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ABSTRACT

Competition between pollinators, such as nectar-eating birds, bats, and small insects, plays an important role in understanding resource distribution among feeding guilds (Murray et al. 2000). This study suggested that territorial behaviors exhibited by hummingbirds are not hardwired, but rather, they may be affected by abiotic factors such as weather conditions. An individual may increase its energy budget through selective defense of a plant. Hummingbird and butterfly visits to and agonistic interactions (i.e. chases) at a *Stachytarpheta jamaicensis* plant were observed for a total of 40 hours and weather conditions were quantified. As the activity of butterflies (a competing species) increased in good weather, hummingbird defense of a plant decreased for species known to be territorial. Conversely, during adverse weather conditions, butterfly activity was depressed and energy used for defense of a plant was beneficial for hummingbirds. Observations showed that species typically known for traplining also displayed territorial behavior during these conditions. Multiple regression analyses showed that hummingbird visitation increased significantly as wind speed increased ($R^2 = 0.11$, $F = 0.05$, $p < 0.037$, N= 668). Butterfly visitation increased significantly with an increase in light intensity ($R^2 = 0.55$, $F = 0.0001$, $p < 0.012$, N= 926) and decreased with increased cloud cover ($R^2 = 0.55$, $F = 0.0001$, $p < 0.004$, N= 926) and index of rainfall ($R^2 = 0.55$, $F = 0.0001$, $p < 0.008$, N= 926). One-way ANOVAs showed that there were significant differences between the number of interactions and all weather parameters (temperature $F = 76.14$, $p < 0.0001$, df = 152; light $F = 29.57$, $p < 0.0001$, df = 123; wind $F = 9.66$, $p < 0.0001$, df = 123; cloud $F = 24.00$, $p < 0.0001$, df = 123; rain $F = 13.44$, $p < 0.0001$, df = 123).

RESUMEN

La competencia entre los polinizadores, como los pájaros, murciélagos, e insectos pequeños que son nectarívoros, es una parte integral de la distribución de recursos entre gremios (Murray et al. 2000). Este estudio sugirió que los carácteres territoriales exhibidos por los colibríes no son completamente innatos;por el contrario, son modificados por condiciones abióticas como el clima. El individuo puede aumentar su presupuesto energético por medio de la defensa selectiva de una planta. Las visitas e interacciones agonísticas (persecución) por los colibríes y las mariposas en una planta de *Stachytarpheta jamaicensis* fueron observadas durante un total de 40 horas y las condiciones climáticas fueron cuantificadas. Cuando la actividad de las mariposas (un competidor de colibríes) aumentó durante clima óptimo, la defensa de una planta por los colibríes desminuyó en el caso de las especies territorial. Por el contrario, durante clima desfavorable, la actividad de las mariposas desminuyó y la energia usada para defender la plantabenefició a los colibríes. Se observó que las especies conocidas como colibríes errantes también mostraron un carácter territorial durante estas condiciones. Análisis de regresiones múltiples encontraon que las visitas de colibríes aumentaron con el incremento en la velocidad del viento ($R^2 = 0.11$, $F = 0.05$, $p < 0.037$, N= 668). Las visitas de mariposas aumentaron con el aumento en la intensidad de la luz ($R^2 = 0.55$, $F = 0.0001$, $p < 0.012$, N= 926) y desminuyó con el aumento del índice de nubosidad ($R^2 = 0.55$, $F = 0.0001$, $p < 0.004$, N= 926) y de precipitación ($R^2 = 0.55$, $F = 0.0001$, $p < 0.008$, N= 926). Los análisis de varianza mostraron diferencias significativas entre el número de interaciones y todos los parámetros del clima (temperatura F =

76.14, $p < 0.0001$, df = 152; luz $F = 29.57$, $p < 0.0001$, df = 123; viento $F = 9.66$, $p < 0.0001$, df = 123; nubosidad $F = 24.00$, $p < 0.0001$, df = 123; precipitación $F = 13.44$, $p < 0.0001$, df = 123).

INTRODUCTION

Hummingbirds (Trochilidae) are the predominant pollinators among the birds of montane Central America. In Monteverde, Costa Rica, nearly 9% of the flora is hummingbird pollinated. Bats and various insects, including butterflies, beetles, and moths, constitute the rest of the pollinating fauna with about 85% of plants adapted specifically for dispersal by insects (Murray et al. 2000). A high demand by many pollinators creates a competitive dynamic that allows animals to share resources inter-specifically through territoriality and antagonistic interactions (Miller 1967). Resource use by hummingbirds is separated into two categories: territorial or traplining (Hilty 1994), and species are categorized by their most common (i.e. typical) behaviors (Stiles and Skutch 1989; Table 1). Territorial species guard plants that are rich in nectar and will exhibit aggressive behaviors, such as chasing, in order to restrict flower access for other potential visitors. A study done by Primack and Howe (1975) on the competition between hummingbirds and skipper butterflies on a *Stachytarpheta jamaicensis* plant found that the aggressive behavior of a territorial *Amazilia* hummingbird restricted visitation of skippers to a lower part of the plant. Further, it was observed that hummingbird intruders were also chased away frequently.

Physiological differences between hummingbirds and butterflies, such as in thermoregulatory systems, may constrain butterfly visits to a food source but not restrict hummingbirds. According to Suarez and Gass (2002), in subalpine meadows where morning are cold, hummingbirds are able to achieve a net energy gain in the face of the high energetic costs associated with thermoregulation and flight. Endothermy in hummingbirds allows them to maintain a stable body temperature while poikilothermic butterflies require radiation from the sun or other heat sources in order to regulate their fluctuating core temperature. This indicates that weather conditions such as light intensity and cloud cover should have an impact on the number of visits to flowers and, hence, the interactions between the two taxa. Thomas et al. (1986) found that during adverse weather conditions (e.g. low temperature and high wind speed), butterfly visitation decreased on a *Hamelia patens* plant while hummingbird visitation and defense of the plant increased. During optimal weather conditions (e.g. higher temperatures and low wind speed), butterfly visitation was greatest and hummingbird activity was depressed. This also meant that interactions between hummingbirds and butterflies were less frequent due to the decrease in the number butterfly visitors. During the butterflies' peak activity, the resource was depleted so that the cost of defending the plant for the hummingbird exceeded the benefits.

These results show that territorial hummingbirds may not be restricted by weather conditions but they may be constrained by the energy cost of defending a plant against numerous competitors (Thomas et al. 1986). Although nectar is high in caloric value, the energy needs of hummingbirds are great due to the animals' small body size and rapid metabolic rates, making their use of resources important to sustaining their caloric needs (Stiles and Skutch 1989).

This study addresses the effect of weather on the visitation by hummingbirds and butterflies on *Stachytarpheta jamaicensis* (Verbenaceae) and the dynamics of interspecific competition between these visitors. I suggest that adverse weather conditions will have a positive correlation with hummingbird territoriality and a negative correlation with butterfly visitation, while in optimal weather conditions butterfly visitation will be greatest and hummingbird territoriality will decrease. Evidence for these hypotheses may show that resource use exhibited by hummingbirds is facultative, not hard-wired, and abiotic factors, such as weather, may contribute to changes in these typical behaviors.

MATERIALS AND METHODS

This study was carried out over a three-week period during the early November 2005 transition from wet to dry season, on private property in Cañitas, Monteverde, Costa Rica where an *S. jamaicensis* (180 cm tall and 508 cm wide) was planted as an ornamental. Weather measurements were taken every 20 minutes between the hours of 0820-1220, and included temperature (º C), wind speed (m/s), cloud cover index (scale of 0-2; 0 clear, 1 mostly clear, 2 no visible sun outline), light intensity (LUX), and rainfall index (scale of 0-3: 0 no precipitation, 1 mist, 2 visible drop formation, 3 heavy rainfall). The numbers of visitations by hummingbirds and butterflies and interactions (i.e. chases) between hummingbird-hummingbird (h-h), butterfly-hummingbird (b-h; butterfly chases hummingbird), hummingbird-butterfly (h-b; hummingbird chases butterfly), and butterfly-butterfly (b-b) were recorded at a distance of 5 meters from the plant. A visit was when an animal would arrive to the plant, feed (sometimes several times in one visit) and then leave the plant. Adverse weather conditions were considered any combination of conditions where there was high precipitation (index of rainfall 2-3), low temperature (16-20 ºC), high wind speed (2.0-5.0 m/s), low light (10-50 LUX) or cloudy conditions (index of cloud cover 2). Multiple regression analyses were performed to compare all weather parameters versus the number of visitations and the number of interactions. One-way ANOVAs were performed to compare the mean at which interactions occurred during each weather parameter. A post-hoc Fisher's PLSD was used to determine the significance between interaction sets for each weather parameter.

RESULTS

Visitation Results

Multiple regression statistics showed that wind speed had a significant effect on hummingbird visitations to *S. jamaicensis* while light intensity, cloud cover, and rainfall all showed significant effects on butterfly visitations. With increasing wind speed, the number of hummingbird visitations also increased ($R^2 = 0.11$, $F = 0.05$, $p < 0.037$, N= 668; Figure 1). Butterfly visitations increased significantly as light intensity increased ($R^2 = 0.55$, $F = 0.0001$, $p < 0.012$, N= 926; Figure 2). As cloud cover and rainfall increased, butterfly visitations decreased significantly ($R^2 = 0.55$, $F = 0.0001$, $p < 0.004$, N= 926; Figure 2; $R^2 = 0.55$, $F = 0.0001$, $p < 0.008$, N= 926; Figure 2). All other parameters were shown to be non-significant.

Interaction Results

Temperature- A one-way ANOVA showed a significant difference between the temperatures and each interaction set observed ($F = 76.14$, $p = < 0.0001$, $DF = 152$; Figure 3). Furthermore, a post-hoc Fisher's PLSD showed that mean temperatures for b-b interactions were greatest at significantly higher temperatures (mean = 21.59 ºC) while h-h interactions were greatest at lower temperatures (mean = 17.39 ºC). Both b-h and h-b were greatest at the highest temperatures (mean = 22.44 ºC, 22.81 ºC respectively).

Light intensity- There was a significant difference between the light intensities for each interaction set observed (one-way ANOVA, $F = 29.57$, $p = < 0.0001$, $DF = 123$; Figure 3). The post-hoc Fisher's PLSD showed that the number of interactions for each set decreased significantly as light intensity decreased in the following order: b-b (mean = 82.11 LUX), b-h (mean = 55.27 LUX), h-b (mean = 37.76 LUX), h-h (mean = 31.11 LUX).

Wind speed- There was a significant difference between the wind speed and each interaction set observed (one-way ANOVA, $F = 9.66$, $p = < 0.0001$, $DF = 123$; Figure 4). Fisher's PLSD showed that interactions for b-b and b-h were significantly less frequent at high wind speed (mean = 1.27, 1.21 m/s respectively) than h-h (mean = 1.71 m/s). Interactions of h-b were most frequent at significantly lower wind speed than all others (mean = 0.70).

Cloud cover- There was a significant difference between the cloud cover and each interaction set observed (one-way ANOVA, $F = 24.0$, $p = < 0.0001$, $DF = 123$; Figure 4). Fisher's PLSD showed that the number of interactions for each set increased significantly as cloud cover increased in the following order: b-b (mean = 0.65), b-h (mean =1.33), h-b (mean =1.57), h-h (mean = 1.76).

Rainfall- There was a significant difference between the rainfall and each interaction set observed (one-way ANOVA, $F = 13.44$, $p = < 0.0001$, $DF = 123$; Figure 4). Fisher's PLSD showed that the number of interactions for each set increased significantly as rainfall increased in the following order: b-b (mean = 0.15), b-h (mean = 0.17), h-b (mean =0.50), h-h (mean = 0.87).

DISCUSSION

Weather conditions did have an effect on hummingbird and butterfly visits and interactions at *S. jamaicensis*. Specifically, significant results for light intensity, rainfall, and cloud cover demonstrated that as adverse weather increased, hummingbird visitation increased, while butterfly visitations decreased. Greater numbers of hummingbird visits during high wind speeds lent support for the hypothesis that adverse weather conditions would result in an increase in hummingbird visitation. Likewise, greater light intensity, and reduced cloud cover and rainfall, supported an increase in butterfly visitations due to optimal weather conditions. However, the R^2 value for wind speed was low, indicating a weak relationship, and that other factors were involved in determining hummingbird visits. Because this study was done in the beginning of the migratory or breeding season for certain species (Stiles and Skutch 1989), some days may have had more visits by transitory species or an increase in the number of hummingbirds exhibiting territoriality which decreased the number of total visits due to individuals guarding instead of coming and going from the plant as frequently (see description of visit in Methods).

Although, the number of visits for both animals did not have significant results for all weather parameters, trends show that hummingbird and butterfly visits are negatively correlated (Figure 5). As butterfly visits increased with optimal weather conditions, hummingbird visits decreased, and as adverse weather conditions increased, butterfly visits were depressed and hummingbird visits increased. The same trends were shown for all other weather parameters except for temperature. This could be because, although temperatures were high, other weather parameters may have been great as well. For instance, on warm days, wind speeds could have been high, reducing the number of butterfly visits. These trends show that the number of butterfly visits affects the number of hummingbird visits and that butterfly visits are related to weather conditions.

There was a significant difference between interactions and all weather parameters. As cloud cover and rainfall increased, h-b interactions increased, while under high light intensity, they decreased, showing that hummingbirds displayed more aggressive behavior in these adverse conditions than in optimal ones. This supports previous findings by Thomas et al. (1986), which showed that butterfly visitation was reduced by adverse weather conditions while hummingbird visitation and defense increased. Interactions between b-b and b-h were greater compared to h-h during high light intensity, and higher temperatures while h-h interactions increased compared to b-b and b-h during high wind speeds, increased cloud cover and high rainfall. It was also observed that hummingbird species that were listed in Stiles and Skutch (1989) as typically territorial species (Table 1) would show traplining behavior during periods of high butterfly activity at the plant and species typically known as trapliners would exhibit territoriality when butterfly activity at the plant was low. This change in behavior is consistent with energetic constraints on hummingbirds for defending a plant against large numbers of butterflies (Thomas et al. 1986) because traplining behavior is more beneficial to a territorial species if the net energy gain is greater by visiting many plants, or in the case of typically traplining species, the energy gain is greater for defending a plant that does not have as many competing animals.

These results show that abiotic factors do play a role in the behavior of hummingbird resource use. Feeding behaviors of hummingbirds are not hard-wired, but are adjusted for when energy gain is greatest for the individual. Visits in adverse weather are limited for poikilothermic butterflies that really on abiotic factors in order to thermoregulate, but are possible for endothermic hummingbirds that are more adaptable to changing weather conditions. In this way, hummingbirds may switch their typical resource-use behaviors in order to energetically benefit them best. This facultative behavior may allow more species to share the same plants through niche partitioning, and on the broader scale, allow more animals to effectively compete within feeding guilds.

Comments and Future studies

According to the results, differences between h-b and b-h interactions did not follow the prediction that as optimal conditions increased b-h interactions would be higher, and as adverse conditions increased, h-b interactions would be higher. I believe this was because these interactions were rare in the field (for b-h N = 6, for h-b N = 12) and therefore sample size was small and varied between the two sets. Even so, chases between the two were recorded. This supports Primack and Howe's (1975) finding that hummingbirds exhibit aggressive behavior against other hummingbirds and against butterflies. I believe there could have been significant results related to weather, had there been more time to collect a larger sample size.

This study was done during the transition period between wet and dry season. This time of year could have an influence on behaviors due to migrating species of both hummingbirds and butterflies, or the onset of mating season, which would cause animals to become more aggressive at food sources. Future studies could show how these behaviors differ across seasons.

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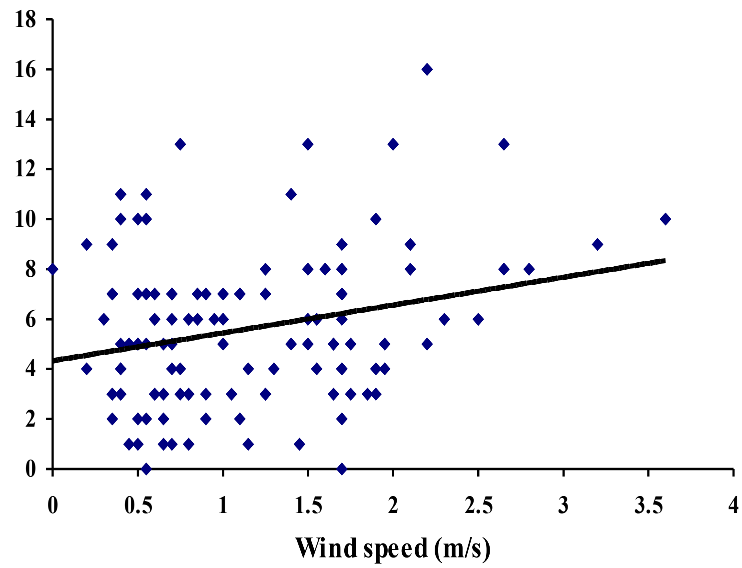

FIGURE 1. Relationship between the number of individuals of butterflies observed visiting *S. jamaicensis* and wind speed. As wind speed increases do hummingbird visits. See text for details.

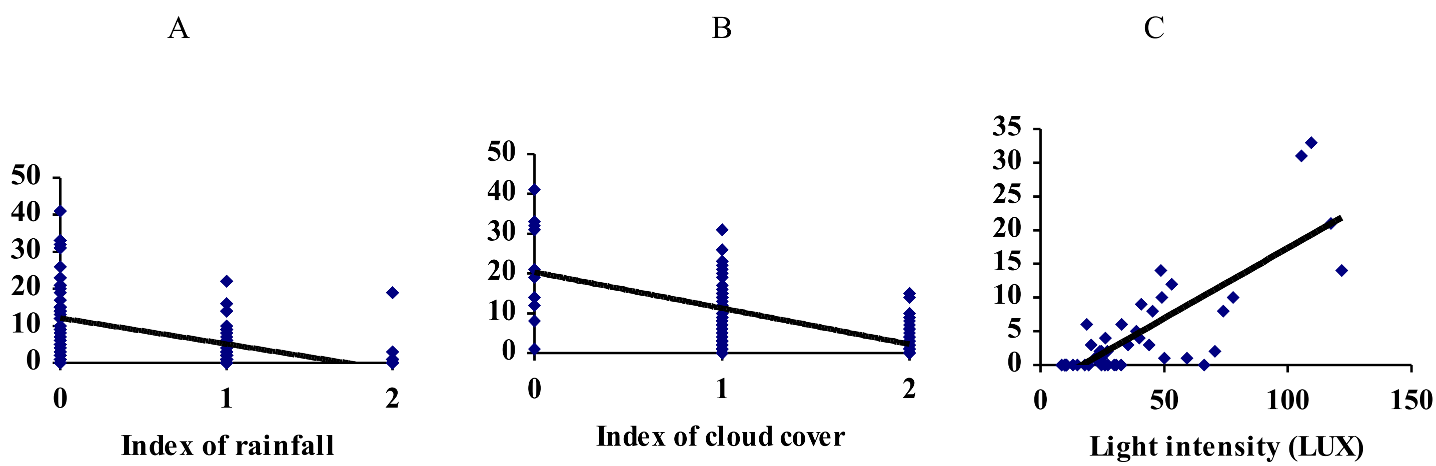

FIGURE 2. Relationship between the number of individuals of butterflies observed visiting *S. jamaicensis* and A) Index of rainfall B) Index of cloud cover C) Light intensity. As adverse weather increases (A and B) butterfly visits decrease. As optimal weather increases (C) butterfly visits increase.

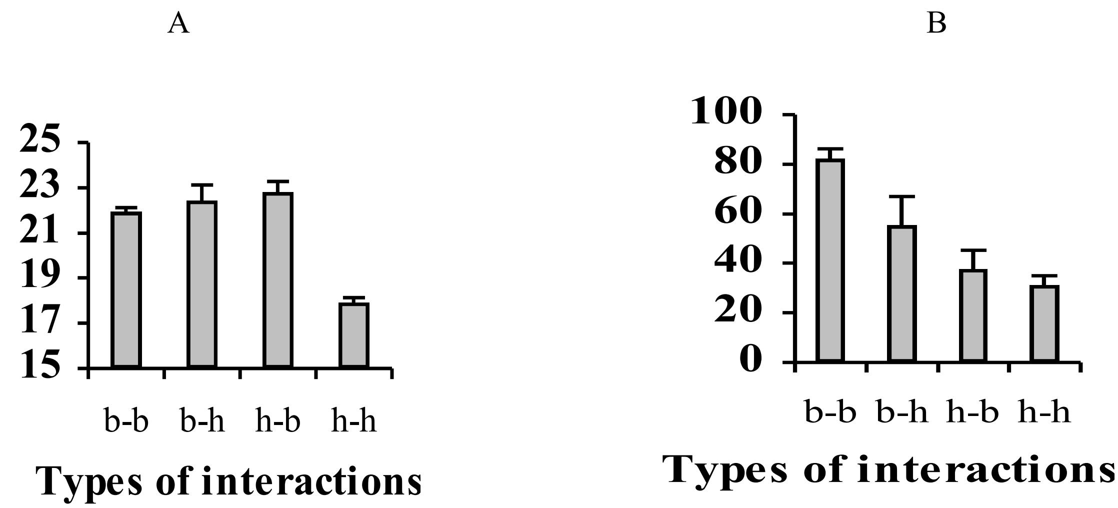

FIGURE 3. Mean at which greatest number of interactions occurred at *S. jamaicensis* versus optimal weather conditions A) Temperature B) Light intensity. b-b = butterfly chases butterfly, b-h = butterfly chases hummingbird, h-b = hummingbird chases butterfly, h-h hummingbird chases hummingbird. b-b and h-h chases negatively correlated. b-b interactions greatest during optimal weather conditions (see text). Bars represent standard error.

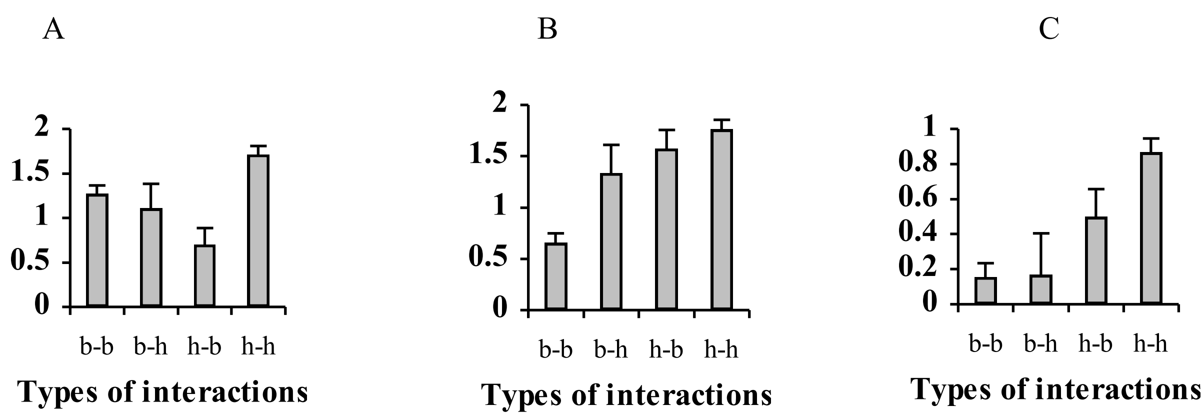

FIGURE 4. Mean at which greatest number of interactions occurred at *S. jamaicensis* versus adverse weather conditions A) Wind speed B) Index of cloud cover C) Index of rainfall. b-b = butterfly chases butterfly, b-h = butterfly chases hummingbird, h-b = hummingbird chases butterfly, h-h hummingbird chases hummingbird. b-b and h-h chases negatively correlated. h-h interactions were greatest during adverse weather conditions (see text). Bars represent standard error.

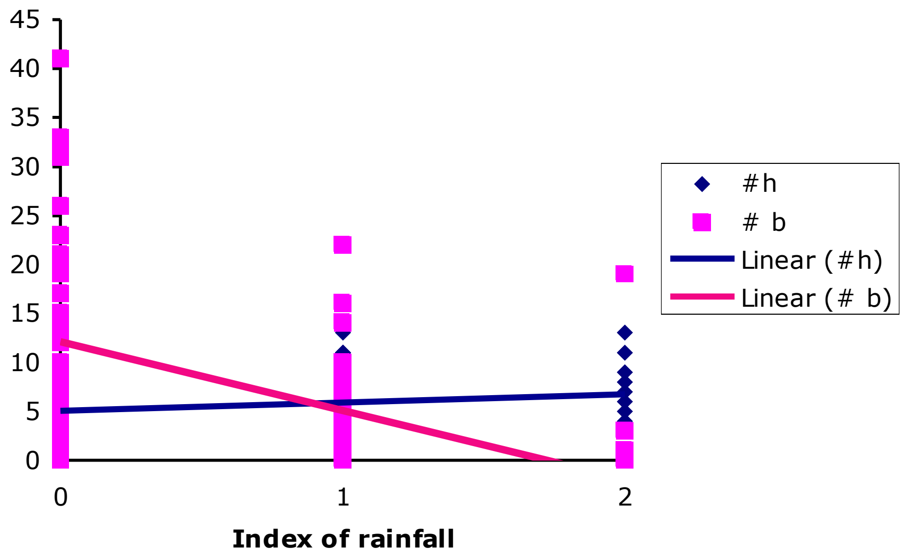

FIGURE 5. Trend lines applied to the number of hummingbird and butterfly visits as a function of rainfall. As butterfly visits decreased with increasing rainfall hummingbird visits increased with increasing rainfall. Hummingbird visits and butterfly visits are negatively correlated. For all other parameters showed similar trends (see text). This was not a statistical text.

TABLE 1. List of hummingbird (Trochilidae) species observed at *Stachytarpheta jamaicensis* and their typical feeding behaviors according to Stiles and Skutch (1989)

Species Name	**Common Name**	**Territorial**	**Trapliner**
Colibri thalassinus	Green Violet-ear	X	
Eupherusa eximia	Striped-tailed Hummingbird	X	
Elvira cupreiceps	Coppery-headed Emerald		X
Calliphlox bryantae	Magenta-throated Woodstar	X	
Archilochus colubris	Ruby-throated Hummingbird		X