

May 2011

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Floral Color Change and Maintenance of Old Flowers in *Lantana camara* (Verbenaceae)

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ABSTRACT

Young flowers of *Lantana camara* are yellow and positioned in the center of the inflorescence with a ring of older, red flowers around them. This study investigates how changes in flower color and presence/absence of nectar influence robbers and pollinators of *L. camara*. It was found that a significant proportion of older, red flowers (mean = 20.3 percent) contain nectar. In addition, the majority of yellow and red flowers (estimated 90 percent) appear to have pollen and are receptive to pollination. Both pollinators and robbers preferred yellow flowers. Pollinators took nectar from a greater proportion of yellow flowers (e.g. 57 percent) versus red flowers (15 percent). In addition, pollinators showed no preference for inflorescences with the characteristic ‘bulls-eye’ pattern: all yellow inflorescences (AY) that were the same size as normal (N), ‘bulls-eye’ inflorescences, received more visits from butterflies (22 versus 10 per hour), and had more nectar removed (only 12.6 percent of AY flowers had nectar versus 37.5 percent of N flowers). Robbers were about ten times more likely to rob inflorescences with only yellow flowers than inflorescences containing yellow and red flowers (e.g. mean robbery per inflorescence was 3.71 and 0.334, respectively), even when reward and inflorescence size were similar. In addition, a ring of red flowers reduced robbery of yellow flowers by a factor of 37. Robbers may pollinate *L. camara*, as inflorescences visited only by robbers contained significantly more flowers with pollen on or near the pistil (1.64 flowers/infl) than inflorescences that were not visited (0.364 flowers/infl). *L. camara* plants may enhance fitness benefits by prohibiting large-scale robbery from yellow flowers yet provide some reward for robbery in red flowers as a way to assure their pollination.

RESUMEN

Las flores juvenes de *Lantana camara* son amarillas y se posicionan en el centro de la inflorescencia rodeadas por un anillo de flores rojas más viejas. Este estudio investiga como los cambios en el color de las flores y la presencia/ausencia de néctar influencia la visitación por ladrones de néctar y polinizadores de *L. camara*. Se encontró una proporción significativa de flores rojas viejas conteniendo néctar (promedio = 20.3%). Además, la mayoría de las flores rojas y amarillas (alrededor del 90%) parecen tener polen y estar receptivas para la polinización. Ambos polinizadores y ladrones de néctar prefieren las flores amarillas. Los polinizadores toman néctar en una mayor proporción de las flores amarillas (p.e. 57%) contra las flores rojas (15%). Además, los polinizadores no muestran preferencia por las inflorescencia con el patrón de “ojo de toro”: las inflorescencias completamente amarillas que fueron del mismo tamaño que el “ojo de toro” recibieron más visitas por mariposas (22 contra 10 por hora), y más néctar fue removido (12.6% de flores tienen néctar contra 37.5%). Los ladrones fueron cerca de diez veces más propensos a robar en inflorescencias con solo flores amarillas que en aquellas inflorescencias que contenían flores rojas y amarillas (p.e. promedio de robos por inflorescencia fue de 3.71 y 0.334 respectivamente), aún cuando el premio y el tamaño es similar. También, el anillo de flores rojas disminuye el robo en flores amarillas por un factor de 37. Los ladrones pueden polinizar *L. camara* ya que las inflorescencias visitadas únicamente por ladrones contienen significativamente más flores con polen en o cerca del pistilo (1.64 flores/inflorescencia) que las inflorescencias que no fueron visitadas (0.364 flores/inflorescencia). *L. camara* puede aumentar su éxito reproductivo prohibiendo robos a larga escala en las flores amarillas pero dando cierta recompensa a los robos en flores rojas como un mecanismo para asegurar la polinización de las mismas.

FLORAL TRAITS SHOULD MAXIMIZE THE LIKELIHOOD that visitors will pollinate while minimizing robbery (Weiss 1995, Maloof and Inouye 2000). In some plants, flowers remain on the inflorescence and change color as they age (Weiss 1991, Weiss 1995). This may increase attractiveness to pollinators (Weiss 1991, Weiss 1995) and/or protect younger, not-yet-pollinated flowers from nectar robbers (Barrows 1976, Maloof and Inouye 2000).

Retention of post color change flowers around the outside of an inflorescence may augment its attractiveness to pollinators through color cues or by increasing its size (Barrows 1976, Weiss 1991, Weiss 1995). Both of these possibilities have been considered in the tropical woody shrub, *Lantana camara*. This plant has yellow, orange, and red flowers (Barrows 1976). Yellow flowers are produced first in the center of the inflorescence and then subsequently darken to orange and then red, creating a characteristic 'bulls-eye' pattern (Barrows 1976). These flowers cannot self-pollinate (Barrows 1976). Since flowers that have changed color are assumed to have little or no nectar or pollen, color changes direct pollinators to more rewarding and viable younger flowers within an inflorescence (Barrows 1976, Gori 1989, Weiss 1991, Weiss 1995). In one survey of 97 butterfly visits, butterflies went to yellow over orange-red flowers 99 percent of the time (Barrows 1976). In addition, pollinators may be particularly attracted to the 'bulls-eye' pattern on *L. camara* inflorescences. One study found that pollinators prefer normal inflorescences (with the 'bulls-eye' pattern) over inflorescences with only yellow flowers (Zurinkas 2003). However, this study did not control for inflorescence size: yellow inflorescences were smaller than normal inflorescences (Zurinkas 2003). Size may be an important consideration; it has been found that butterflies choose larger over smaller inflorescences independent of the level of nectar reward offered or the color of the inflorescence (Weiss 1991). Thus, more visits to normal inflorescences could have been solely due to larger size. The larger size of *L. camara* inflorescences also allows butterflies with longer body lengths to serve as pollinators, as compared with the smaller inflorescences of *L. trifolia* (Schemske 1976). This is because older flowers are a landing platform that allows larger butterflies to holdfast as they forage on the interior flowers (Schemske 1976).

While the retention of older flowers may create a physical barrier to robbers, the impact of floral color change on these organisms is relatively unknown. Barrows (1976) reported, after examining a limited sample of flowers, that a ring of older orange and red flowers on *L. camara* inflorescences reduced nectar robbing of the interior yellow flowers from 71 to 23 percent. Nectar robbers may show a preference for younger pre-change flowers, as do pollinators (Weiss, 1991). These robber interactions are important to consider as robbers may decrease the fitness of the plant, though they occasionally pollinate as well (Kendell and Smith 1976, Maloof and Inouye 2000, Richardson 2004). A review of 18 studies found that negative, neutral, and positive net effects of robbery were equally likely (Maloof and Inouye 2000).

I examined floral color changes in *L. camara* inflorescences in regard to pollinator and robber behavior. Many of the hypotheses for how these changes impact pollinators and robbers are based on assumptions (older flowers have no nectar), conflations (size with 'bulls-eye' pattern), a limited sample (reduction of robbery in yellow flowers), or remain largely untested (robbers as pollinators). I intended to resolve these shortcomings by considering whether: 1) older flowers have no nectar and are reproductively unviable, 2) older flowers block yellow flowers from robbery, 3) floral color change is a cue to robbers as well as pollinators, 4) 'bulls-eye' coloration attracts pollinators independent of size, and 5) robbers can serve as pollinators. Answering these questions is essential in fully understanding the functionality of color changing

flowers in *L. camara*: how these changes relate to pollinator and robber attraction, and whether the robbers are really only robbers.

METHODS

The study was conducted in Monteverde, Costa Rica, in April 2011. Study sites were a small field located across from the Monteverde Butterfly Garden that contained approximately 50 small *L. camara* plants and a garden at the Cloud Forest School that contained several large *L. camara* plants. Both sites were located in Pacific slope Premontane Moist habitats. In the following subheadings, study sites (Field and Garden) are indicated in parenthesis.

PLANT PHENOLOGY: COLOR, REWARD, AND REPRODUCTIVE POTENTIAL (FIELD).—To investigate the timing of changes in color and reward in *L. camara*, seven actively flowering inflorescences with unopened flowers were covered with a mesh bag (day 1) to exclude robbers and pollinators. The number of flowers of each type (unopened, yellow, orange, red) was recorded the next day (day 2) at 0630, 0930, 1230, 1530, and 1830, and then at 1230 for the next four days.

To examine the reproductive phenology of *L. camara*, five inflorescences that had not been previously touched were collected and examined under a dissecting microscope. Flowers were dissected using a razorblade. The presence of pollen (both on the anthers and near the pistil) was recorded. In addition, the appearance of the pistil—whether it was moist, erect, and generally healthy looking, was noted.

NECTAR CONSUMPTION AND VISITATION (FIELD).—To see whether orange and red flowers contain nectar and to assess whether pollinators prefer yellow flowers over orange and red, 20 inflorescences were bagged on 14 plants one evening. In addition, 20 inflorescences on the same 14 plants were marked with a piece of masking tape but otherwise left untouched. Care was taken so that every bagged inflorescence had an unbagged companion on the same plant. All inflorescences were normal (N inflorescences), meaning they contained yellow, orange, and red flowers. In addition, inflorescences were of similar size and condition. The next day these inflorescences were examined at 0630 (dawn), 0930, 1230, 1530, and 1830 (dusk). This experiment was conducted throughout the day because the schedule of nectar production in *L. camara* is unknown and to assure that nectar not taken was not reabsorbed throughout the day. At each of the five time periods, one bagged and unbagged inflorescence on four plants (total of 16 inflorescences) was examined in detail. The number of flowers of each color as well as the number of flowers with nectar were recorded for each inflorescence. The presence of nectar was detected by gently removing the flower from its calyx and firmly pressing the base of the flower between two fingers. If a visible drop appeared, the flower was considered to offer a nectar reward. This method follows Barrows (1976).

To test whether butterflies prefer inflorescences with ‘bulls-eye’ coloration independent of size, I compared nectar in N inflorescences to all yellow inflorescences (AY inflorescences) of the same size. AY inflorescences were found on two plants in the field, and observation revealed that they contained approximately the same distribution of nectar as N inflorescences (i.e. flowers on the edge were less likely to contain nectar). Thus, these inflorescences appeared to be identical to N inflorescences, with the exception that all flowers were yellow. Four AY inflorescences were bagged along with four inflorescences from normal plants in close proximity. Four additional AY and N inflorescences on the same plants were marked but

otherwise untouched. The next day at 1230, the number of flowers and the number with nectar on each inflorescence were recorded.

To compliment the above experiment, visitation for N and AY inflorescences was compared. Ten AY and 10 N inflorescences in close proximity were watched for an hour. A visit was a butterfly landing on an inflorescence.

ROBBERY (FIELD AND CLOUD FOREST SCHOOL).—To see whether old flowers block robbery and color change serves as a cue for robbers, 32 N inflorescences and 15 AY inflorescences were marked on 17 plants across from the butterfly garden on a sunny morning at 0630. Orange and red flowers were removed on 15 of the 32 N inflorescences to create 15 yellow inflorescences (Y inflorescences). This left 17 N inflorescences. All inflorescences were examined for robbery and robbed flowers were removed. Robbery was readily apparent as a small hole at the base of the corolla. After robbery was removed, N and AY inflorescences contained 20-30 flowers and Y inflorescences contained 8-15 flowers. That evening, at 1600, the same inflorescences were checked for robbery that had accumulated that day. The amount of robbery and the color of the flower robbed were recorded.

This same comparison was repeated at the Garden. At 0630, approximately 40 N inflorescences (the actual number varied between 18 and 24) on three plants with seemingly equal amount of robbery were marked. From half, orange and red flowers were removed to create 20 Y inflorescences. Robbed flowers were removed. Flower ranges on inflorescences were the same as above. At 1600, these inflorescences were examined for robbery in the same way as before.

To erase possible effects of differential nectar quantity in flowers of different color/age, the previous experiment was repeated with 10 N, 10 Y, and 10 added-nectar (AN) inflorescences on the same three plants. AN inflorescences were created by adding nectar to orange and red flowers on normal inflorescences with a syringe. Nectar added was a 30 percent sugar solution, which matched the sugar content of *L. camara* flowers as previously measured with a refractometer.

To isolate the effect of size on robber preference, the experiment was repeated with 10 Y, and 10 red inflorescences (R inflorescences) on each of the three plants. R inflorescences contained only red flowers and were created by removing enough flowers on inflorescences with only red flowers to have a range of 8-12 flowers. The range of the Y inflorescences was reduced from the usual 8-15 flowers to 8-12 flowers to match that of R inflorescences.

Finally, to assess robbery on the AY inflorescences while controlling for per-plant differences, nine AY inflorescences were picked from across the butterfly garden, placed in water, and brought to the Cloud Forest School. These were placed in small plastic vials filled with water and taped to Plant 1 in the garden (see results) at 0630. At the same time, 11 N and 10 Y inflorescences (usual flower ranges) were marked on the same plant. Robbed flowers were removed, and all inflorescences were examined at 1600 with the same methods as always. This experiment was conducted because I had previously observed (unexpectedly) that AY inflorescences received a very small amount of robbery, and wished to investigate whether this was an inherent property of the inflorescences.

POLLINATION (CLOUD FOREST SCHOOL).—At 0630, 11 normal inflorescences on the usual three plants in the Cloud Forest School were checked for robbery, robbed flowers were removed, and the inflorescences were bagged so that neither pollinators nor robbers could reach them. At the

same time, 14 normal inflorescences were subjected to the same treatment, and then the opening of the flower was sealed with a small drop of glue to prevent pollinators (but not robbers) from accessing them. Fourteen additional inflorescences were subjected to the same treatment but left as is. Later that day, at 1530, all inflorescences were collected and examined for pollen deposition around the pistil under a dissecting microscope. Pollen was easily seen once flowers had been removed from the base of the inflorescence, leaving behind the pistil. The number of flowers with pollen deposited around or on the pistil per inflorescence was recorded.

RESULTS

PLANT PHENOLOGY: COLOR, POSITION, REWARD, AND REPRODUCTIVE POTENTIAL.—New flowers began opening at dawn and the majority (92 percent of 84 flowers examined) were open by 0800 (figure 1). All of the 84 yellow flowers that opened on day 2 stayed yellow the whole day, only darkening a bit towards the evening. By the next morning, the 84 flowers were orange. Flowers lasted 4 days total (~50 percent of flowers that opened on day 2 were missing on the morning of day 6).



FIGURE 1. Lantana color changes over time. These two pictures depict the same inflorescence separated by 24 hours. New flowers opened in the morning and turned orange by the next day. Flowers lasted approximately 4 days.

Examination of five inflorescences under the dissecting microscope revealed that most flowers (an estimated 95 percent), including red ones, had viable looking pistils: these were moist and erect, and showed no signs of decay. Only red flowers very near the outside of the inflorescence had pistils that looked withered (~10 percent of red flowers). Furthermore, the majority of flowers, including red ones, had pollen on the anthers (~90 percent), although observation revealed that pollen in yellow flowers was the most abundant. More flowers closer to the edge of the inflorescence had pollen deposited around the pistil (17.2 percent of 58 red-orange flowers versus 4.2 percent of 24 yellow flowers), yet many flowers even on the edge (82.8 percent) did not appear to be pollinated.

NECTAR CONSUMPTION AND VISITATION.—I observed *Anartia* and *Danaus* butterflies as the primary pollinators of the *L. camara* plants under study. *Trigona* bees were observed as robbers. Patterns of nectar differed between bagged and unbagged flowers (figure 2). Nectar in bagged yellow flowers peaked in the middle of the day (1230) and all examined had nectar (figure 2a). In contrast, bagged yellow flowers were least likely to have nectar at 1230 (only 43 percent of yellow flowers had nectar, figure 2b). Thus the proportion of flowers with nectar dropped by 57

percent as compared to the bagged flowers. Orange flowers in both the bagged and unbagged condition were most-likely to have nectar earlier in the day, at 0930 (69 and 38 percent of flowers had nectar, respectively) after which the proportion of orange flowers with nectar sharply dropped off (35 and 10 percent had nectar at 1230). There are no data for orange flowers after 1230 because these had darkened so much by the time that they could no longer be distinguished from red flowers. About 20 percent of bagged red flowers contained nectar. Nectar in red flowers peaked during the evening in both conditions (40 percent bagged had nectar and 10 percent unbagged had nectar), and in the unbagged condition they had the least nectar at 1230 (0 percent had nectar—a drop of 15 percent when compared to bagged flowers). It appears that yellow and red flowers replenish their nectar stores throughout the day.

Groups differed in proportion of flowers with nectar between N and AY inflorescences (Chi-squared, $X^2 = 5.71$, $df = 1$, $p = 0.017$, figure 3). Bagged N inflorescences had slightly more nectar at 1230 than bagged AY inflorescences (46 and 40 percent respectively), but this difference was not statistically significant (Chi-squared, $X^2 = 1.02$, $df = 1$, $p = 0.312$). On the other hand, unbagged N inflorescences had nearly three times as much nectar as unbagged AY inflorescences (37.5 versus 12.6 percent; Chi-squared, $X^2 = 16.9$, $df = 1$, $p < 0.0001$).

Butterflies visited AY inflorescences nearly twice as often as N inflorescences: visitation was 22 and 10 in one hour, respectively (Chi-squared, $X^2 = 4.5$, $df = 1$, $p = 0.034$).

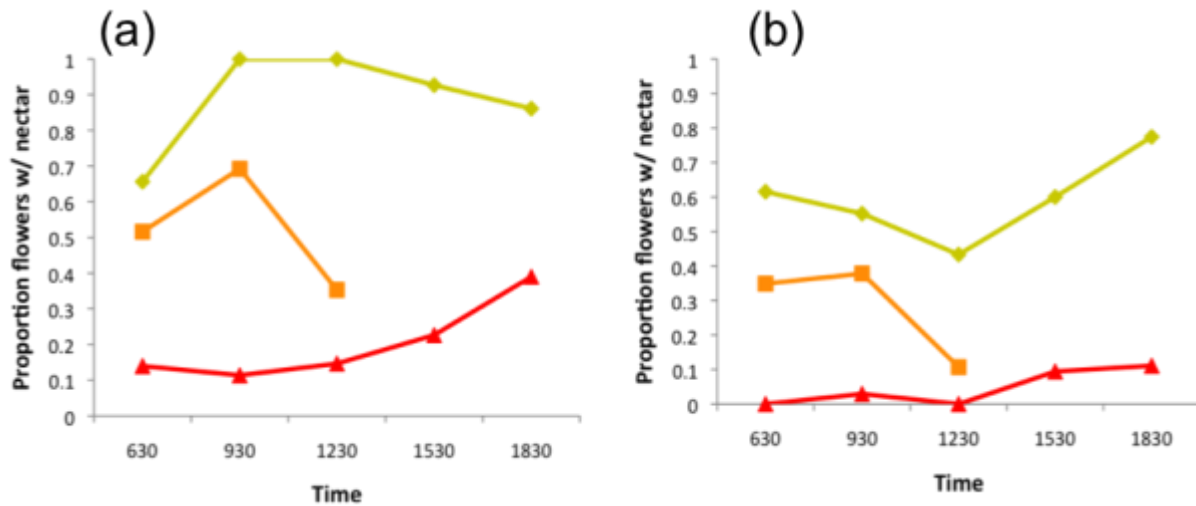


FIGURE 2. Proportion of yellow, orange, and red *L. camara* flowers for bagged (a) and unbagged (b) inflorescences with nectar at five times of day. Proportions for yellow flowers are shown in yellow (top line), while those for orange (middle line) and red (bottom line) are shown in orange and red, respectively. Four inflorescences for each time period were examined (20-30 flowers per inflorescence).

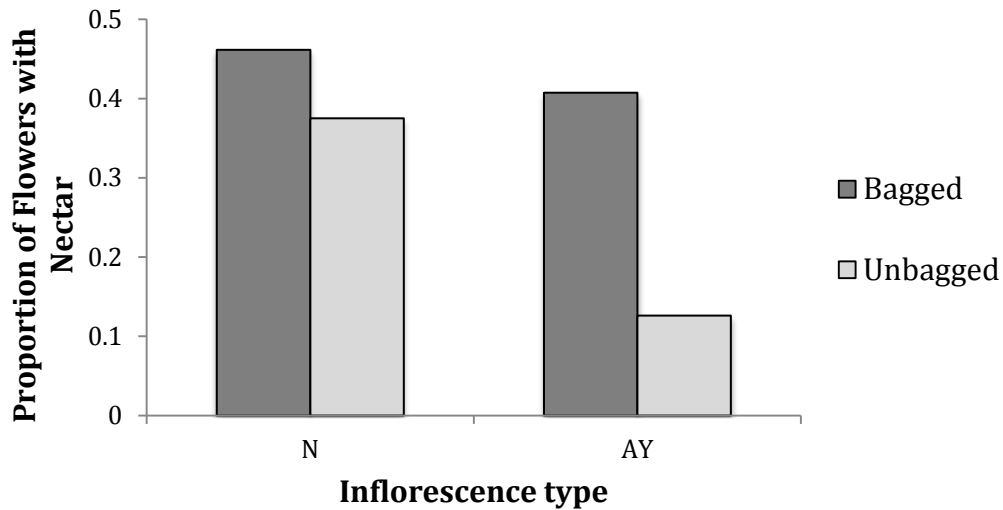


FIGURE 3. Proportion of *L. camara* flowers with nectar in bagged and unbagged inflorescences on normal inflorescences (N) and all yellow inflorescences (AY). All flowers on each inflorescence were counted. Groups differed in proportion with nectar (Chi-squared test). There was no difference between bagged N and AY inflorescences, but the difference between unbagged inflorescences was significant (Chi-squared test). From left to right, n = 117, 104, 108, and 103 flowers.

ROBBERY.—Of the N, Y, and AY inflorescences examined for robbery in the butterfly garden, Y experienced the most robbery per inflorescence (mean \pm 1 standard error = 2.7 ± 0.958 flowers per inflorescence), followed by N inflorescences (1.7 ± 1.08), and finally by AY inflorescences, which experienced almost no robbery (0.13 ± 0.13). However, these differences were not significant (One Way ANOVA, $F = 2.33$, $df = 2$, $p = 0.110$) because one plant of the 17 sampled dominated robbery: 93.8 percent and 90.2 percent of the total robbery on N and AY inflorescences, respectively, took place on this plant. I had previously observed that this plant received a disproportionate amount of robbery, and that AY inflorescences were robbed only on extremely rare occasions (most days they had no robbery at all).

Y inflorescences at the Cloud Forest School experienced about ten times more robbery per inflorescence than N inflorescences (3.71 ± 0.323 versus 0.334 ± 0.340) and this difference was significant (Two Way ANOVA, $F = 51.6$, $df = 1$, $p < 0.0001$, figure 4). There was also a significant difference between plants (Two Way ANOVA, $F = 8.18$, $df = 2$, $p = 0.0005$), but this was because Y inflorescences on plant 1 had much more robbery than those on plants 2 and 3 (6.39 ± 0.864 versus 2.42 ± 0.662 and 2.33 ± 0.744 , respectively). In addition, yellow flowers were 37 times more likely to be robbed on Y inflorescences than those on N inflorescences: 37 percent of yellow flowers were robbed on Y inflorescences while only 1 percent of yellow flowers were robbed on normal inflorescences (n = 792).

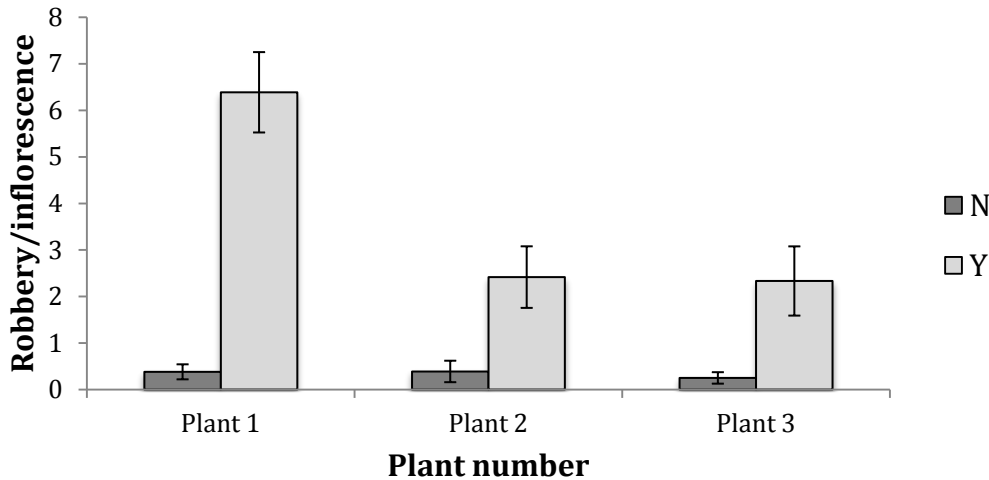


FIGURE 4. Robbery per inflorescence for normal (N) and yellow (Y) inflorescences on three *L. camara* plants. Error bars represent one standard error. Y inflorescences were created by removing orange and red flowers from N inflorescences. Y inflorescences experienced significantly more robbery than N inflorescences, and those on plant 1 had significantly more robbery than Y inflorescences on plants 2 and 3 (Two Way ANOVA, Tukey's HSD test, $p < 0.05$). From left to right $n = 20, 24, 21, 18, 18,$ and 24 inflorescences).

ROBBERY—CONTROLLING FOR REWARD. Robbery per inflorescence was significantly different between Y, N, and AN inflorescences (Two Way ANOVA, $F = 80.6, df = 2, p < 0.0001$, figure 5). Once again, Y inflorescences had significantly more robbery than other groups, with 6.67 ± 0.47 instances per inflorescence. AN inflorescences had about twice as much robbery as N inflorescences (1.83 ± 0.34 versus 0.900 ± 0.227); however, this difference was not significant (Tukey's HSD test, $p > 0.05$). Plants 1, 2, and 3 were not significantly different from each other (Two Way ANOVA, $F = 0.870, df = 2, p = 0.423$).

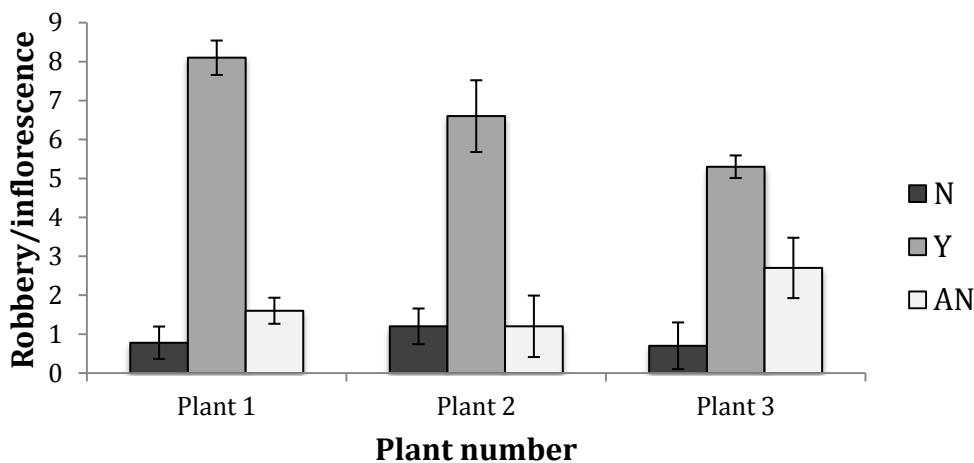


FIGURE 5. Robbery per inflorescence between normal (N), yellow (Y), and added nectar (AN) inflorescences on three *L. camara* plants. Error bars represent one standard error. Y inflorescences were created by removing orange and red flowers from N inflorescences. AN

inflorescences were created by adding nectar (30% sugar) to orange and red flowers on N inflorescences. Robbery per inflorescence was significantly different between inflorescence types, but not between plants (Two Way ANOVA). Differences between N and AN inflorescences were not significant (Tukey's HSD test, $p > 0.05$). $n = 10$ inflorescences for each bar.

ROBBERY—CONTROLLING FOR SIZE. Robbery per inflorescence was significantly different between R and Y inflorescences (One Way ANOVA, $F = 184.4$, $df = 1$, $p < 0.0001$, figure 6). Y inflorescences had a large amount of robbery (8.13 ± 0.415) while R had very little—slightly less than the usual for N inflorescences (0.227 ± 0.415). There was no significant difference between plants (Two Way ANOVA, $F = 0.973$, $df = 2$, $p = 0.384$).

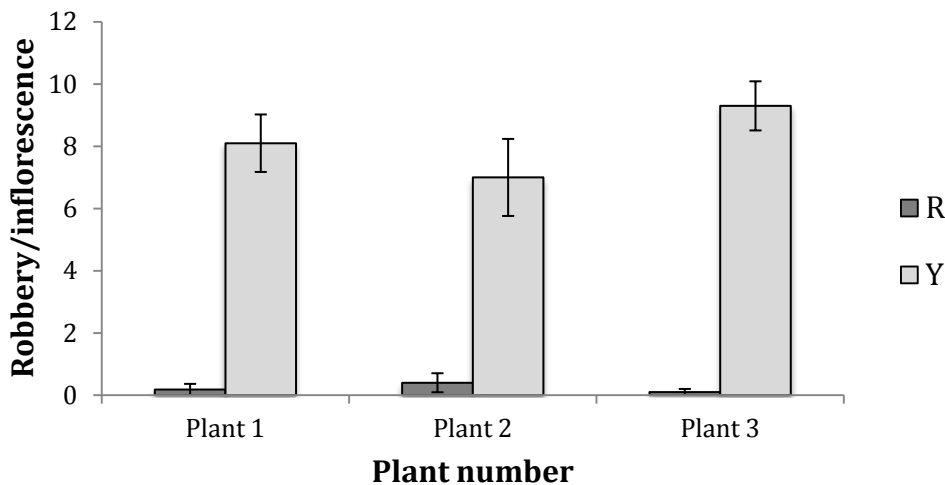


FIGURE 6. Robbery per inflorescence between red (R) and yellow (Y) inflorescences on three *L. camara* plants. Error bars represent one standard error. Y inflorescences were created by removing orange and red flowers from N inflorescences, and R inflorescences were created by removing flowers from all red inflorescences. Both Y and R inflorescences had 8-12 flowers. Robbery per inflorescence was significantly different between inflorescence types but not between plants (Two Way ANOVA). $n = 11$ inflorescences for the first bar, and 10 for the rest.

ROBBERY—AY INFLORESCENCES. Robbery per inflorescence for Y, N, and AY inflorescences at the Cloud Forest School (AY had been transplanted from the field near the butterfly garden) differed between groups (One Way ANOVA, $F = 90.1$, $df = 2$, $p < 0.0001$). Y inflorescences had 5.6 ± 0.830 instances of robbery per inflorescence, while N and AY inflorescences had much less: 0.81 ± 0.791 and 0.00 ± 0.875 , respectively. It is noteworthy that once again AY inflorescences experienced less robbery than N inflorescences; however, this difference was not significant (Tukey's HSD test, $p > 0.05$).

POLLINATION.—Inflorescences that both pollinators and robbers could access, that only robbers could access, and that neither pollinators nor robbers could access had significantly different amounts of pollen deposited near or on the pistil (One Way ANOVA, $F = 15.0$, $df = 2$, $p < 0.0001$, figure 7). Inflorescences that both pollinators and robbers could access had about twice as many pistils with pollen on them than those that only robbers could access (3.07 ± 0.450).

versus 1.62 ± 0.269 , Tukey's HSD test, $p < 0.05$), while those that neither could access had significantly less pollen deposited on them (0.36 ± 0.203 , Tukey's HSD test, $p < 0.05$).

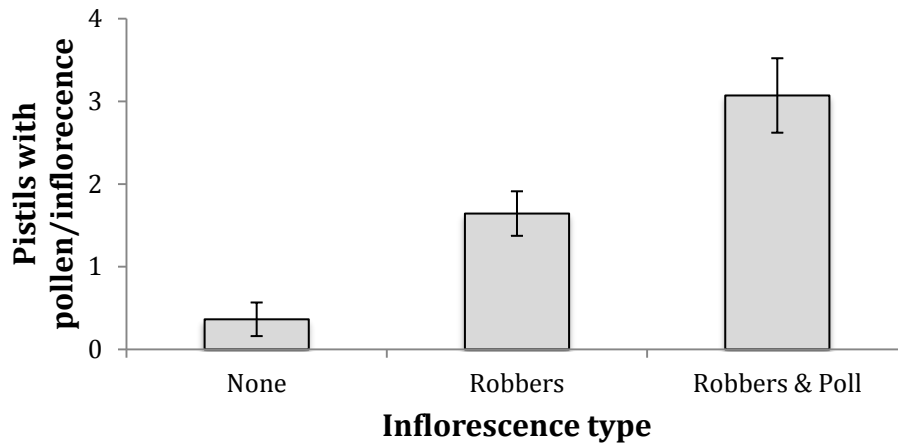


FIGURE 7. Pistils with pollen per inflorescence for three types of inflorescences. 'None' signifies that neither pollinators nor robbers could access them, 'Robbers' that only nectar robbers could access them, and 'Robbers & Poll' that both pollinators and nectar robbers could access them. Error bars represent one standard error. The three conditions were significantly different from each other (One Way ANOVA). From left to right $n = 11$, 14 , and 14 inflorescences.

DISCUSSION

In contrast with the results of Barrows (1976), it was found that both orange and red flowers contain nectar. It appears that the plant reabsorbs nectar from yellow and then orange flowers as they turn red and then maintains those smaller nectar quantities in red flowers by placing nectar in them throughout the day. The plant invests the most heavily in yellow flowers, which also receive more visits than the other flowers (as evidenced by the larger drop in proportion with nectar for yellow unbagged flowers). This supports the idea that pollinators use the color yellow as a cue for rewarding flowers (Barrows 1976, Weiss 1995). All flowers had nectar removed, which means each type of flower was visited by pollinators and/or robbers throughout the day.

Examination of flowers under a dissecting microscope revealed that most flowers, including orange and red ones, were capable of pollinating and being pollinated. This conflicts with previous claims by both Barrows (1976) and Weiss (1991, 1995) that red flowers contain spent male and female parts. In addition, although more red flowers than yellow appeared pollinated, the majority were not. These results, as well as those of the previous paragraph, imply that there is more to these older, red flowers than previously thought. *L. camara* plants are still investing energy (nectar and reproductive capability) in mostly unpollinated, older flowers.

'Bulls-eye' coloration does not attract pollinators when size is controlled. More nectar was taken from AY versus N inflorescences, even though they contained approximately the same number of flowers. Visitation data substantiates this, as butterflies were more likely to visit the AY inflorescences. This conflicts with Zurinkas (2003) and suggests that there is no functional significance to the 'bulls-eye' pattern in terms of pollinator attraction.

The presence of orange and red flowers around the outside of the inflorescence severely decreases robbery of yellow flowers. In fact, I found that orange and red flowers are much more effective at this than originally reported by Barrows (1976), who found that their presence reduced robbery by a little over a factor of three. I found, after examining a sample several times larger than Barrows', that robbery was reduced by a factor of 37. This occurs because orange and red flowers physically block the corollas of yellow flowers from access by robbers. Furthermore, the presence of older flowers decreases total robbery per inflorescence by about 10 times: these flowers do not just block yellow flowers from getting robbed, they dissuade large amounts of robbery overall. The most likely explanation for this is that robbers have learned that older flowers often do not contain nectar, and therefore avoid inflorescences containing them in order to forage more optimally. It may be that this occurs due to associative learning, as has been proposed for pollinators (Weiss 1991). Post-change flowers may be serving an important adaptive function if large-scale robbery reduces fitness of *L. camara*.

Like pollinators, robbers appear to use color as a cue for identifying rewarding flowers. Y inflorescences were much more likely to be robbed than inflorescences containing yellow, orange, and red flowers, even when presence of nectar and inflorescence size were controlled. It appears that robbers are hijacking color cues that are meant to aid pollinator efficiency for their own purposes, and this behavior is likely at net cost to the plant (once again, this is assuming that large-scale robbery of yellow flowers reduces fitness of *L. camara*).

My results provide some evidence that robbers are serving as pollinators of *L. camara*. Inflorescences that only robbers could access had significantly more flowers with pollen deposited on or near the pistil than those that neither pollinators nor robbers could reach. However, these data must be interpreted with caution, as robbers could simply be knocking pollen from the same flower onto the stigma. *L. camara* cannot self-pollinate (Barrows 1975), so this action would not enhance the fitness of the plant. *Trigona* bees, the only robbers seen in this study, are often associated with negative effects on seed set (Maloof and Inouye 2000). One study of the tropical treelet, *Quassia amara*, found that exclusion of robbers resulted in 4-12 times greater seed production than in control flowers (Roubik et al. 1985). With all this in mind, I propose that large-scale robbery of *L. camara* inflorescences, especially the most active and rewarding yellow flowers, may decrease the fitness of the plant—most likely through a reduction in pollinator visitation (Maloof and Inouye 2000). This makes sense in light of the fact that a ring of red flowers is so effective at reducing robbery, and may have arisen due to selective pressure from robbers. Another possibility is that these flowers are the outcome of pressure to enlarge the landing platform or to increase the attractiveness of the inflorescence with larger size, as has been suggested by Schemske (1976) and Weiss (1991), but it seems like an outstanding coincidence that they would also be so successful at reducing robbery at the same time. It is likely that all these forces have contributed to the maintenance of older flowers.

However, given that robbers are capable of pollinating, it makes sense to maintain limited nectar quantities and reproductive capabilities in orange and red flowers. In this way, the plant is balancing fitness benefits from pollinators and robbers, or at least making the most of a bad situation: pollinator interactions are not greatly disrupted, since robbers cannot reach the yellow flowers and are dissuaded from (likely detrimental) large-scale robbery, yet the plant still receives some pollination from robbers at a low cost. This hypothesis fits well with the results and explains why post-change flowers contain nectar and are reproductively active. Of course, this could be solely for the pollinators' benefit, but the results of previous studies suggest that pollinators visit older flowers very rarely: about 1 percent of the time (Barrows 1976). These

limited pollinator interactions with older flowers may not be beneficial enough to explain the plant's energy investment. A future study examining seed set in N and Y inflorescences with differential robber visitation would be helpful in testing my hypothesis and resolving this question.

Finally, it appears that there is genetic variation in the population of *L. camara*, as AY inflorescences—discovered during the course of the study—contained no orange or red flowers, yet had the same distribution and amount of nectar as N inflorescences. Despite these similarities, AY inflorescences appeared to be highly resistant to robbery, even when attached to a plant at the Cloud Forest School garden, where robbery was high. The mechanism and selective forces associated with this resistance remain unknown.

This study has shed light on how color changes influence the behavior of pollinators and robbers. The results suggest that these changes serve a dual function of directing pollinators to rewarding flowers and reducing robbery with the end of maximizing pollination from legitimate pollinators and possibly robbers. Findings for *L. camara* may apply to the many species with similar floral changes; however, idiosyncrasies due to the identity of the legitimate pollinator and the robbers are likely. Exploring these idiosyncrasies with *L. camara* in mind may be the next step in fully understanding the significance of floral color changes to plant fitness.

ACKNOWLEDGEMENTS

I thank Alan Masters for his support in the development, execution, and analysis of this study. Emily Shelly and Laura Hurley were particularly helpful in their review of the written work. Those at the Cloud Forest School in Monteverde who granted access to the study site are appreciated.

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