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Nectar robbery and pollination by hummingbirds in relation to morphological and physiological features of Gesneriaceae

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ABSTRACT

Many flowers depend on hummingbirds for pollination. However, some hummingbirds are known to rob flowers rather than pollinate them. High robbery rates could decrease pollination reproductive fitness in these plants. Corolla length, bract coverage, nectar volume and sugar concentration, were hypothesized in this study to affect robbery rates. A long corolla, short bract, and high nectar volume and concentration were hypothesized to increase the rate of robbery. Pollination rates were also expected to increase with a high nectar volume and sugar concentration. Data were collected on *Alloplectus tetragonus, Besleria Formosa,* and *Drymonia rubra* (Gesneriaceae) in the Santa Elena Reserve for 21 days. *Alloplectus tetragonus* had the longest corolla and shortest bract. *Besleria formosa* had the shortest corolla and *D. rubra* the longest bract. The nectar volume and concentration were examined daily for 16 days. All species varied significantly by day in nectar volume and concentration, except for *D. rubra* and *B. Formosa* in nectar volume. Although there were significant differences between all characteristics examined, robbery and pollination rates were not significantly different. Thus, these characteristics were combined in different ways for each species, but resulted in the same outcome: low rates of robbery and pollination. *A. tetragonus* and *B. Formosa* produced small amounts of dilute nectar and did not provide a great reward for nectar robbers while *D. rubra* had large bracts to protect against robbery.

RESUMEN

Muchas flores necesitan los colibríes para polinización. Pero algunos colibríes roban las flores en vez de polinizándolas. Altas tasas de robos puede bajar tasas de polinización y afectar la reproducción en esas plantas. Estudie tres especies de flores: *Alloplectus tetragonus*, *Besleria Formosa*, y *Drymonia rubra* (Gesneriaceae). Observe características diferentes de las flores, como la longitud de la corola, el tamaño de la bráctea, el volumen de néctar, y la concentración de azúcar. Pensé que la tasa de robos crecería con una corola larga, una bráctea pequeña, y altos volúmenes de néctar y concentraciones de azúcar. Estudie en La Reserva de Santa Elena en noviembre, 2000. Encontre diferencias significativas entre los especies de las flores, pero no habían diferencias entre la tasa de robos o polinización. Alloplectus tetragonus fue el mas largo y B. Formosa el mas corto. Drymonia rubra tenia las brácteas mas grandes y A. tetragonus las mas cortas. Drymonia rubra tenia una concentración de azúcar muy alta y produjo néctar casi todos los días. Alloplectus tetragonus y B. Formosa produjeron menos con concentraciones mas bajas. No produjeron néctar en los primeros días de su vida. También, D. rubra solo vivió como cuatro días mientras A. tetragonus vivió por mas de quince días. Estas características fueron diferentes para cada especie, pero su suma resulto en la misma tasa de robos y polinización. Alloplectus tetragonus y B. Formosa

probablemente no tenían suficiente néctar para consumirlos, y D. rubra tenia brácteas grandes. Los roedores probablemente visiten otras flores que siempre tienen néctar. Finalmente, puede ser que la tasa de robos es más alta cuando no hay comida suficiente, como en el tiempo seco.

INTRODUCTION

A wide variety of flowers are dependent on Hummingbirds for pollination. The hummingbirds feed on nectar and in the process often pollinate the plant. Plants often force animals to visit many flowers by secreting small quantities of nectar per flower (Heinrich and Raven 1972 in Feinsinger 1983). Pollinators, however, try to maximize energy intake and minimize energy expenditure. Some hummingbirds are known to rob nectar, which is when they bypass the opening of the corolla and pierce its side near the base to extract nectar. Flowers with long corollas often experience high rates of nectar robbery since fewer species may access the nectar that lies deep within the corolla (Nilsson 1988 in Fenster 1991). This may have negative effects on the plant for not only is the robber failing to pollinate the plant, but it is also decreasing the nectar volume, making the flower less attractive to legitimate pollinators (Lyon and Chadek 1971 in Feinsinger 1983).

Flowers pollinated by hummingbirds generally share a number of characteristics. They are often solitary or loosely clustered in a horizontal or pendant position with flexible pedicels (Endress 1994). Most are diurnal, scentless, and are red or yellow. They often have a long tubular corolla, robust tissues, and lack a perch (Endress, 1994). In addition, they often have large amounts of dilute nectar of low viscosity with low amino acid content (Stiles 1981 in Endress 1994).

Hummingbird species and the plants they pollinate may be divided into two guilds: those that are trapliners and those that are territorial (Table 1). Trapliners follow foraging routes with scattered but predictable high-yield locations, which they regularly exploit over a long period of time (Endress 1994). Thus, traplined plants often exhibit steady flowering patterns and are usually found in the understory as herbs, shrubs, vines, or epiphytes. They are usually found in small clumps in closed forest and have long curved perianths (Endress 1994). Hermits, those with long, curved bills, pollinate these long flowers and prefer a high volume and sugar concentration of nectar (Feinsinger 1983). Alloplectus tetragonus and D. rubra are among those plants with a long corolla ($\geq$ 30mm).

Territorial hummingbirds compete and partition flowers and are often short-billed (Snow and Snow 1972, 1980). Short-billed hummingbirds tend to visit short, straight flowers that produce less nectar (Feinsinger 1983). Plants visited by territorial hummingbirds are generally in large, monoclonal stands at forest edges and open habitats. They secrete less nectar than hermit-pollinated flowers (Feinsinger 1983). B. Formosa has a short corolla ($\geq$ 25mm) and is probably rarely robbed (Feinsinger 1987).

Some hummingbird species are known to be good pollinators, whereas others are known to be robbers. Of those found in the Monteverde Cloud Forest Preserve, the Green Hermit (Phaethornis guy, culmen length of 47mm) was responsible for 68.2% of

legitimate pollination on long flowers (Feinsinger 1986). The Violet Sabrewing (Campylopterus hemileucurus, culmen length of 34.4mm) was responsible for most of the remaining legitimate visits. On the other hand, the Purple-throated Mountain-gem (Lampornis calolaema, culmen length of 23mm) was responsible for 96.9% of all visits to short flowers and less than 5% of legitimate visits to long corollas (Feinsinger 1986). The Green Violet-ear (Colibri thalassinus), the Fiery-throated hummingbird (Panterpe insignis), the Coppery-headed Emerald (Elvira cupreiceps), and the Striped-tailed hummingbird (Eupherusa eximia) all have short bills. The Striped-tailed hummingbird (culmen length of 22.8mm) makes the remaining visits to short corollas, but gains most of its energy by piercing long corollas (Feinsinger 1987).

My study examined the effects of corolla length, bract coverage, nectar volume, and sucrose concentration on the robbery and pollination rates of Alloplectus tetragonus, Besleria Formosa, and Drymonia rubra. It is hypothesized that larger bracts and a shorter corolla will result in reduced robbery rates. Both robbery and pollination rates are expected to increase with higher sucrose concentrations and nectar volumes for this would provide more nutrients to the robber or pollinator.

MATERIALS AND METHODS

Study Site

The study area was within The Santa Elena Reserve of the Arenal Conservation Area in Costa Rica. The Santa Elena Reserve (SER) is about 310 hectares large at 1700m and is located on the Atlantic slope north of Monteverde and Santa Elena (Haber et al 2000). The study area includes Holdridge life zones 3 and 4 (Haber et al. 2000). Zone 3 is found at elevations between 1,500m and 1,600m, and Zone 4 is found above 1,600m on the Pacific slope and above 1,400m on the Caribbean slope (Fogden 1993).

Morphological and Physiological Characteristics

Three species of Gesneriaceae were studied: *Alloplectus tetragonus*, *Besleria Formosa*, and *Drymonia rubra*. First, twenty or more flowers were sampled from each species to determine mean corolla length, bract size, nectar volume, and sucrose concentration. Calipers were used to measure the length of the corolla, from the base of the calyx to the most distal part of the petals. The relative bract size was estimated by taking the ratio of the bract length to the total corolla length.

Twenty flowers of each species were covered with mesh bags before opening to measure nectar volume and sucrose concentration. This prevented rainwater from diluting the sugar concentration and hummingbirds from extracting the nectar. They were then checked throughout their life span for 16 days from November 3 to November 19 to

determine how nectar production correlates with the age of the flower. A capillary tube was used to extract and measure the nectar volume. A caliper was used to measure the amount of the tube that was filled with nectar. A Reichert hand refractometer was used to measure the sucrose concentration of the nectar. This data was also used to determine the first day of nectar production and the life span of each flower.

Robbery and Pollination Rates

Estimates of robbery rates were determined for each species of Gesneriaceae. Mature flowers were marked as either damaged or undamaged. Forty-one individuals of *A. tetragonus* and *B. Formosa* each were sampled as well as 33 of *D. rubra.* A damaged flower is one that has a hole or tears near its base. Flowers were marked with string so as not to recount them, and the rate of robbery was determined by taking the ratio of total damaged flowers to the total number of flowers sampled. Estimates of pollination rates were also determined for the Gesneriads. The stigma was removed from about twenty flowers of each species during the mature stage of development and was stored in tinfoil. Pollen was identified by comparing it to pollen on the anther of the same species. Pollen of each species had already been identified by looking at the anthers under the microscope.

Finally, hummingbirds were observed to determine which species are present. Hummingbirds were observed in the forest and at the feeders at the information center of the reserve. The Guide to the Birds of Costa Rica was used to identify them.

Statistical Analyses

A number of statistical analyses were conducted. First, Chi square tests were performed to determine whether there were significant differences between species in nectar robbery rates and pollination rates. One-way ANOVA tests were used to analyze the differences in corolla length, bract coverage, total nectar volume, average sugar concentration, the first day of nectar production, and the life span of each species of flower. The Kolmogorov-Smirnov test was used to test for normality among the above characteristics. Friedman tests were used for each species to analyze how nectar volume and sucrose concentration changed each day.

RESULTS

First, there was not a significant difference between species in robbery or pollination rates. *Alloplectus tetragonus* was robbed eight times, *B. Formosa* four times, and *D. rubra* three times (Chi Square, $X^2 = 1.76$, d.f. = 1). The frequency of pollination was not

significantly different either (Chi Square, $X^2 = 2.45$, d.f. = 1). Ten of 22 *A. tetragonus* were pollinated, 6/22 *B. Formosa*, and 5/20 *D. rubra* were pollinated.

Although there were not significant differences between species in robbery or pollination rates, there were in all other characteristics tested. The length of the corolla was significantly different with *A. tetragonus* the longest and *B. Formosa* the shortest (Figure 1). There was also a significant difference in the ratio of bract length to corolla length. *D. rubra* had the greatest coverage by its bract, and *A. tetragonus* the least (Figure 2).

Nectar production also varied between species in a variety of ways. First, the total volume produced by each species was significantly different. *Drymonia rubra* produced the greatest amount of nectar, followed by *A. tetragonus* and *B. Formosa*, which were similar in the volume of nectar produced (Figure 3). They also produced significantly different sugar concentrations of *Drymonia rubra* produced nectar with the highest concentration and *B. Formosa* the lowest (Figure 4). However, there was not a significant difference between B. Formosa and A. tetragonus (Fisher's PLSD, p=0.1425). They also differed in the first day of nectar production. *Alloplectus tetragonus* produced nectar on the seventh day, *B. Formosa* on the fourth day, and *Drymonia rubra* on the second day (Figure 5). Finally, each species differed in the average life span of its flowers. *D. rubra* lived for an average of 4.30 days, *A. tetragonus* for 6.45 days, and *B. Formosa* for an average of 14.36 days.

In addition, both nectar volume and sugar concentration were analyzed over time for each species of Gesneriaceae (Tables 2 and 3). The volume of nectar in *B. Formosa* did not vary significantly with each day (Friedman test, tied p=0.0909, corrected $X^2 = 12.308$), nor did the volume of *D. rubra* (tied p= 0.1116, corrected $X^2 = 6.000$). The volume of *A. tetragonus* did vary significantly with each day, gradually increasing in volume as time went on (tied p = 0.0223, corrected $X^2 = 11.412$). The sugar concentration in nectar varied significantly with each day in all three species. *D. rubra* showed the greatest concentration on the second day (tied p= 0.0002, corrected $X^2 = 19.889$). *Alloplectus tetragonus* increased in sugar concentration each day (tied p = 0.0182, corrected $X^2 = 11.882$), and *B. Formosa* also increased its sugar concentration each day (tied p = 0.0328, corrected $X^2 = 10.500$).

DISCUSSION

All three species of Gesneriaceae differed significantly in morphological and physiological characteristics, but experienced very similar robbery and pollination rates. Thus, it may seem that each of my hypotheses was rejected and none of the studied characteristics have an effect on robbery or pollination rates. However, I argue that corolla length, bract coverage, nectar volume, sugar concentration, and nectar production rate are all uniquely at work on each species, ending with a similar outcome. While *D. rubra* makes use of large bracts to protect itself against robbery, *A. tetragonus* and *B.*

Formosa produce smaller amounts of weaker nectar to make themselves less attractive to robbery.

First, *D. rubra* produced high sugar concentrations and high volumes of nectar beginning nearly the first day after opening. If then produced nectar continuously for a duration of about four days, which is in accordance with Wiehler who found *D. rubra's* longevity to be four days (1983). Since robbers probably prefer flowers with greater nectar volume and concentration, I hypothesized that these flowers would experience greater robbery rates. This was supported by the finding that hummingbirds in a lab preferred the most concentrated solution, up to 49% (Hainsworth and Wolf 1976 in Bolten 1978). There are few reasons why *D. rubra* may not have experienced higher pollination or robbery rates. For one, Baker (1975) found that as the sugar concentration increases, the viscosity increases as well, which leads to a low foraging efficiency for hummingbirds. Thus, hummingbirds may actually choose flowers that do not have such a high sugar concentration. Secondly, *D. rubra* had significantly larger bracts than the other species, which may compensate for its high nectar volume and sugar concentration.

Unlike *D. rubra*, *A. tetragonus* had very short bracts. Besides short bracts, it had the longest corolla of the three species. Although this study did not show significant differences in robbery or pollination rates due to corolla length, another study found a positive correlation between the length of the corolla tube and the percentage of nectar robbery (Le 1994). This result was expected since a long corolla would limit the number of species that can access the nectar found deep within (Nilsson 1988 in Fenster 1991). Perhaps *A. tetragonus* was not more susceptible to robbery because of its low levels of nectar production. It produces low volumes of nectar at fairly low sugar concentrations later on it its life. In addition, many individuals never produced nectar. Thus, potential robbers and pollinators may be less attracted to this species of flower. Its meager rewards may not outweigh the energy spent to get them.

Finally, the defense mechanism of *B. Formosa* may function in the same way. It produces the least amount of nectar at the lowest concentration. It also begins producing nectar late in its life and has a very long life span (about 14 days). Each flower is unpredictable in its nectar production and low in volume and concentration at best. Therefore, *B. Formosa* should not be highly sought after by nectar robbers. Additionally, *B. Formosa* has a short corolla and should not be robbed even by short-billed hummingbirds.

Pollination rates among species did not vary significantly between species either, even though nectar production among species did. Low rates of nectar production, as seen in *B. Formosa* and *A. tetragonus*, may be beneficial for pollination rates as well as minimizing robbery rates. While some flowers are empty, others are still producing nectar. Since the 'cheaters' cannot be discerned from other flowers, the pollinator will still visit them. Thus, the flower expends less energy and is still successfully pollinated. This is known as the 'lucky hit' strategy (Southwick 1982). This theory is supported since *D. rubra,* which did have high rates of nectar production, did not experience significantly greater rates of pollination.

Finally, there may not have been many nectar robbers present in the forest during the study period or the foraging pressures may have not been high. Hummingbirds that are known to rob flowers, such as the Stripe-tailed hummingbird, may have been primarily feeding on other flowers. This is supported by the fact that I only saw Striped-tailed hummingbirds at the feeders by the information center, whereas I saw Green Hermits pollinating D. rubra nearly everyday. Perhaps when resources are more limited, nectar robbery rates would increase, and morphological and physiological characteristics would affect robbery rates.

This study provided insight to the cycle of nectar production in three species of Gesneriaceae, as well as morphological adaptations that may influence robbery and pollination rates. While significant differences were found in these characteristics between each species, there were not significant differences in robbery or pollination rates. These characteristics may simply not have an effect on robbery or pollination rates or robbery rates may have been so low that their effect was not manifested. It would be interesting to determine robbery rates at different times of the year to see if they change. If robbery rates do increase, one might expect the above characteristics to better protect certain species of flowers from robbery.

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Table 1. Hummingbirds seen in the Santa Elena Reserve between November 1 and November 20, 2000.

Hummingbird Species	Present	Guild
Green Hermit	Yes	Trapliner
Violet Sabrewing	Yes	Trapliner
Stiped-tailed hummingbird	Yes	Territorial
Coppery-headed Emerald	Yes	
Purple-throated Mountain-gem	Yes	Territorial
Green-crowned Brilliant	Yes	Trapliner

Table 2. The daily change in sugar concentration in three species of Gesneriaceae.

species	Tied P	Corrected X'	n	day	Sugar concentration	*Se*
Drymonia rubra	0.0002	19.889	17	1	8.86	3.15
				2	15.12	3.55
				3	10.52	3.21
				4	11.67	3.59
Alloplectus tetragonus	0.0182	11.82	15	1	0	0
				2	0.07	0.07
				3	3.61	1.93
				4	4.6	1.84
				5	6.5	2.46
Besleria formosa	0.0328	10.5	9	1	0	0
				2	0	0
				3	0.78	0.78
				4	6.5	1.93
				5	6.8	2.45

Table 3. The daily change in nectar volume in three species of Gesneriaceae

species	Tied P	Corrected X'	n	day	Nectar concentration	*Se*
Drymonia rubra	0.1116	6	6	1	0.52	0.27
				2	2.37	0.8
				3	3.31	0.49
				4	0.8	1.47
Alloplectus tetragonus	0.0223	11.412	15	1	0	0
				2	0.07	0.07
				3	0.15	0.08
				4	0.27	0.11
				5	0.65	0.32
Besleria formosa	0.0909	12.308	8	1	0	0
				2	0.01	0.01
				3	0.02	0.01
				4	0.12	0.04
				5	0.21	0.09
				6	0.11	0.06
				7	0.12	0.06
				8	0.22	0.09

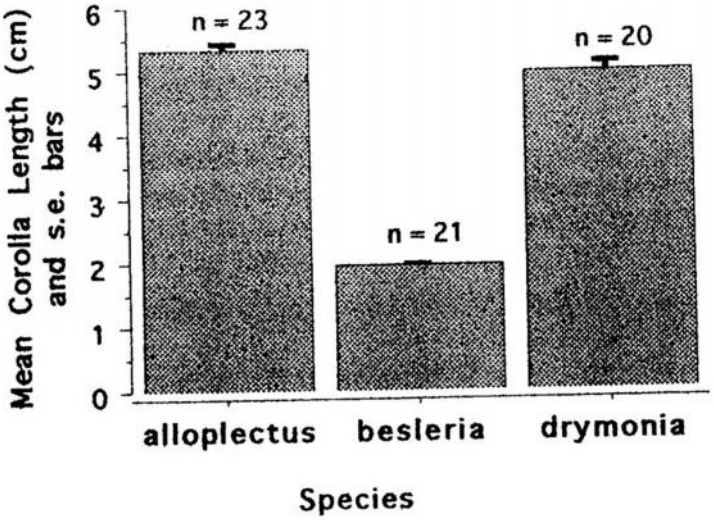

Figure 1. The mean corolla length of three species of Gesneriaceae. Differences between lengths were significant (One-way ANOVA, $F = 439.294$, d.f. $=1$, $p < 0.0001$). The number of individuals (n) is listed above.

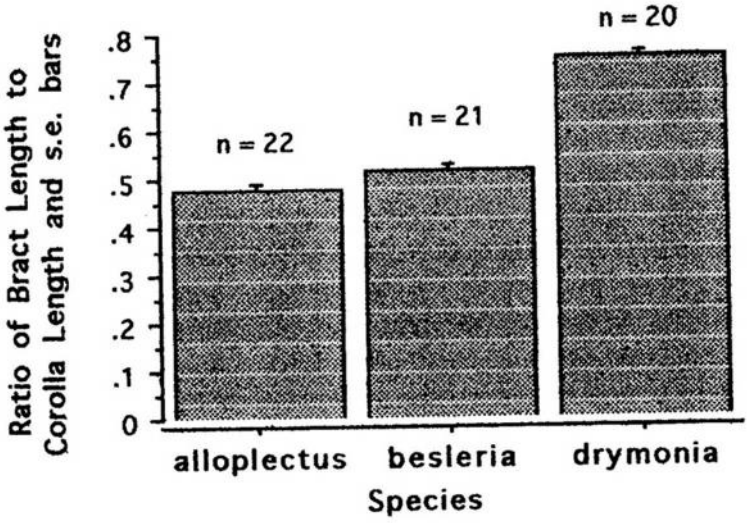

Figure 2. A comparison of bract coverage of three species of Gesneriaceae. There was a significant difference between all species (One-way ANOVA, $F = 161.145$, d.f. $= 1$, $p < 0.0001$). The number of individuals (n) is listed above.

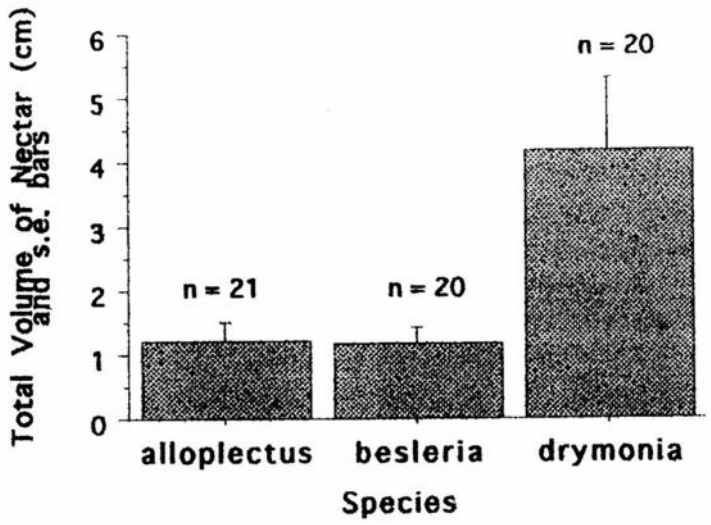

Figure 3. The total volume of nectar in three species of Gesneriaceae (One-way ANOVA, F = 6.101, d.f. = 1, p = 0.0039). There were significant differences between *A. tetragonus* and *D. rubra* (Fisher's PLSD, p = 0.0035), and between *B. formosa* and *D. rubra* (p = 0.0037). There was not a significant difference between *A.tetragonus* and *B. formosa* (p = 0.9873). The number of individuals (n) are listed above.

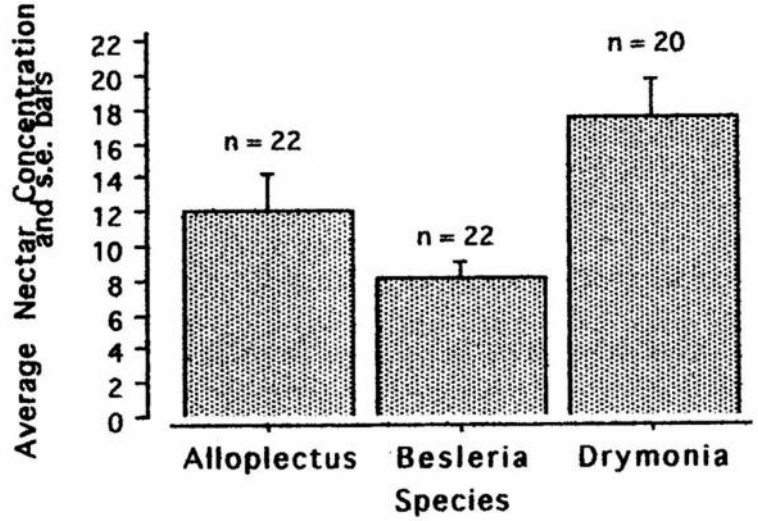

Figure 4. The average sugar concentration of three species of Gesneriaceae varied significantly (One-way ANOVA, F = 6.389, d.f. = 1, p = 0.003). There was not a significant difference in sugar concentration between *A. tetragonus* and *B. formosa* (Fisher's PLSD, p = 0.1425). The number of individuals (n) is listed above.

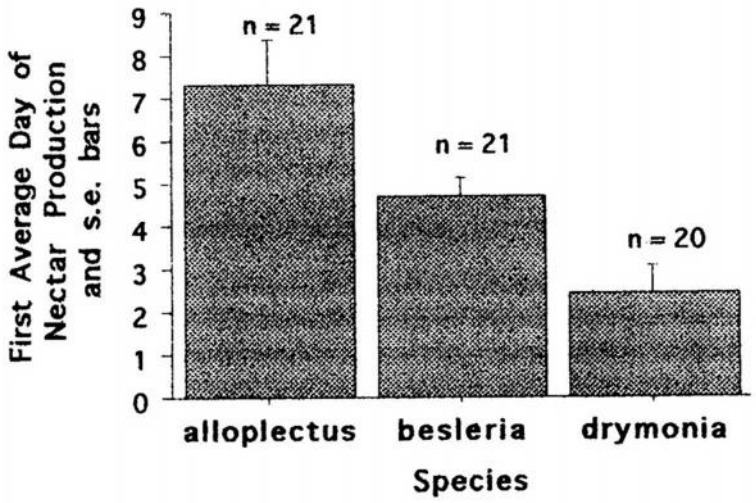

Figure 5. The first day of nectar production varied significantly between three species of Gesneriaceae (One-way ANOVA, F = 10.014, d.f. = 1, p = 0.0002). The number of individuals (n) is listed above.