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Impact of reward on floral mimics Lantana camara (Verbenaceae) and Epidendrum radicans (Orchidaceae)

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Impact of Reward on Floral Mimics *Lantana camara* (Verbenaceae) and *Epidendrum radicans* (Orchidaceae)

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ABSTRACT

The fitness of a non-rewarding plant species can be increased by the addition of another plant species with similar flowers and reward present if pollinators are unable to distinguish between the two species (Bierzychudek 1981). Floral mimicry occurs between species when three ecological conditions are met: the model and mimic species must coexist within flight range of an individual pollinator, plant species must share pollinator species, and pollinator individuals visiting one plant must also visit one or both of the other plant species (Bierzychudek 1981). Non-rewarding *Epidendrum radicans* (Orchidaceae) has been shown to be a Batesian mimic of rewarding *Lantana camara* (Verbenaceae). Although mimicry increases the fitness of Batesian species when plants are in close proximity, mixed patches are widely spaced, and patch sizes are small (Deacon 2000; Woo 2001), there is little known about floral reward's affect on the relationship. This study uses *L. camara* and *E. radicans* to test the impact of increased reward availability in model plants (*L. camara*) on pollinator visitation rates to both model and mimic plants. Two observation plots were constructed containing *L. camara* and *E. radicans*, where *L. camara* flowers in one plot were injected with a 20% sucrose solution. Plots were observed for butterfly visitation rates and monitored for pollinia removal from *E. radicans*. Increased reward in *L. camara* resulted in fewer visits to *E. radicans* flowers and *L. camara* inflorescences within the treated patch (three-way ANOVA: $F = 24.0506$; $df = 1$; $P < .0001$). In addition, *L. camara* inflorescences were visited longer with increased reward present (three-way ANOVA: $F = 5.88$; $df = 1$; $P < .05$). However, no difference was observed between pollinia removal between patches (Chi-square = 3; $df = 1$; $P > .05$). Different butterfly species had varying rates of visitation to the mimic species in response to an increased reward. *Danaus plexippus* visited 0.75 fewer *E. radicans* flowers, *Leptophobia aripa* visited 0.184 more flowers, and *Anartia fatima* visited 0.039 fewer *E. radicans* flowers (two-way ANOVA: $F = 3.7887$; $df = 2$; $P < .05$). As a result of increased reward, model and mimic species are negatively affected, due to a decrease in pollinator visitation rates. Prior research suggested rewarding flowers benefit most from being in close proximity to one another, in clumped patches (Deacon 2000). The results of this study suggest that *L. camara* may have been selected to produce a reward that favors a large number of visits to many flowers, which benefits the mimic as well. Although mimic flowers were visited, there was no affect on the pollinia removal from *E. radicans*, suggesting that patch size and density ultimately affect pollination rates of deceptive plants.

RESUMEN

El exito reproductivo de una planta que no ofrece ninguna recompensa al agregar una planta con flores similares que ofrezca una recompensa si el polinizador no es capaz de diferenciarlas. La planta que no ofrece recompensa *Epidendrum radicans* (Orchidaceae) es mimética de la especie *Lantana cámara* (Verbenaceae), que si ofrece recompensa. Este estudio utiliza *L. camara y E. radicans* para demostrar el impacto de un aumento en la disponibilidad de recompensa en plantas modelo (*L. camara*), en proporciones de visitas de polinizadores tanto a la planta modelo como a la mimética. Dos parcelas de observación fueron construidas conteniendo ambas especies de plantas, en donde las flores de *L. camara* en una parcela fueron inyectadas con una solución al 20% de sacarosa. Se determinaron las proporciones de visitas por parte de mariposas y la remoción de polinia en *E. radicans*. Aumento en el factor de recompensa en *L. camara* resulta en menos visitas a flores de *E. radicans* e inflorescencias de *L. camara* dentro del parche tratado (ANOVA: $F = 24.0506$; $df = 1$; $P < .0001$). En adición las inflorescencias de *L. camara* fueron visitadas por periodos más largos cuando se aumentó la recompensa (ANOVA: $F = 5.88$; $df = 1$; $P < .05$). Sin embargo no se observó ninguna diferencia en la remoción de polinia entre parches ($X^2 = 3$; $df = 1$; $P >$

.05). Diferentes especies de mariposa presentan diferentes proporciones de visitación a la especie mimética en respuesta al aumento en la recompensa; *Danaus plexippus* visita 0.75 menos *E. radicans* flores, *Leptophobia aripa* visita 0.184 más flores, y *Anartia fatima* visita 0.039 menos *E. radicans* flores (ANOVA: F = 3.7887; df = 2; P < .05). Como resultado del aumento de la recompensa, las especies modelo y miméticas se ven afectadas negativamente, debido al aumento en la proporción de visitas por parte de los polinizadores. Resultados posteriores sugieren un beneficio al aumentar la recompensa floral al estar cerca unos de otros, en parches agregados (Deacon 2000). Los resultados de este estudio sugieren que *L. camara* puede estar seleccionada a producir recompensa que favorece un gran número de visitantes a varias flores, lo cual beneficia al mimético también. Aunque flores miméticas fueron visitadas, no hay un efecto en la remoción de polinia de *E radicans*, sugiriendo que el el tamaño y la densidad del parche afectan finalmente las tasas de polinización de plantas engañosas.

INTRODUCTION

Plant-pollinator associations are not always mutualistic. Plants can attract pollinators using deceptive signals without rewarding them with nectar or pollen (Schluter 2008). Floral mimicry occurs under specific conditions between plants with larger inflorescence size, within small patches, and when model and mimic are in close proximity to one another (Deacon 2000; Dupre 2004; Woo 2001). However, Bierzychudek (1981) and Deacon (2000) suggest mimicry does not occur when plants are within dense patches, because pollinators are able to detect the unrewarding nature of the stand and leave before many flowers are pollinated. Additionally, mimicry is dependent on the foraging habits and presence of pollinators, with some flowering plants relying on deception or the lack of a collectable or consumable substance (Ackerman et al. 1994). Rewards may attract visitors and maintain high levels of pollination, but the cost of the reward production may outweigh the benefits, as nectar production can be expensive (Ackerman et al. 1994).

A non-rewarding species that mimics a rewarding model species and obtains a one-sided advantage through imitation is said to be a Batesian mimic (Dafni 1984; Roy and Widmer 1999). Batesian mimics do not reward pollinators and rely on morphological similarities including floral coloration and other shared attractive floral signals of the model species to successfully attract pollinators (Craig and Johnson 2008; Jersakova 2006; Roy and Widmer 1999; Schluter 2008). Floral mimicry is highly conditional, requiring specific ecological conditions necessary for mimicry to occur between a mimic and model species. These conditions include shared phenologies such as flowering time and color similarities, shared pollinators, and overlapping geographical ranges (Bierzychudek 1981; Schluter 2008).

Lantana camara (Verbenaceae) and *Epidendrum radicans* (Orchidaceae) are common weedy plants of Costa Rica. They have overlapping geographic ranges and prefer highly disturbed regions along roadsides or in pastures from 0-2000 meters in elevation (Gargiullo 2008; Schemske 1983; Todiza 1983). Further, they share similar floral phenologies in that both flower year round with red-orange and yellow inflorescence. These floral species are primarily pollinated by butterfly species, *Anartia fatima* and *Danaus spp*. (Schmeske 1983; Todzia 1983; Wolfe 1987). Studies suggest that the deceptive orchid *E. radicans* achieves higher pollinia removal through resemblance of rewarding Müllerian mimic species *L. camara* and *Asclepias curassavica* (Apocynaceae), and is a Batesian mimic (Deacon 2001; Dupre 2004; Jersakova 2006; Todzia 1983).

Studies of Batesian mimicry suggest deceptive plant species benefit in close proximity to rewarding plants because pollinators are more abundant near rewarding plants and are more likely to leave a plot when non-rewarding deceptive flowers are visited first within patches (Ackerman et al. 1994; Craig and Johnson 2008). However, it remains unclear whether increased visits by pollinators to mimic species within patches results from increased availability of reward. This study returns to the Batesian floral mimicry complex to test the impact of increased reward availability in model plants (*L. camara*) on pollinator visitation rates to model and mimic plants. Based on earlier studies by Ackerman et al. (1994) and Craig and Johnson (2008), I predict that increasing reward in model plants will result in a greater pollinator abundance to mimicry plants, therefore increasing visitation rates to adjacent mimic species and increasing the potential for pollination to occur in mimic plants. Batesian mimicry has both costs and benefits. While not producing a reward is more cost efficient for the plant, Batesian plants are dependent on the density and patch composition of model plants to attract pollinators (Ackerman et al. 1994).

MATERIALS AND METHODS

Study Site

This study took place from October 29, 2008 to November 13, 2008 on an inclined embankment along the roadside near the Miramontes Hotel in Cañitas, Costa Rica. Two sites, A and B, each composed of 11 *L. camara* inflorescences, containing 10-40 individual flowers per inflorescence, and eight *E. radicans* flowers, with one or two flowers per inflorescence were observed. *E. radicans* species were interspersed among the native *L. camara* plants on each site, with plants positioned so flowers were at similar heights. *E. radicans* were moved from a site in San Luis to Cañitas. The entire plant was uprooted and placed directly within the site. Because *E. radicans* has aerial roots, transplanted individuals did not require extra care (Gargiullo 2008). *L. camara* flowers in site B were injected with a 20% sucrose solution, using a 3 mL syringe, to increase the reward volume within the plot site at the beginning of each observation period.

Observations

Sites A and B were observed for the number and species of butterfly pollinators, flower species visited, and length of stay per flower to determine pollinator visitation rates. *E. radicans* flowers' pollen is packaged into pollinia, which attaches onto the base of the butterfly's proboscis when the flower is pollinated (Bierzychudek 1981). To determine the rate of visitation for *E. radicans* flowers, pollinia removal was also monitored within plot A and B. The presence or absence of pollinia was recorded at the beginning and end of each observation period. *E. radicans* flowers with pollinia removed were removed from the site and replaced with a new flower containing pollinia at the beginning of each observation period. Observation periods were roughly 30-90 minutes long. Sites A and B were located approximately 60 meters apart and observed between the hours of 8:30 am and 1:00 pm for a total of 1000 minutes.

Relevant Natural History

L. camara inflorescences were observed in this study as a single compound flower. Because 67% of inflorescences are contiguous or almost composite (Schemske 1976; Schemske 1983), consisting of several small flowers, many butterfly pollinators do not treat flower probing as an individual event. Rather, pollinators probe the majority of the flowers in an inflorescence at each feeding period. One *L. camara* inflorescence (21.8 mm +/- 0.9) is approximately equal to one *E.*

radicans flower (20mm) in diameter, resulting in equivalent floral displays per individual unit (Gargiullo 2008; Schemske 1976). If flowers of *L. camara* were observed for individual probing incidents by butterfly pollinators, differences in expected results would have been greater.

L. camara has axillary inflorescence that are broadly rounded and composed of yellow and orange-red flowers (Schemske 1983). Inflorescence diameter of *L. camara* is 21.8 mm +/- 0.9 (Schemske 1976). *L. camara* inflorescences in the study contain10-40 flowers per inflorescence. Similarly, *E. radicans* are comprised of yellow/orange and red inflorescence, with a flower diameter of approximately 20 mm (Gargiullo 2008; Todzia 1983).

RESULTS

Considering all visiting butterfly species, more nectar did not change visitation rates between patches. Nearly equal numbers of butterflies visited both patches, with 235 butterflies observed in patch A and 222 butterflies observed in patch B (Fig 1: Chi-square = 0.37; df = 1; $P < .001$). Although Plot A and B were visited equally by butterflies, pollinators did show a preference between model and mimic species between plots. In general, inflorescences of *L. camara* were visited more frequently than flowers of *E. radicans*. 182 flowers of *E. radicans* were visited by butterflies in patch A, and 102 flowers were visited in patch B with increased reward. Additionally, 64 more inflorescences of *L. camara* were visited in patch A than in patch B (Fig 2: Chi-square = 6.49; df = 1; $P < .05$; Chi-square = 26.04; df = 1; $P < .001$). Consequently, increasing reward availability within a plot negatively affected model and mimic floral species, as both were visited fewer times within the treated plot, reducing the possibility of pollination to occur.

Although pollinators visited both types of plants more in patch A, butterflies on average spent longer periods of time probing plants in patch B. The explanation of fewer visits to inflorescences and flowers with added nectar is depicted in Figure 3, by average time spent per individual within plots. When nectar was added to patch B, the time spent on inflorescences dramatically increased. Inflorescences of *L. camara* were visited on average 33.072 +/- SE seconds longer in patch B with additional reward present, while flowers of *E. radicans* were observed to be probed for less time in the treated patch B, by 0.329 +/- SE seconds (Fig 3; three-way ANOVA: F = 24.0506; df = 1; $P < .0001$). In plot B, butterflies were observed probing *L. camara* inflorescences for longer periods of time, and visited fewer flowers. This suggests that fewer inflorescences were required by butterflies to be full.

Although three species of butterflies of varying sizes were commonly observed visiting patches, *Anartia fatima* (Nymphalidae: Nymphalinae), *Danaus plexippus* (Nymphalidae: Danainae), and *Leptophobia aripa* (Pieridae), there was no significant difference between the average amount of time spent within the patches or on individual plant species by butterflies (Fig 3; three-way ANOVA: F = 2.8492; df = 1; $P > .05$; three-way ANOVA: F = 0.9127; df = 2; $P > .05$). D. plexippus was observed spending on average the longest time within plot A and B, 37.471 +/- SE, and 86.759 +/- SE, respectively (Fig 6).

Overall, fewer visits to *E. radicans* flowers resulted in a decreasing trend in the number *E. radicans* pollinia removed from patched with nectar added to *L. camara* flowers (B)(Fig 4: Chi-square = 3; df = 1; $P > .05$). Patch A, without additional nectar had 52 pollinia removed, while patch B had 35 pollinia removed from flowers (Fig 4).

When examining the most common butterfly visitors observed within patches A and B by species, *A. fatima*, *D. plexippus*, and *L. aripa* , each responded differently to the increasing reward availability of *L. camara* in patch B. Butterfly species *A. fatima* visited 178 flowers and inflorescences in patch A and 195 individuals in patch B. Butterfly species *L. aripa* visited 45 flowers and inflorescences in patch A and 3 individuals in patch B. Lastly, *D. plexippus* visited 12 individuals in patch A and 18 flowers and inflorescences in patch B (Fig 5: Chi-square = 37.992; df = 2; $P < .0001$). It appears the *D. plexippus* is the major species responsible for pollinia removal from *E. radicans* flowers, as is visited the most *E. radicans* flowers per individual per butterfly species (Fig 7). Additionally, *D. plexippus* was the only species observed visiting more *E. radicans* flowers when the reward to *L. camara* flowers was not enhanced in patch A (Fig 7).

Considering only *E. radicans* flowers, which accounted for 33.3% of total visits, butterfly species differed in the number of flowers visited per individual (Fig 7; two-way ANOVA: F = 2.8188; df = 5; $P < .05$). Trends suggest that *D. plexippus* responded to increased nectar by visiting slightly fewer flowers, 0.75, while *L. aripa* responded to increases in nectar by visiting slightly more flowers, 0.184. Lastly, little change was observed between the number of flowers *A. fatima* visited, 0.039 fewer flowers visited (Fig 7; two-way ANOVA: F = 3.7887; df = 2; $P < .05$; two-way ANOVA: F = 2.8791; df = 2; $P > .05$).

Again, only considering *L. camara* inflorescences, pollinators were observed visiting similar numbers of inflorescences within patches. *A. fatima* and D. *plexippus* were observed visiting on average more *L. camara* inflorescences in patch B, 0.372 and 0.143 more inflorescences respectively. However, *L. aripa* was observed visiting on average 0.373 fewer inflorescences in patch B. Trends were not observed between butterfly species and number of inflorescences visited in response to increased reward (Fig 8; two-way ANOVA: F = 4.9485; df = 5; $P < .001$; two-way ANOVA: F = 0.0552; df = 1; $P > .05$; two-way ANOVA: F = 2.267; df = 2; $P > .05$; two-way ANOVA: F = 1.6144; df = 2; $P > .05$).

DISCUSSION

Previous floral mimicry studies suggest that mimicry occurs under very specific and controlled conditions (Bierzychudek 1981). Dupre (2004) observed a floral mimicry complex occurring between *Lantana camara*, *Epidendrum radicans*, and *Asclepias curassavica*, in which patch sizes and densities were controlled. The data is this study also suggests that mimicry is occurring between *Lantana camara* and *Epidendrum radicans* when plants were combined in small patches, as butterflies visited both model and mimic plants. Unlike the theory presented by Ackerman et al. (1994) in which pollinators are more likely to leave the patch after visiting a non-rewarding flower, pollinators were observed visiting multiple flowers and inflorescences within a patch after visiting the non-rewarding mimic. However, pollinator species prefer the model species containing a reward to the non-rewarding mimic species.

In response to increased nectar availability in inflorescences of *L. camara* in patch B, butterflies visited significantly fewer *E. radicans* flowers and *L. camara* inflorescences. This was due to increases visitation length to *L. camara* inflorescences, reducing foraging activity within patch B. Consequently, increasing nectar within model plants negatively affected visitation rates to model and mimic species, reducing the possibility of pollination to occur. Although no significant differences were observed in pollinia removal between the normal reward patch A and increased reward patch B, trends were observed in which pollinia removal from *E. radicans* flowers decreased with increase reward.

Additionally, trends in butterfly preferences were observed for mimic species. *D. plexippus* appears to be the major species responsible for pollinia removal from *E. radicans* flowers, as it visited the most flowers per individual per butterfly species in both patch types. *D. plexippus* was the only species observed visiting more *E. radicans* flowers when the reward to *L. camara* flowers was at normal levels in patch A.

Because Batesian species do not produce a reward, thus relying on models to aid in the attraction of pollinators (Craig and Johnson 2008; Jersakova 2006; Roy and Widmer 1999; Schluter 2008), Batesian species are dependent on the phenology and attractive characteristics of their models. Therefore, Batesian species pollination success is also dependent on the model species. If model flowers produce high floral densities within a patch and consequently increase the nectar content within the patch, the mimic is also impacted. As observed in this data, mimics are negatively impacted due to increased nectar concentration within patches. Despite the benefits associated with floral mimicry, including less energy invested into reward production, mimics are highly vulnerable, as they have no control over reward production or pollinator attraction (Ackerman et al. 1994).

In this study, both *L. camara* and *E. radicans* benefited from the normal concentration of reward offered by *L. camara*, the model species. This suggests that selection of the model for optimal pollination based on nectar levels offered to pollinators, also evolutionarily assured optimal pollination to the mimic species. However, only one set of mimics was observed within a controlled environment. Therefore, no conclusions can be formed about reward and pollinator interaction for all floral mimics.

To further investigate the study of floral mimicry and the impact of floral reward on pollination, further studies should concentrate on observing more paired patches, with normal reward and with increased reward, as well observing individual flower probing on *L. camara*. Because the Batesian mimic, *E. radicans* is widely accepted as part of a three-plant mimicry complex with Müllerian mimics, *L. camara* and *A. curassavica*, it would be interesting to repeat the studying including model species *A. curassavica*. Lastly, observing the impact of floral abundance and density on mimic pollination rate would further the study in the field of mimicry.

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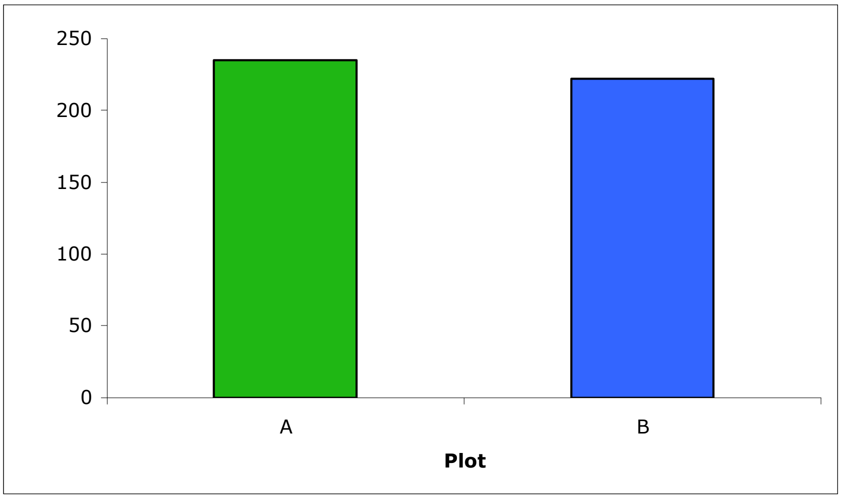


FIGURE 1. Total butterfly visits to inflorescences of *Lantana camara* and flowers of *Epidendrum radicans* in patches with no added reward to *L. camara* flowers (A) compared to those whose flowers had additional 20% sucrose added (B).

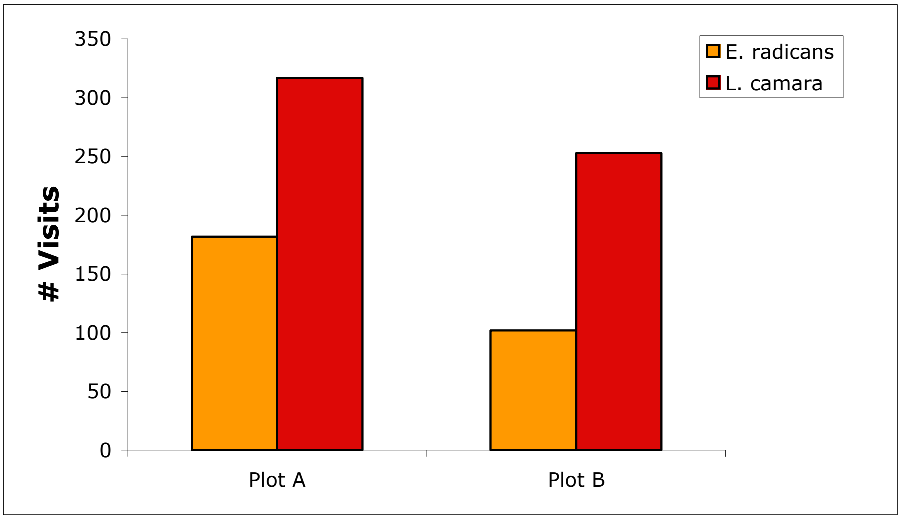
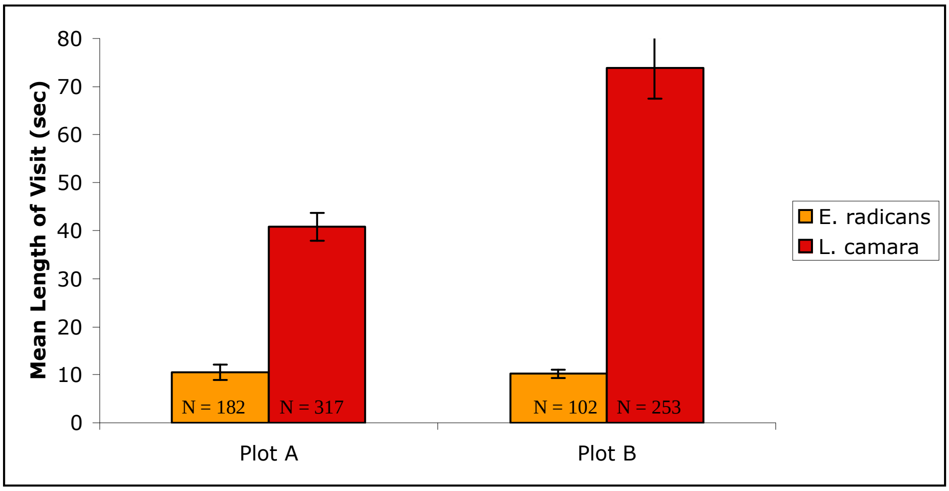


FIGURE 2. Total butterfly visits to flowers of *Epidendrum radicans* (orange) and inflorescences of *Lantana camara* (red) in patches with no added reward (A) compared to *L. camara* inflorescences with an additional 20% sucrose solution (B). The patch with no added reward (A) had 80 more butterfly visits to flowers of *E. radicans* and 64 more butterfly visits to inflorescences of *L. camara.*



FIRGURE 3. Average length of butterfly visitation to flower of *Epidendrum radicans* and inflorescences of *Lantana camara* in patches with no added reward (A) compared to patches where 20% sucrose was added to inflorescences of *L. camara* (B). Inflorescences of *L. camara* within patch (B) were visited on average 33.072 seconds longer. (Error bars represent +/- SE)

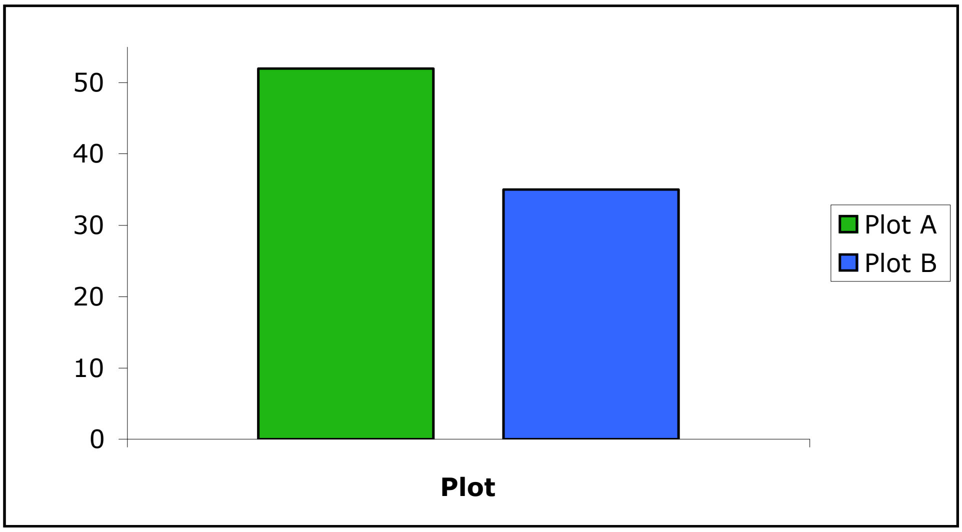


FIGURE 4. Total pollinia removed from flowers of *E. radicans* within patch of no added reward (A) compared to patches with an additional 20% sucrose added to flowers of *Lantana camara* (B). 52 pollinia were removed from flowers of *E. radicans* in patch A, while 35 pollinia were removed from patch B with increased reward.

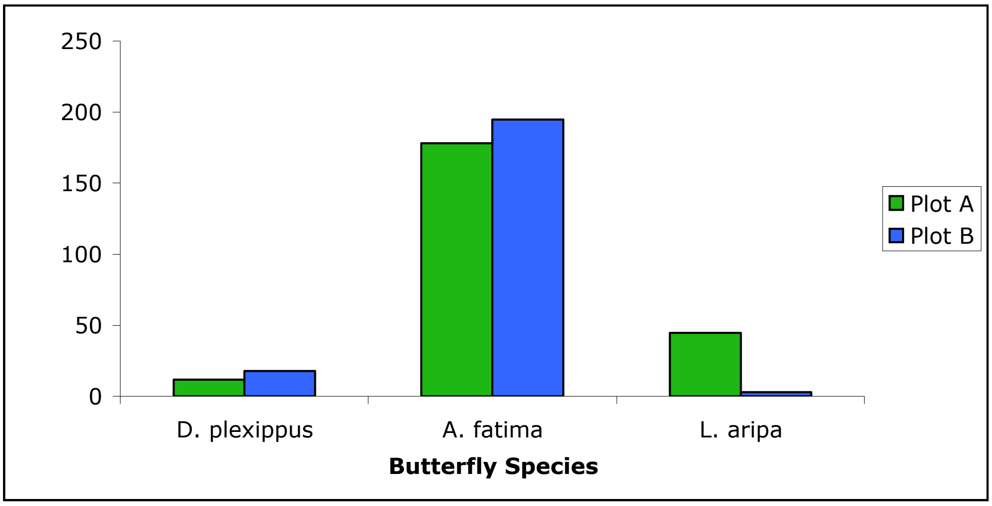


FIGURE 5. Total visits by most common butterflies to flowers of *Epidendrum radicans* and inflorescences of *Lantana camara* in patches without added reward (A) compared to patches with 20% sucrose added to flowers of *L. camara* (B). The most common pollinators within both patch A and B were *Danaus plexippus*, *Anartia fatima*, and *Leptophobia aripa.* Butterfly species *A. fatima* visited 178 flowers and inflorescences in patch A and 195 individuals in patch B. Butterfly species *L. aripa* visited 45 flowers and inflorescences in patch A and 3 individuals in patch B. Lastly, *D. plexippus* visited 12 individuals in patch A and 18 flowers and inflorescences in patch B.

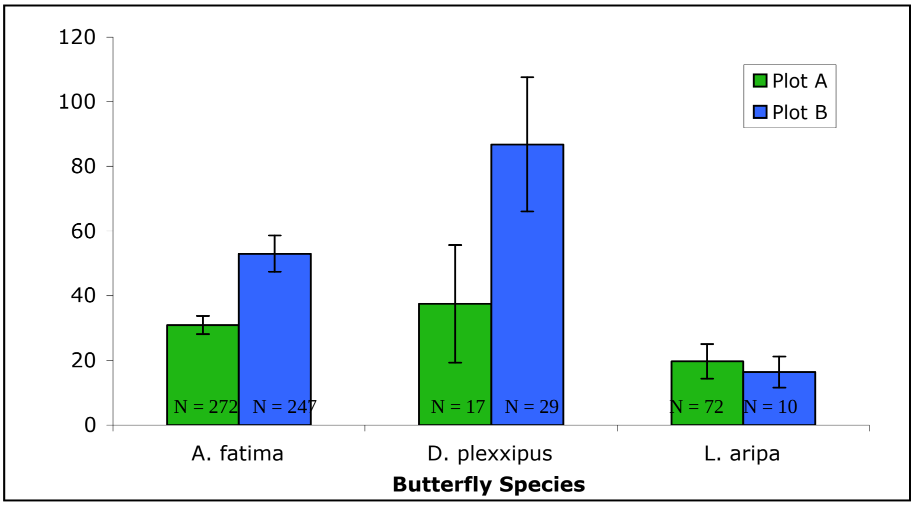


FIGURE 6. Average time spent probing flowers of *Epidendrum radicans* and inflorescence of *Lantana camara* in patches without added reward (A) compared to patches with 20% sucrose added to flowers of *L. camara* (B). Average time is divided for the three most common butterfly species within both patch A and B: *Danaus plexippus*, *Anartia fatima*, and *Leptophobia aripa*. *D. plexippus* spent the on average the longest time within plot A and B, in comparison to the other species, 37.471 +/- SE and 86.759 +/- SE seconds, respectively. (Error bars represent +/- SE)

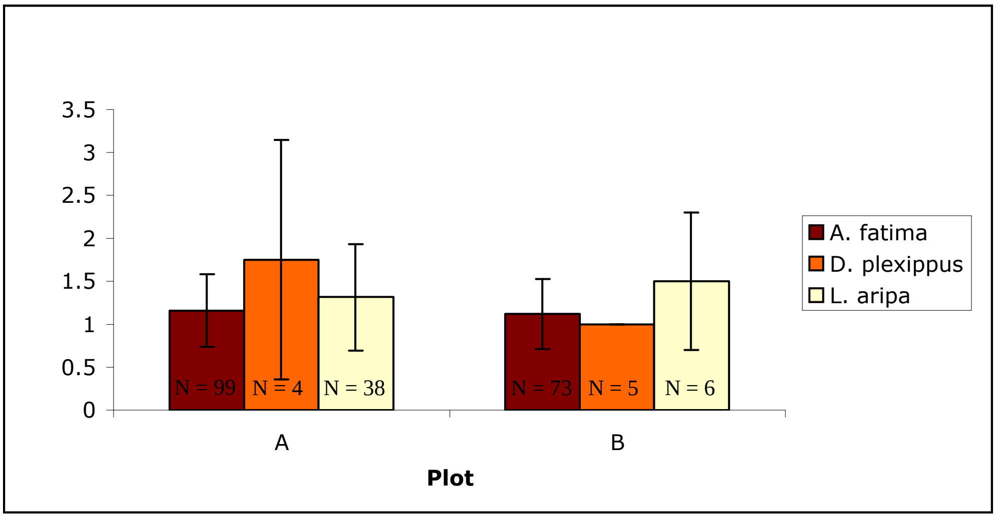


FIGURE 7. The average number of flowers of *Epidendrum radicans* visited by butterfly species *Anartia fatima* (red), *Danaus plexippus* (orange), and *Leptophobia aripa* (white) in patches without added sucrose reward to *Lantana camara* flowers (A) compared to patches with a 20% sucrose solution added to flowers of *L. camara* (B). In response to the added sucrose solution in patch B, *A. fatima* visited on average 0.039 fewer flowers, *D. plexippus* visited on average 0.75 fewer flowers, and *L. aripa* visited on average 0.184 more flowers within patch B. (Error bars represent +/- SD)

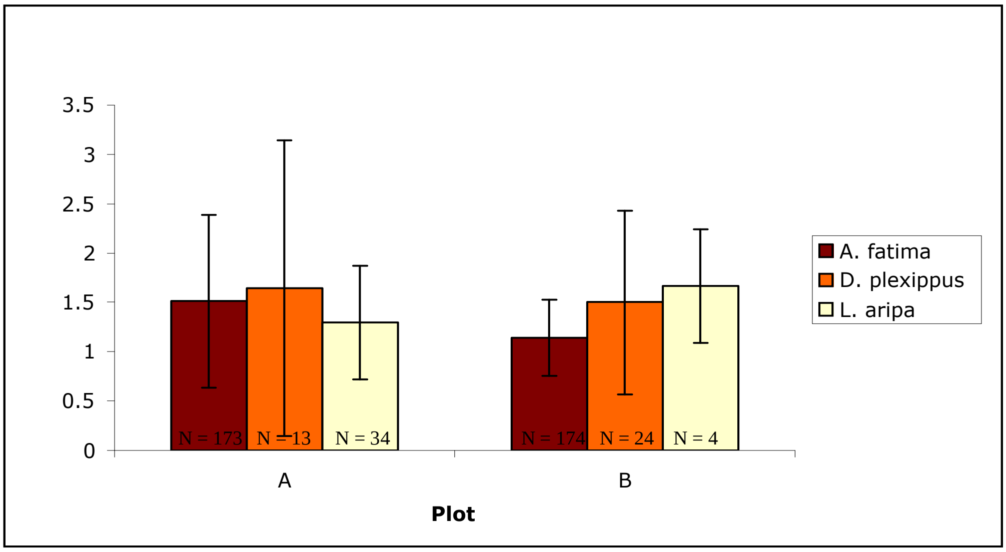


FIGURE 8. The average number of inflorescences of *Lantana camara* visited by butterfly species, *Anartia fatima* (red), *Danaus plexippus* (orange), and *Leptophobia aripa* (white) in patches without added sucrose reward (A) compared to patches with a 20% sucrose solution added to *L. camara flowers* (B). (Error bars represent +/- SD)