table 2).

Pollen from 12 out of the 24 surveyed flowering plants was found on the 54 proboscises. Pollinia from *Asclepias curassavica* (Apocynaceae) were found on two-thirds of all butterfly species collected, while *Lantana camara* (Verbenaceae) pollen was found on about one-fourth of butterfly species. The ten other species of flowering plants were visited by 6 or less butterfly species (Fig. 1).

A significant correlation was observed between length of butterfly proboscis and the number of pollen species on proboscises (Linear regression, $r = .56$, $p < .05$, $N = 54$ individuals). Butterflies with long proboscises had greater pollen species richness than those with short proboscises (Fig. 2). Longer proboscises carried up to twice the number of pollen species as short proboscises.

Long and short proboscis butterflies carried pollen of both long and short corolla flowers. No significant trend was observed between proboscis length and length of corollas visited by butterflies (Linear regression, $r = .13$, $p > 0.05$, $N = 84$). *Oerstedella centrodenia* (Orchidaceae), *Pentas lanceolata* (Rubiaceae), *Kohleria sp.* (Gesneriaceae), and *Malvaviscus penduliflorus* (Malvaceae) with corolla lengths of 7.5 mm, 16.1 mm, 22.5 mm and 34.5 mm respectively, were visited by butterflies that had proboscises whose lengths were less than that of their corresponding corollas (Fig. 3) (10 instances). Eighty-six percent of pollen grains found on proboscises were from flowers with corolla lengths 10 mm or less.

DISCUSSION

The hypothesis that long proboscises would have greater pollen richness than short proboscises was supported. This result may be do to the fact that butterflies with long proboscises have more flower feeding options and therefore visit flowers of all corolla lengths. These long proboscis butterflies feed opportunistically in the community.

In further support of this conclusion, no correlation was observed between length of proboscis and lengths of corollas visited. Butterflies with short proboscises have the potential to pollinate long corolla flowers even though nectar sources are unreachable. This may possibly be due to the fact that long corolla flowers have different placement of pollen and nectar than small corolla flowers (Endress 1994). In this case, actual corolla length may be an overestimate of distance to nectar source. *Kohleria sp.* and *M. penduliflorus* (hummingbird pollinated plants) possibly evolved long anthers to maximize chances of pollen dispersal when hummingbird visitation is limited (Feinsinger 1983). These long anthers increase chances of pollen transfer; butterflies, insects and wasps that land on these anthers can act as pollen transporters. *O. centrodenia* and *P. lanceolata* lack jutting anthers and therefore their pollen was probably gathered by short proboscis butterflies through random pollen transmission. This is likely to occur in communities with butterflies that feed on a wide range of corolla lengths. Long proboscis butterflies may leave long corolla pollen on short corolla flowers, allowing later transfer of that pollen by short proboscis butterflies. With opportunistic feeding of butterflies, both long and short corolla flowers are expected to receive a high amount of pollen from foreign species.

In this study, short proboscis butterflies probably failed to realize that nectar was unreachable in long corolla flowers. Over time, butterflies should learn that nectar rewards are not reachable resulting in decreased visitation to that long corolla species. This may account for the small amount of short proboscis butterfly visitation to long corolla plants.

A. curassavica and *L. camara* may possibly have been visited by the greatest number of butterfly species due to its high density in the pasture. The high accessibility to nectar of short corolla flowers may also contribute to high butterfly species visitation. Other physiological characteristics of the flower such as nectar output could also play a role in high species visitation (Proctor et al. 1996).

With long and short corolla pollen carried by all lengths of proboscises, specialization of butterfly pollinators on plants is not prominent in the community. This non- specificity results in higher community stability due to plant species having a variety of butterfly species pollinators (Bawa 1990). Negative effects on an ecological community due to lack of specialization may also be observed. With less specialization, a decrease in pollen transfer to conspecifics is observed. Higher competition for potential pollinators also increases within plant species. Lack of specialization of butterflies on flowering plants in this study has both positive and negative effects on community composition and stability.

Pollination loads on proboscises suggest that butterfly pollination of flowers in the studied community is not specific. Long proboscis butterflies do have a nectar foraging advantage over short proboscis butterflies. But why have these long proboscis butterflies evolved when short proboscis butterflies can, as shown, pollinate long corolla flowers? Further study may show that long proboscis butterflies have high frequency of visitation to long corolla flowers. This possible result increases specificity and gives rise to explanations of long proboscis evolution in this community.

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Table 1. Corola lengths of 12 different flowering plants within 300m^2 of the study site. The 12 different pollen types corresponding to these species were found on the 54 butterfly proboscises sampled in this study.

Species of Flowering Plant	**Length of Corolla (mm)**
Asclepias curassavica (Apocynaceae)	0.2
Unidentified Aster (Fig. 5)	3
Rubus roseifolius (Rosaceae)	4
Lantana camara (Verbenaceae)	4.5
Epidendrum radicans (Orchidaceae)	7
Hidalgo ternate (Asteraceae)	7.5
Oerstedella centrodenia (Orchidaceae)	7.5
Duranta erecta (Verbenaceae)	8.5
Impatiens walleriana (Balsaminaceae)	10
Pentas lanceolata (Rubiaceae)	16.1
Kohleria sp. (Gesneriaceae)	22.5
Malvaviscus penduliflorus (Malvaceae)	34.5

Table 2. Number of individuals collected from 29 different butterfly species in pasture bordered by fragmented Lower Montane Moist Forest in Cañitas, Costa Rica.

Butterfly Species	Numbers of Individuals Collected
Anartia fatima	12
Heliconius clysonmus	4
Paplio polyxines	3
Siproeta epaphus epaphus	3
Pieriballia Mandela noctipennis	3
Anthanassa sp.	2
Consul electra	2
Dircenna relata	2
Catasticta strigosa actinotis	2
Dircenna klugii	1
Mechanitis polymnia isthmia	1
Cissia similis	1
Dircenna chiriquensis	1
Phoebis sannae	1
Eretris suzannae	1
Lycorea cleobaea atergatis	1
Ithomia patilla	1
Euptychia millis	1
Metal mark sp.	1
Enantia melite amalia	1
Pereute charops	1
Eurema proterpia	1
Eueides lineate	1
Chloreuptychia arnaea	1
Actinote leucomelas	1
Phoebis argante	1

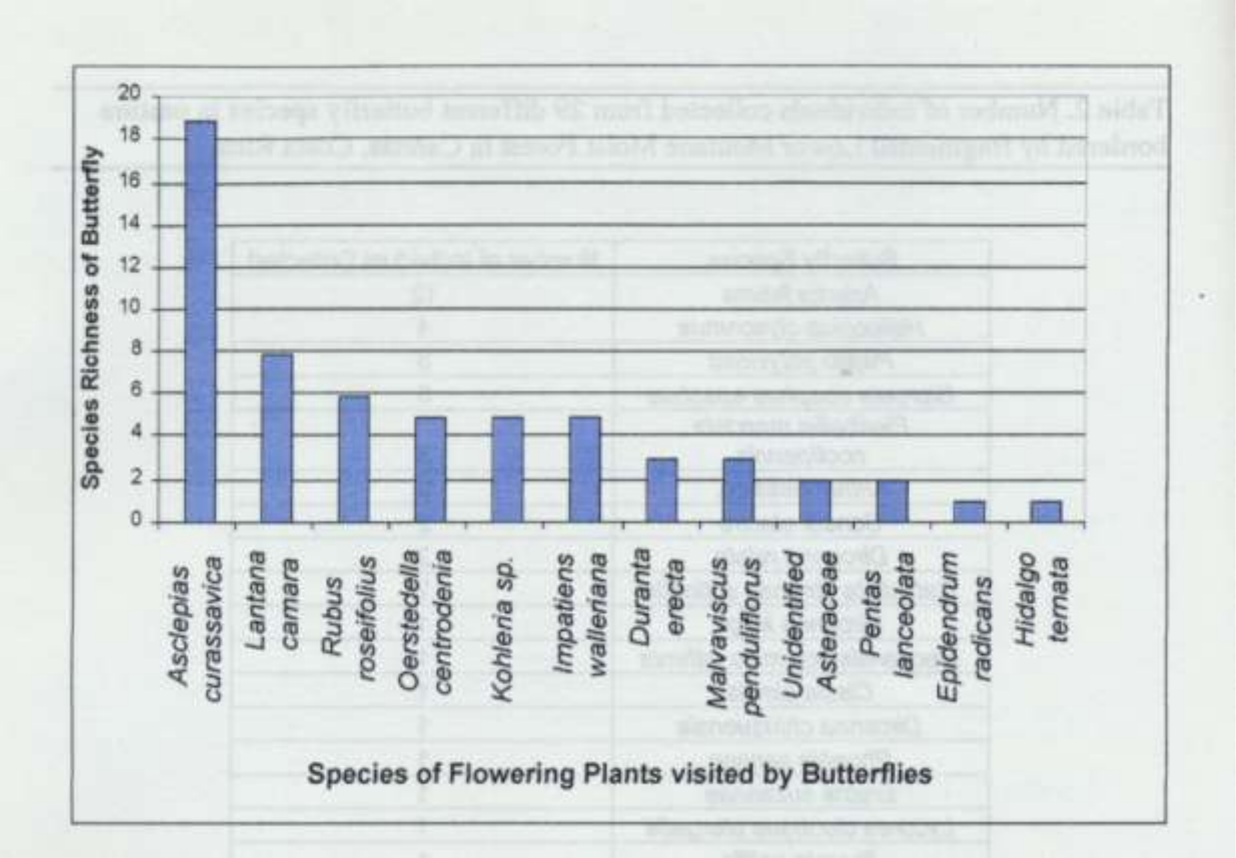

FIGURE 1: Number of butterfly species containing pollen from specific flowering plants in a fragmented Lower Montane Moist Forest in Cañitas, Costa Rica. Butterflies were collected and pollen samples were observed from October 25th to November 15th. *Asclepias currasivica* (Apocynaceae) showed visitation by the greatest number of butterfly species (19) followed by Lantana camara (Verbenaceae) (8). The ten other flowering plants were visited by six or fewer butterfly species.

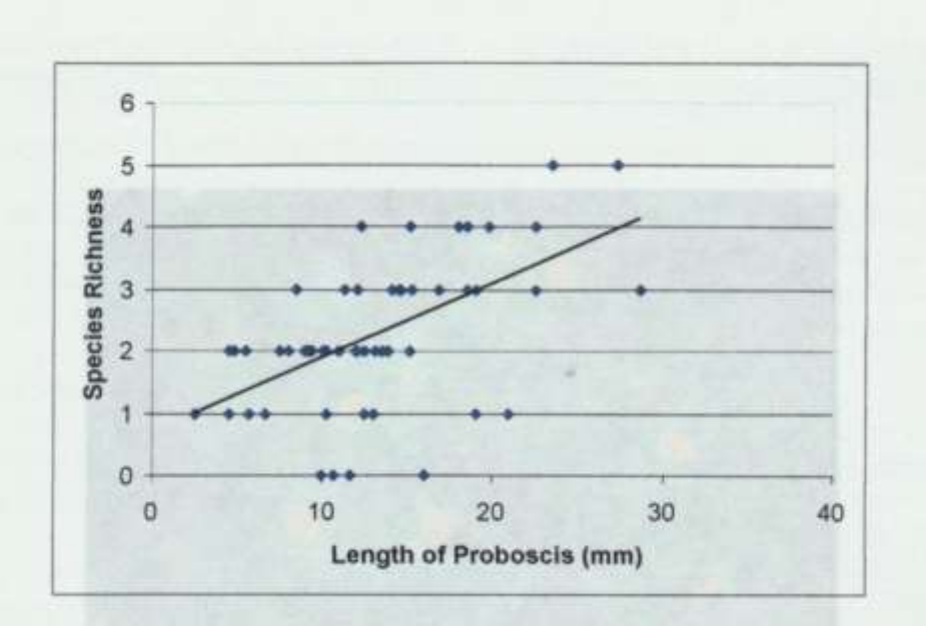

FIGURE 2: Effect of butterfly proboscis length on species richness of pollen found on proboscises. Fifty-four individuals of 29 different butterfly species were collected from a fragmented Lower Montane Moist Forest in Cañitas, Costa Rica from mid-October to mid-November. Increases in length of proboscis conferred increases in pollen richness (Linear regression, r = 56, p < .05, N = 54 individuals).

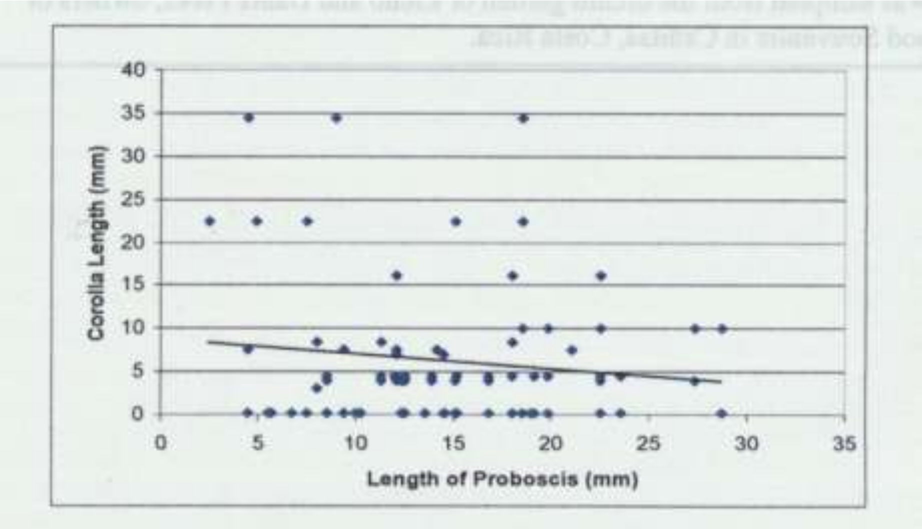

FIGURE 3: Relation between length of butterfly proboscis and length of corolla flowers visited. A total of 84 pollen samples from 54 butterfly proboscises from Lower Montane Moist Forest in Cañitas, Costa Rica were identified. Collection took place from October 25th to November 15th. No significant correlation was observed between proboscis length and corolla length of flowers visited (Linear regression, r = .13, p > 0.05, N = 84).

FIGURE 4: Unidentified flowering plant of the Asteraceae family. Pollen from this flower was sampled from the orchid garden of Licho and Danis Perez, owners of Rosewood Souvenirs in Cañitas, Costa Rica.