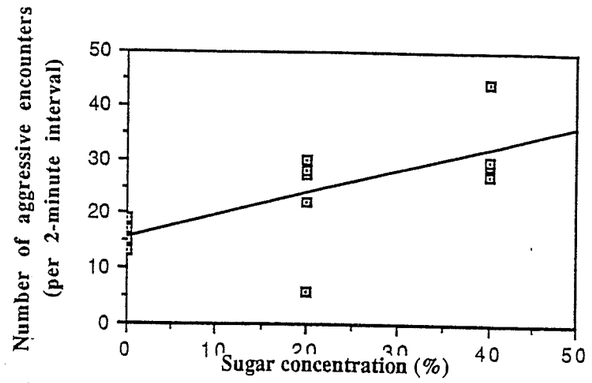
Figure 2 Aggressive encounters vs. level of sugar concentration in feeders per 2 minute interval.



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THE EFFECT OF COROLLA LENGTH ON NECTAR ROBBERY

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Abstract (A.M.)

Our study examined the frequency of nectar robbery in five species of hummingbird pollinated flowers. We tested whether corolla length influences the likelihood of nectar robbery. Statistical analysis of our data showed that frequency of nectar robbery increases as corolla length increases. This is most likely due to the fact that flowers with longer corollas are less accessible to short-billed nectar robbers and therefore such birds must extract the nectar illegitimately through the base of the flower.

Other factors exist that may influence the frequency of nectar robbery in addition to corolla length. Two such factors were given secondary consideration in our study. Preliminary studies indicate that frequency of nectar robbery may also be influenced by the sugar content of nectar as well as the density of flowers within an area.

Introduction (T.G.)

It has been noted that the coevolution of flowers and their pollinators has led to specialized morphologies (Janzen, 1983). An example of this is found in Monteverde, Costa Rica, where hummingbird beak shapes correspond closely to certain flower morphologies. Both hummingbirds and flowers derive benefits from their relationship. For example, the flower offers the hummingbird a highly concentrated energy source. The hummingbird, because of its specialized beak, concentrates on fewer flower species. This increases the likelihood that one plant's pollen will reach another individual of the same species, increasing chances of reproduction. It has also been noted that this specialized hummingbird/flower relationship is particularly important in cold, wet mountainous regions like Monteverde. The flowers' nectar provides a reliable energy source that enables the hummingbirds to survive in harsher conditions, and the hummingbirds provide the main source of pollination because there are fewer insects and bats to act as pollinators in this climate (Stiles and Skutch, 1989).

This morphological development has created specific pollinating relationships between long billed hummingbirds and flowers with long corollas. As a result, other birds cannot access this nectar legitimately. Rather than collect nectar via the corolla, shorter-billed hummingbirds "rob" flowers with long corollas by piercing the bottom of the flower and collecting the nectar directly. By accessing the nectar through the base of the flower, the robber never comes in contact with the anther, and thus never pollinates the flower. This absence of pollinator and drainage of nectar would seem to be a cost to the flower.

Does this specialized system that is known to be beneficial to both individuals have a cost associated with it? We decided to look at this question by examining robbery in relation to specialization. If robbery does increase as specialization increases, then it would seem that there is a cost associated with this coevolutionary system. We thus hypothesized that the percentage of robbed flowers should increase as corolla length increases.

Methods (A.M.)

We measured nectar robbery and corolla length in flowers found along the Rio Eterno, George Powell and Nuboso trails in the Monteverde Cloud Forest Reserve, Costa Rica. In particular, we studied the following five species: Razisea spicata, Raunia triflora, Drymonia rubra, Hansteinia blefharorhachis, and Dicliptera iopus. With the exception of R. spicata, all flowers found along the paths were measured. R. spicata was so abundant we could not measure them all and instead chose R. spicata flowers randomly, approximately every 200 meters. For each flower, species name, corolla length, evidence or robbery and whether or not the flower or inflorescence was found singly or in a clump of flowers of the same species was recorded. Corolla length was measured to one tenth of a millimeter. Robbery was defined by the presence of a small slit at the base of the flower's corolla. Clumps were defined as flowers that were found within three meters of at least two other plants of the same species (with flowers). Flowers were usually measured while still attached to the plant, however occasionally flowers that were found along the path's edge were measured and used in our study. To obtain an indication of nectar sugar concentration, we removed nectar from flowers with a pipette and analyzed the nectar with a refractometer. The flowers used for sugar content analyses were collected from the Campbell farm, southwest of the reserve. Due to the low abundance of R. triflora, D. rubra, and D. iopus, only R. spicata and H. blefharorhachis could provide enough nectar for an accurate measurement of sugar content.

Results (T.G.)

By using a regression, we found that percentage of robbed flowers increased significantly as corolla length increased ($r^2 = 0.149$, $r = 0.386$, $p < 0.01$, $n = 217$: Graph I, Table 1).

We measured percentages of robbed, clumped flowers versus robbed, non-clumped flowers. Percentages in the five species ranged from 0% to 85% for the clumped flowers, and 0% to 82% for the non-clumped flowers (Table 2).

We also measured nectar sugar content for R. spicata and H. blefharorhachis, using nectar from 15-20 flowers of each species. We obtained one refractometer reading for each, finding

values of 21.75% and 12.75%, respectively.

Discussion (L.T.)

The significant regression supports our hypothesis. Therefore, it is quite possible that the limited access to the flower forces other organisms to rob the flower in order to obtain the nectar reward. However, we must also recognize that only 14.9% of the robbery is accounted for by corolla length. Some of the other factors which may influence robbery of nectar are those flower characteristics which initially attract the robbers. These might include: color, fragrance, sugar content of nectar, nectar volume, geographical location of the plant, or location of the flower on the plant itself. In addition, ease of access through the structure of the flower (ie. thickness) or plant density may also be factors. In consideration of these possible factors, we did preliminary research on sugar content and plant density.

We compared the nectar sugar content of R. spicata and H. blefharorhachis. R. spicata had a higher sugar concentration of 21.75% while H. blefharorhachis had a concentration of only 12.75%. This suggests that it also may be true that those species with a high nectar sugar concentration are more subject to robbery than those with a low nectar sugar concentration.

In examining density, we calculated the percentage of flowers that had been robbed in the two categories, clumped and non-clumped, for each species (see Table II). Three of the five species showed that a higher percentage of clumped flowers were robbed than non-clumped flowers, which may mean that flowers in higher density are at a greater risk of robbery because it is more efficient for a robber to forage where it can obtain a high yield for its time spent. The results for the H. blefharorhachis are directly opposite in regard to robbery of clumped vs. non-clumped flowers. The explanation for this may come from hummingbird behavior. If hummingbirds are receiving high rewards from the flowers they visit, like the long-corollaed, sugar rich R. spicata, they tend to trap line their flowers rather than defending them in territories. Shorter, less nectar-rich flowers may be trap-lined, or they may be defended in territories (Kricher, 1989). If H. blefharorhachis fits into this latter category, it may explain why they have a higher proportion of robbery in non-clumped flowers. Territorial birds would defend the clumped flowers, leaving the non-clumped to be preyed on by robbers. We cannot make any assumptions about the fact that D. iopus has the same percentage robbed in each category because we did not find a single robbed flower. If someone were able to determine the nectar volume or sugar concentration of these flowers we could see if these factors, as opposed to density, are the reasons why they are less desirable to robbers. Separating the effects of these three variables is also important to clarify their influence on our study of corolla length.

Since robbery must impart some cost on a plant, one might question the fitness of those species which have developed long corollas and have thus been put at risk. If the flower must replace robbed nectar then it has this energy cost for which it received no reproductive benefit. If

they do not replace nectar, one might question how long on an evolutionary scale their long-billed pollinators will continue to visit a plant at which they run the risk of receiving no reward. However, for now it appears that the flowers may not be suffering enough from these costs to outweigh the benefits. R. triflora and R. spicata, two of the most heavily robbed flowers (see Table I), are also by far the most commonly found. As we have no way of assessing their present fitness, we cannot tell if the plant is at a stabilized point of abundance or if they were previously more common and are now experiencing lower numbers. It is quite possible, however, that in spite of the cost to the plant, robbery actually increases the fitness of the plant. Since the hummingbird cannot determine whether or not the flower contains nectar when it enters it, not finding any forces the bird to move on to another flower in order to find enough sugar energy (Gill, 1987). Visits to other flowers aid in cross pollination and distribute the plant's genes into the population. We acknowledge two sources of error. We obtained some of the flowers which we sampled from the ground around the plant. If the plant is more likely to drop robbed flowers, then our data may have been skewed. Also, in the nectar sugar concentration comparison that we did, we were able to obtain only very small amounts of nectar and so had no chance to try replicates for accuracy.

We recommend further study on the other possible influences affecting robbery and also on the effect robbery has on the plant itself.

Table 1 Mean length, standard deviation, and percentage of robbed flowers for five hummingbird-pollinated species found at Monteverde, Costa, Rica, 1991. n=217

Species	Mean Length	S. D.	Percent Robbed
Ravnia triflora	64.78 mm	7.40	72%
Razisea spicata	56.22 mm	4.17	79%
Drymonia rubra	49.18 mm	7.65	52%
Hansteinia blefharorhachis	27.75 mm	1.87	54%
Dicliptera iopus	21.26 mm	3.40	0%

Table 2 Percentage of robbed clumped vs. not clumped flowers, as measured at Monteverde, Costa, Rica, 1991.

	Percent Robbed			
Species	Clumped		Not Clumped	
Ravnia triflora	84%	n=25	73%	n=38
Razisea spicata	85%	n=26	66%	n=22
Drymonia rubra	70%	n=10	40%	n=20
Hansteinia blepharachachis	40%	n=35	82%	n=17
Dicliptera iopus	0%	n=19	0%	n=2

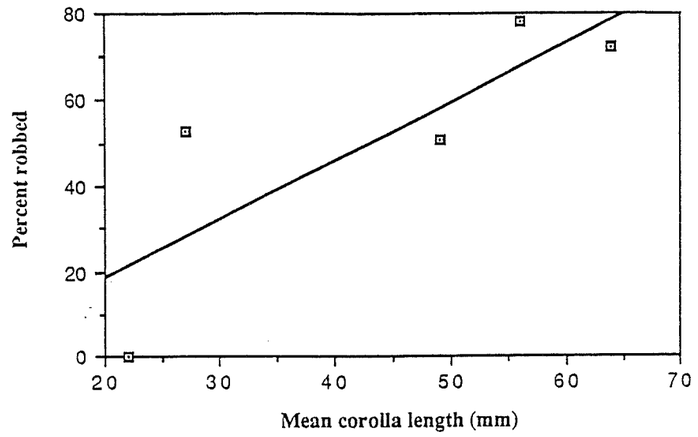

Figure 1 Trend for percent robbed flowers as corolla lenght increases as measured at Monterverde, Costa Rica, 1991 (n=217).

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