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Are there evidences of a complex mimicry system among *Asclepias curassavica* (Apocynaceae), *Epidendrum fulgens* (Orchidaceae), and *Lantana camara* (Verbenaceae) in Southern Brazil?[1]

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ABSTRACT – (Are there evidences of a complex mimicry system among *Asclepias curassavica* (Apocynaceae), *Epidendrum fulgens* (Orchidaceae), and *Lantana camara* (Verbenaceae) in Southern Brazil?). The goal of this paper was to test the presence of mimicry in *Asclepias curassavica* L., *Epidendrum fulgens* Brong., and *Lantana camara* L. The study was carried out at the Parque Estadual de Itapeva, RS, southern Brazil, from 2004 to 2006. Flowering period of each of the three species was followed up; focal observations of butterflies visiting flowers, from fixed point and during random walks were carried out. We also estimated the frequency of pollinaria removal in the orchid, as well as its mode of reproduction. All these variables were important for testing the mimicry hypothesis. Despite some temporal coincidences in the flowering period of two plants in the system, there was no statistical association among the three plants as to flowering period. Twenty-nine species of butterflies, as potential pollinators, were recorded, particularly *Agraulis vanillae maculosa*, *Dryas iulia alcionea*, *Urbanus simplicius*, *Tegosa claudina*, and *Heliconius erato phyllis*, which were the more frequent visitors of the three plants. There was association between the number of visits to *L. camara* and *E. fulgens*, based on Pearson correlation ($r = 0.4603$; $n = 19$; $P = 0.0473$). Pollinaria removal of *E. fulgens* was low, as measured by the percentage of removal (range: 0 – 10%). The analysis of the mode of reproduction of this orchid showed its pollinator-dependence, since no fruits were formed by spontaneous self-pollination. In contrast, the percentage of fruit set that resulted from geitonogamy and xenogamy was, in average, 86%. The results here shown are not conclusive as to the occurrence of a mimicry system among the three plants.

Key words - butterflies, diurnal floral visitors, floral mimicry

RESUMO – (Há evidências de um sistema complexo de mimetismo entre *Asclepias curassavica* (Apocynaceae), *Epidendrum fulgens* (Orchidaceae) e *Lantana camara* (Verbenaceae) no Sul do Brasil?). O objetivo deste trabalho foi testar a presença de mimetismo em *Asclepias curassavica* L., *Epidendrum fulgens* Brong. e *Lantana camara* L. O trabalho foi realizado no Parque Estadual de Itapeva/RS, no sul do Brasil, entre 2004 e 2006. O período de floração de cada uma das três espécies foi acompanhado; foram realizadas observações focais de borboletas visitantes florais a partir de um ponto fixo e observações através de caminhadas aleatórias. Também estimou-se a freqüência de remoção de polinários na orquídea, bem como o seu modo de reprodução. Todas estas variáveis foram importantes para testar a hipótese do mimetismo. Embora tenham ocorrido algumas coincidências temporais nos períodos de floração entre duas das plantas do sistema, não houve associação estatisticamente significativa no período de floração das três plantas. Foram registradas 29 espécies de borboletas, dentre as quais *Agraulis vanillae maculosa*, *Dryas iulia alcionea*, *Urbanus simplicius*, *Tegosa claudina* e *Heliconius erato phyllis* foram as mais freqüentes nas visitas às três plantas. A correlação de Pearson mostrou que há associação entre o número de visitas realizadas a *L. camara* e *E. fulgens* ($r = 0{,}4603$; $n = 19$; $P = 0{,}0473$). A remoção de polinários em *E. fulgens* foi baixa, medida pela percentagem de remoção (amplitude: 0 – 10%). A análise do modo de reprodução mostrou a dependência da orquídea em relação a polinizadores, uma vez que nenhum fruto foi produzido a partir da autopolinização espontânea. Em contraste, a percentagem de frutos formados resultantes de geitonogamia e xenogamia foi em média 86%. Os resultados aqui relatados não são conclusivos quanto à existência de um sistema mimético entre as três plantas.

Palavras-chave - borboletas, mimetismo floral, visitantes florais diurnos

Introduction

Mimicry, especially in butterflies, is considered the best example of an adaptation where the genetic basis is well understood, natural selection agents are known, and the evolutionary dynamics is predictable. Moreover, "it is a microcosm for evolutionary theory in general, with ramifications into the evolution of polymorphism, transitions between adaptive peaks, origins of biodiversity,

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and the evolution and maintenance of community patterns" (Joron & Mallet 1999). However, despite some fine studies published on this subject, mainly with butterflies, little is known about plant mimicry. Firstly, the traditional division between Batesian and Müllerian mimicry does not apply to plants. Batesian mimicry is characterized by the coexistence in the same population of an organism that is unpalatable or otherwise protected, being mimicked by a second organism, palatable or defenseless. A classic example is the case of the Monarch butterfly (*Danaus plexippus*) and its mimic, the Viceroy (*Limenitis archippus*); in Brazil there are plenty of examples, but one very common is that between the butterflies *Parides agavus* (model, distasteful) and *Heraclides hectorides* (mimic) (Araujo & Valente 1981). One of the differences between Batesian and Müllerian mimicry is that in the latter, both model and mimic are unpalatable or protected (usually called co-mimics); perhaps the most spectacular example is the one formed by different species of *Heliconius*, particularly between *H. erato* and *H. melpomene* all around Brazil and South America (Sheppard *et al*. 1985). The fact that this simple division is problematic stimulated Vane-Wright (1976) to propose a general classification of mimetic systems based on the original tripartite system of Wickler (1968). This system is based on three elements, S_1, the model, S_2, the mimic and R, the operator (the one which is uncapable to distinguish S_2 from S_1). Assuming that each element can interact with each other in two ways (positive or negative) there will be eight (2^3 = two possible interactions, three elements of the system) different types of mimicry. Moreover, since the elements S_1, S_2, and R can belong to different species, or instead, to the same species or combinations of the same and different species, five different types of mimicry can exist. In the whole, a matrix of 40 (8 × 5) different types of mimicry can be predicted (see Vane-Wright 1976 for a complete explanation). The genetic foundation of plant mimicry, on the other hand, is completely unknown, and the rare studies focus on the selective agents responsible for the evolution of this adaptation (for a notable exception see Johnson 1994; Johnson *et al*. 2003).

Floral mimicry in *Asclepias curassavica, Epidendrum radicans,* and *Lantana camara*, which are very common in the Neotropics, is perhaps the most frequently described in literature. In spite of being morphologically distinct, these plants show many features in common: flower in dense umbel-like inflorescences, inflorescence size, number of flowers per inflorescence, extensive period of flowering, pollination mainly by butterflies, and perhaps more significantly, a conspicuous pattern of red and yellow flowers. The presumptive existence of mimicry among them, usually described according to the classical Batesian-Müllerian approach, was discussed by Boyden (1980), who simply describes the visit of 10 butterflies (*Danaus plexippus*) to flowers of *Epidendrum ibaguense*, each of them with pollen from *Lantana camara* in their head and thorax and pollinaria of the orchid in their legs, and Bierzychudek (1981) who, otherwise, used a set of variables different from our work, to test the hypothesis of mimicry among *Lantana camara*, *Asclepias curassavica* and *Epidendrum radicans* from Costa Rica. Endress (1994) and Roy & Widmer (1999), on the other hand, simply refer to these plants as a possible example of floral mimicry. The present paper transposes the problem to the system found in Southern Brazil, where the only difference is in the orchid species which is *Epidendrum fulgens.* However, differently from the previous papers, we set the study under the tripartite system proposed by Wickler (1968) and expanded by Vane-Wright (1976).

Given the situation described above, to search for evidences that could indicate that *Asclepias curassavica*, *Epidendrum fulgens*, and *Lantana camara* constitute a floral mimicry system, the present work has the following objectives: 1. to describe the flowering period of the three plants; 2. to investigate the potential pollinators of this supposed system, particularly butterflies; 3. to detect the removal frequency of pollinaria in the orchid species; 4. to describe the mode of reproduction of the orchid.

Material and methods

Fieldwork was carried out at Parque Estadual de Itapeva (Itapeva State Park – 49°43'39" W and 29°20'34" S), municipality of Torres, Rio Grande do Sul, the southernmost state in Brazil. The Park is located in the hydrographic basin of the river Mampituba, representing *ca*. 1,000 ha of the remnants of the Northern Coastal Plain of Rio Grande do Sul. A rich diversity of ecosystems, such as *restingas* (marine deposits along the coast and their vegetation), *mata paludosa* (a sort of swamp forest), a lake and several ponds, is found in the park.

According to Leite & Klein (1990), the phytoecological unit is "Área das Formações Pioneiras Marinhas – *Restingas* e *Dunas* (Area of Marine Pioneer Foundations – *Restingas* and Dunes)" which is characterized by vegetation directly influenced by the sea, distributed on recent Quaternary sandy soils with saline constitution, subject to high solar radiation and strong wind action. This vegetation includes different environments, such as the beach strip, fixed dunes, flattened and deflation plains, and rock ridges. Climate type is Cfa – Humid Subtropical Climate (Koeppen 1948). Average annual temperature is 17.9 °C, and rainfall is 1,423 mm (Waechter 1985).

Three sampling areas were chosen for our observations and tests: one on dunes heavily covered by vegetation, where *L. camara* and *E. fulgens* co-occurred; another, in the flattened zone of the Park, where again *L. camara* and *E. fulgens* co-occurred, and a third one next to the houses where administrative people of the Park live, and where only *L. camara* and *A. curassavica* co-occurred. In none of the sampled areas the three species of plants occurred simultaneously. The linear distance from one area to the other was approximately 700 m.

Flowering – *A. curassavica*, *E. fulgens*, and *L. camara* (figures 1-3) flowering were followed from March 2005 to March 2006. Ten plants were monitored per species, and the number of flowers was recorded.

Potential pollinators – Focal observations of butterflies visiting the flowers were carried out by observation from a fixed point and, alternatively, by observations in random walks. Observation from a fixed point was characterized by choosing five inflorescences of a group of individuals of each species studied in November and December of 2004; January, November, and December of 2005; and January of 2006. Observation period was of approximately seven hours daily per plant species, summing up 105 hours of observations. The number of visits made by butterflies and daytime of landing was recorded in a field spreadsheet. During random observations, butterflies were observed along tracks of approximately 200 m each, which included two species of plants: *A. curassavica* and *L. camara* or *E. fulgens* and *L. camara*. The tracks were traveled during approximately four hours/day, summing up 36 hours, from February to May, 2005. Landing time and corresponding plant were recorded in the field spreadsheet. Fieldwork was usually carried out between 9h00 and 16h00.

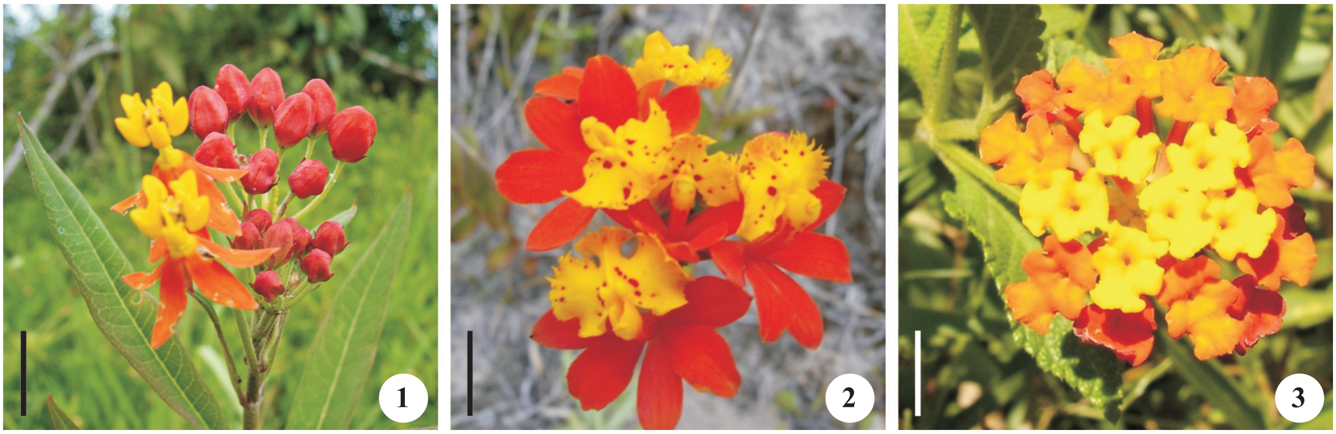
Epidendrum fulgens pollinaria removal – To detect the frequency of pollinaria removal from the orchid relative to nectar source (*L. camara*), six 40 m transections were chosen between February and March of 2005, summing up 240 m. In these transections, five orchid inflorescences were labeled at every 10 m, and the number of pollinaria recorded per flower. Inflorescences were labeled in the morning, and checked by the end of the afternoon. A group of 60 inflorescences was initially labeled, and other 60 inflorescences were labeled two days later. To record the frequency of pollinaria removal, the first group was checked again 48 hours latter, and the second group of inflorescences, checked again 24 hours latter, always in the afternoon.

Epidendrum fulgens mode of reproduction – Field experiments were done to investigate the mode of reproduction of the orchid (the mimic species in our system), and specially to test its dependence on pollinators. We designed four experimental groups, three of them being different sorts of hand pollination: self-pollination, with pollinaria removed from one flower and deposited in the same flower; geitonogamy, with pollinaria removed from one flower and deposited in another flower of the same inflorescence; xenogamy where emasculated flowers received pollinaria from a different individual. A fourth experimental group of flowers were left intact and were simply covered, as a control group for spontaneous self-pollination. In all these treatments the inflorescences were subsequently covered with a thin cloth tissue ("organza").

Testing of statistical hypotheses, whenever necessary, were done by the Chi-Square distribution and Pearson correlation, with angular transformation (Zar 1996). Estimates of the correlation coefficients were obtained by the software BioEstat 5.0 (Ayres *et al*. 2008).

Voucher specimens were deposited in ICN (Universidade Federal do Rio Grande do Sul) herbarium (*D. Fuhro 01*, *D. Fuhro 02*, *D. Fuhro 03*, *D. Fuhro 04*).

In the analyses to follow, we excluded *A. curassavica* in some of them due to its occurrence being restricted to only one of the areas studied, and mainly because its number of flowers was poor as compared to the other two species. However, we think it is indeed an important element in the complex ecological interactions that constitute the presumptive mimicry system among the three species of plants and their potential pollinators, the butterflies.



Figures 1-3. Inflorescences of *Asclepias curassavica* L. (1), *Epidendrum fulgens* Brongn. (2), and *Lantana camara* L. (3). Bar = 1 cm.

Results

Flowering – The peak flowering of *Epidendrum fulgens* occurred between December 2005 and February 2006 (figure 4); flower percentage started to increase on November 2005, and decreased in March 2006, reaching the same levels as in the previous year. *Lantana camara* flowering was irregular, with a peak between October and November 2005, and decreasing thereafter. However, the emergence of flowers did not stop, indicating that *L. camara* is probably one of the main food items for butterflies in this area, as far as these three species are concerned. The peak flowering of *Asclepias curassavica* occurred only in April, followed by a decrease, and a slight re-emergence in July, October, and November 2005 and in March 2006. Statistically, there was no association among the flowering of these plants (*A. curassavica* and *E. fulgens*: $r = -0.2774$, $n = 13$, $P = 0.3588$; *A. curassavica* and *L. camara*: $r = 0.2170$, $n = 13$, $P = 0.4764$; *E. fulgens* and *L. camara*: $r = 0.0894$, $n = 13$, $P = 0.7714$). However, a flowering overlap among the three plants occurred during a short period.

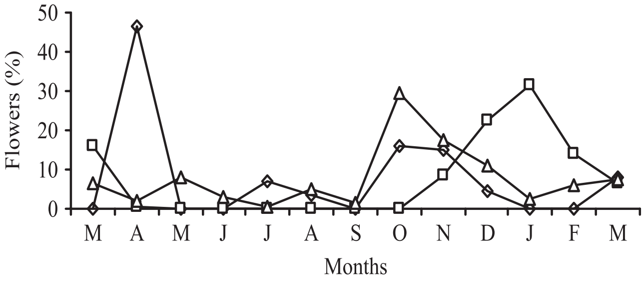


Figure 4. Flowering of *Asclepias curassavica* (◇), *Epidendrum fulgens* (□) and *Lantana camara* (△) from March, 2005 to March, 2006.

Potential pollinators – Twenty-nine species of butterflies were recorded (table 1). Among them, *Agraulis vanillae maculosa*, *Dryas iulia alcionea*, *Urbanus simplicius*,

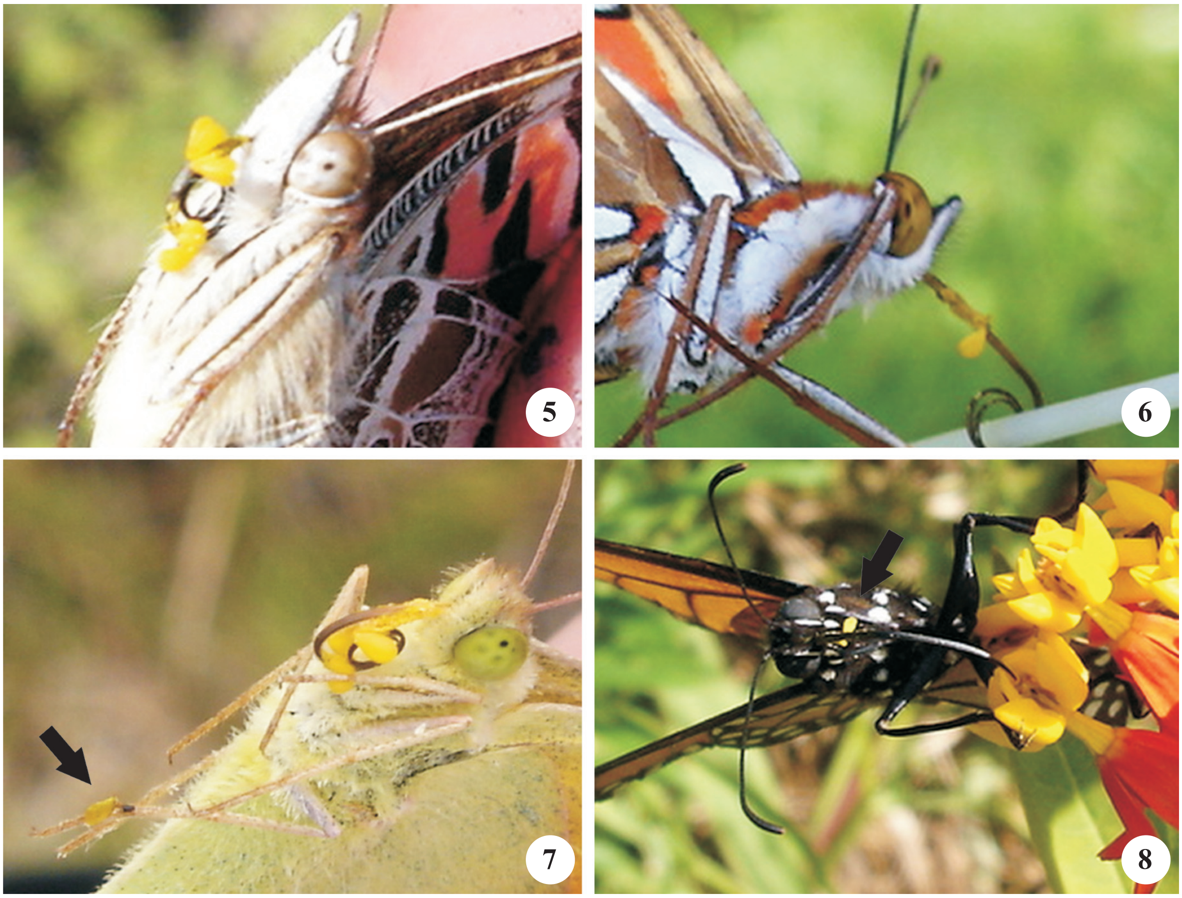
Table 1. Number of recorded visits of butterflies as potential pollinators of *Asclepias curassavica, Epidendrum fulgens and Lantana camara*, from November/2004 to January/2006. Each column represents the sum of observations in different years.

Species	*Lantana camara*							*Epidendrum fulgens*							*Asclepias curassavica*						
	N	D	J	F	M	A	M	N	D	J	F	M	A	M	N	D	J	F	M	A	M
Agraulis vanillae maculosa	175	81	130	01	01			01		06							14				
Dryas iulia alcionea	15	32	09	01	03	16	20	01			01						01				01
Urbanus simplicius	01			02	01	13	04	01				04	01		01						
Tegosa claudina			01		01		01	01		01											01
Heliconius erato phyllis							28	01													01
Anartia amathea roeselia							20								04						
Danaus plexippus erippus								01							01		01				04
Danaus gilippus gilippus		01														01					
Dryadula phaetusa							02							01							
Eueides isabella dianasa	01					02									01						
Junonia cf. *genoveva*							15				01										
Vanessa braziliensis	01							01				01									
Heraclides hectorides	01						09	01													
H. thoas brasiliensis	03							01													
Eurema spp.		01				01		01	01	01											
Protesilaus sp.	37		01	01				01			01										
Phoebis argante argante														03							01
Parides bunichus perrhebus				01			11							01							
Ortilia ithra															05						
Actinote mamita								01													
Anartia jatrophae jatrophae											01			01							
Heraclides anchisiades					01																
Colias lesbia lesbia											01										
Tmolus echion			03																		
Urbanus cf. *teleus*	10																				
Heliopetes omrina									01												
Melipotis sp.												01									
Philorus sp.									01												
Phocides polybrius phanias									01												

Tegosa claudina, and *Heliconius erato phyllis* visited all three plants. In addition, butterfly species that visited at least two of the three plants must be considered, particularly those which visited the flowers of *E. fulgens* and *L. camara*: *Junonia* cf. *genoveva*, *Vanessa braziliensis*, *Heraclides hectorides*, *H. thoas brasiliensis*, *Parides bunichus perrhebus*, *Protesilaus* sp., and *Eurema* spp. The pierid *Phoebis argante argante* was never observed on *Lantana* flowers. The remaining species were visitors of only one plant species. Figures 5-8 show some remarkable instances of the presence of orchid flower pollinaria in the proboscis of the butterflies; particular attention should be paid to the presence of pollinaria of both species, *E. fulgens* and *A. curassavica*, in one individual of *Colias lesbia lesbia* (figure 7). Although not shown here, the same occurred with *Danaus* spp. In the whole, our records of butterflies as potential pollinators increased in 23% the number of such records in the literature (table 2).

Taking into account the butterflies that visited particularly *L. camara* and *E. fulgens*, the association among the number of visits to both species was tested by Pearson correlation. The results showed significant association among visitors of both plant species ($r = 0.4603$; $n = 19$; $P = 0.0473$). The low magnitude of this association can be confirmed by the coefficient of determination (r^2), that is, only 21% of the butterfly visits to *Epidendrum* are explainable by the visits to *Lantana*.

Epidendrum fulgens pollinaria removal – The removal of *E. fulgens* pollinaria was low (table 3), *i.e.*, there is no decreasing trend relative to nectar source as *L. camara* distance increases, as expected. The highest frequency was only 10% at a distance of 30 m (transection 5, afternoon), preceded by a 3% frequency at 20 m, and 0% at 10 m. Therefore, the fact that *E. fulgens* is close to *L. camara* does not indicate a "benefit" for that species in terms of increasing the number of visits received,



Figures 5-8. Butterflies with pollinaria on their mouthparts and legs in Parque Estadual de Itapeva. 5. *Vanessa braziliensis* (note pollinaria attached to the proboscis). 6. *Agraulis vanillae maculosa* (one pollinaria of *Epidendrum fulgens* clearly visible in the proboscis). 7. *Colias lesbia lesbia* with *Asclepias curassavica* pollinaria attached on one of its legs (arrow) and *E. fulgens* pollinaria in the proboscis. 8. *Danaus gilippus gilippus* visiting *A. curassavica*. Note *E. fulgens* pollinaria (arrow) in the proboscis.

Table 2. List of butterfies as floral visitors of the three plant species as reported in studies on pollination, flower mimicry, food source or direct field observations. (*A.c.* = *Asclepias curassavica*; *E.p.* = *Epidendrum* spp.; *L.c.* = *Lantana camara*; SC = Schemske (1976); BA = Barrows (1976); BO = Boyden (1980); BI = Bierzychudek (1981); BE = Berchtold (1981); CO = Corrêa *et al.* (2001); BR = Barros *et al.* (2001); PI = Pinheiro (pers. comm.) and PS = present study.)

Family	Species	*A. c.*	*E. p.*	*L. c.*
Nymphalidae	*Actinote mamita*		PS	
	Agraulis vanillae maculosa	PS	PS – PI	SC – BA – BR – PS
	Anartia amathea roeselia	BE – PS		PS
	A. fatima	BI	BI	SC – BA – BI – BR
	A. jatrophae jatrophae	BE	PS	SC – BA – BI – BR
	Chlosyne sp.		BI	BI
	Danaus gilippus gilippus	BE – PS		BA – PS
	D. plexippus erippus	BE – BO – PS	BO – PS	SC – BA – BO
	Dione julia			SC
	Dryas iulia alcionea	BI – PS	PS	SC – PS
	Dryas iulia cillene			BR
	Dryadula phaetusa		PS	PS
	Euptoieta claudia			BR
	E. hegesia			BR
	Eueides isabella dianasa	PS		PS
	Heliconius erato phyllis	PS – CO	PS	PS – CO
	Heliconius sp. 1			SC
	Heliconius sp. 2			SC
	Junonia cf. *genoveva*		PS – PI	PS
	Junonia sp.			BR
	Ortilia ithra	PS		
	Precis lavinia			SC
	Tegosa claudina	PS	PS	PS
	Thessalia theona			SC
	Vanessa braziliensis		PS – PI	PS
Papilionidae	*Battus belus*			BR
	B. polydamus polydamus			SC – BR
	Heraclides hectorides		PS	PS
	H. anchisiades			PS – BR
	H. thoas brasiliensis		PS	PS – SC
	Parides bunichus perrhebus		PI	PS
	Protesilaus sp.		PS	PS
	Papilio polyxenes			BR
Hesperiidae	*Autochton longipennis*			SC
	Heliopetes omrina		PS	
	Hesperiidae sp.			BA
	Pyrgus spp.			SC
	Phocides polybius phanias		PS	
	Urbanus simplicius	PS	PS	PS
	Urbanus cf. *teleus*			PS
	Urbanus sp.			BA
	Urbanus sp. 1			BR
	Urbanus sp. 2			BR
	Urbanus spp.			SC
Lycaenidae	*Rekoa palegon*	PS		
	Tmolus echion			PS
Pieridae	*Ascia monuste*			SC – BR
	Colias lesbia lesbia		PS – PI	
	Eurema daira			SC – BA
	Eurema sp.			SC
	Eurema spp.		PS	PS
	Lycorea ceres			BA
	Pieridae sp.			BA
	Phoebis argante argante		PS	SC – BR
	P. sennae marcellina			SC
	Phoebis sp.			BR

Table 3. Frequency of *Epidendrum fulgens* pollinaria removal according to distance from resource origin (nectar of *Lantana camara*). (M = morning; A = afternoon; 24 h, 48 h = resampling of the same flowers.)

		Nº pollinaria removed / Total no. of flowers			
Transect	Period	10 m	20 m	30 m	40 m
1	M	0	0	0.029	0.034
	A	0	0	0.029	0.034
	24 h	0	0	0	0.036
2	M	0.080	0	0	0
	A	0.033	0	0	0
	24 h	0.033	0	0	0
3	M	0	0.037	0	0
	A	0	0	0	0
	24 h	0	0.034	0	0
4	M	0	0	0	0
	A	0	0	0	0
	48 h	0	0	0	0.056
5	M	0	0	0	0.048
	A	0	0.033	0.103	0.048
	48 h	0	0.031	0.042	0.000
6	M	0.042	0.067	0.063	0.029
	A	0.042	0.067	0.067	0.029
	48 h	0.043	0	0	0

as it does not offer resources to the flower visitor. The low frequency of pollinaria removal was reinforced by the 24- and 48-hour observations, as a higher removal frequency would be expected for the same plants. Statistical analysis was considered unfeasible, since there was no recognizable pattern.

Epidendrum fulgens mode of reproduction – Table 4 summarizes the results on the mode of reproduction of *E. fulgens*. This plant is self-compatible and no statistical differences were observed among the cross-pollinated flowers and self-pollination, as to the number of fruits (χ^2 = 0.1058; 2 d.f.; *P* = 0.9952). No fruits were observed in spontaneous self-pollination, thus *E. fulgens* is pollinator-dependent.

Table 4. Experimental pollinations and fruit-set in *Epidendrum fulgens*.

	Flowers Nº	Fruits	
		Nº	%
Self-pollination (*)	25	21	0.84
Geitonogamy (*)	26	22	0.85
Xenogamy (*)	31	27	0.87
Spontaneous self-pollination	30	0	0

(*) groups statistically compared (χ^2 = 0.1058; 2 d.f.; *P* = 0.9952).

Discussion

Although *L. camara* and *E. fulgens* do not have a synchronized flowering period they still have flowers simultaneously during approximately four months. This suggests the use of pollinators' memory for nectar source (*L. camara*), which would be beneficial for the orchid, because it would increase the probability of visits to the orchid by pollinators, although it does not produce nectar. Additionaly, *L. camara* produces exposed pollen as well, which can be used by other insects, particularly Hymenoptera. As for the butterflies sampled in the present study, only *Heliconius erato phyllis* used this food source. The fact that *Heliconius* butterflies are pollen feeders is well known; moreover, Beltrán *et al.* (2007) showed that this behavioral trait had a single origin in the phylogeny of the group.

It is easy to see that the number of *E. fulgens* flowers increases after the peak of *Lantana* blooming. Moreover, out of the five butterfly species that visit the three plant species, marking-release-recapture data on four of them (*Dryas iulia alcionea*, *Heliconius erato phyllis*, *Agraulis vanilae maculosa*, and *Tegosa claudina*) indicate average lifetimes longer than 40 days, *i.e.,* sufficient time to use the information on *Lantana* flowers stored in their memory, and to use it when *Epidendrum* blooming increases (Téo Halfen, unpublished results). This suggests the possible presence of mimicry between two or more species in the studied setting, in which the orchid provides false information (it seems to have nectar, but it does not – Fuhro 2006), deceiving pollinators. Vogel (1993) stressed this aspect when observing that flowers that offer nectar are used as models by "food-deceptive flowers", without nectar, and that the latter may use a "standard appearance" to lure visitors. On the other hand, Schemske (1976) suggested that many plants develop inflorescences to maximize foraging efficiency (floral display), favoring some pollinators, while preventing others from entering the pollination system, such as the case of *L. camara, A. curassavica*, and *E. fulgens* flowers. Field observations showed that, in *L. camara*, yellow flowers are frequently visited by butterflies. Yellow is a positive sign for the flower visitor, as it indicates the presence of nectar. After pollination, flowers turn orange to red. Maintaining the flowers red, with no nectar, would attract potential pollinators of the same inflorescences and/or of distant plants (Weiss 1991). So, if *E. fulgens* uses this "standard appearance", it would benefit not only from the presence of *L. camara*, but also from other species that bloom in the area.

Butterflies with *E. fulgens* pollinaria adhered to their proboscis were observed in areas where this plant was not present. This indicates that butterflies traveled among areas, increasing cross-visitation. For instance, an individual of the butterfly *Danaus plexippus plexippus* carrying *E. fulgens* pollinaria in its proboscis and, simultaneously, *A. curassavica* pollinaria on its legs, was captured within an area where only *A.curassavica* and *L. camara* were present.

Our data indicate that butterflies visiting the flowers of *L. camara* as a source of nectar and pollen, have a probability of 46% to visit a flower of *E. fulgens*. So, visiting one plant species and another is not a random behavior. If they formed a pair of mimetic species this is exactly what one would expect. Eventually a criticism could be done to this analysis, relying in the absence of another test to correlate the visit to *Lantana* to any other flower nearby. However, the important point to be stressed here is that if no correlation was found in the visits between *Lantana* and *Epidendrum*, that would weaken the idea of a mimicry system between them. *Asclepias* was not included in this correlation analysis, as it did not occur close to the orchid, therefore violating one of the requirements for the occurrence of a sensorial mechanism that induces visits to the mimic.

From the theoretical standpoint, two circumstances can be expected as to the amount of pollinaria removed from the orchid associated to the presence of *L. camara*: (1) the closer orchid individuals are to *L. camara*, the higher the probability of pollinaria removal, and as this distance increases, the probability of pollinaria removal diminishes; (2) the higher the number of *L. camara* individuals located close to the orchid (that is, their density), the higher the probability of pollinaria removal as well (adapted from Bierzychudek 1981). In the present study, only the first probability was tested. Our results are not consistent with these expectations, despite a significant correlation in the visits to *L. camara* and *E. fulgens* reported in the preceding paragraph.

Surely, the results presented here are not conclusive as to the presence of a mimetic system among *A. curassavica*, *E. fulgens* and *L. camara*, although there are indications that this may be true. For instance, the color of the flowers of the three species is similar, with red around yellow. In addition, the results of the test on the relative frequency of butterfly visits to pairs of species showed a significant association between *L. camara* and *E. fulgens*. This situation is similar to that reported by Bierzychudek (1981), who moreover observed that in some regions of Central and South America changes in the color of *L. camara* flowers are associated with concurrent changes in the color of *E. secundum* flowers. Based on this information, it is tempting to speculate in which category of the system proposed by Vane-Wright (1976) the plants studied here, particularly *L. camara* and *E. fulgens*, could be included. We attempted to do this in figure 9: there, butterfly represents the operator (R), an organism that is not able to discriminate the model (S_1) from the mimic (S_2). The former, as it produces nectar and attracts pollinators, would be the model (*L. camara*), whereas the orchid (*E. fulgens*) would be the mimic, as it does not produce nectar, thereby deceiving the visitor but otherwise benefiting from the color similarity of its flowers to those of *L. camara*. The benefit to the orchid is the releasing of its pollinaria followed by its dispersal by the butterfly. The negative sign associated to *L. camara* indicates that the presence of the mimic is a disadvantage for the model, and the two positive signs of the operator suggest that its natural tendency is to approach both plant species. Vane-Wright (1976) refers to this type as Class V, "antergic inviting mimicry"; in his own words, "this represents a form of mimetic competition, whereby

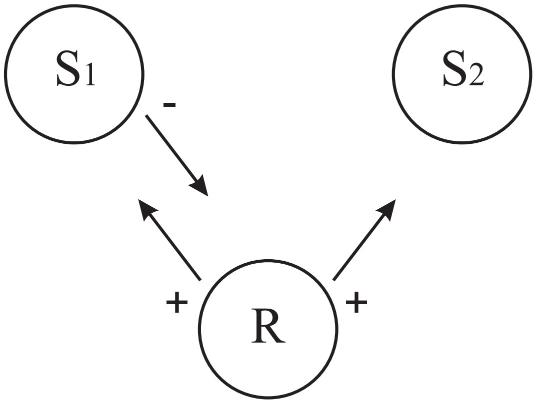


Figure 9. Diagram of the suggested model of a possible mimetic relationship between *Lantana camara* (S_1 = model) and *Epidendrum fulgens* (S_2 = mimic). The operator (R) is a butterfly. Adapted from Vane-Wright (1976).

the mimic simulates a signal of positive interest to the operator, as a result of which the model loses in some way. The mimic is always of some potential value to the operator". In the present study, we decided not to use the classical Batesian mimicry and Müllerian mimicry, such as did Boyden (1980), Bierzychudek (1981) and Johnson (1994), because these terms are applied specifically to distasteful animals and their mimics.

One of the assumptions of mimicry evolution is that the number of mimics must be fewer that those of the model (Sheppard 1965). In the present study, *E. fulgens*, the supposed mimic, does not follow this requirement, as it occurs in higher frequency than the other two plants (a preliminary estimate indicated approximately a ratio of 1 *L. camara* to 10 *E. fulgens*; for *A. curassavica*, the ratio is even greater). This may indicate that the ecological success of this orchid does not depend on the presence of *L. camara*, or *A. curassavica*, and that these exceptions to the rules of mimicry could have decisively contributed to the fact that no strong evidences of mimetic interaction between *L. camara* (or *A. curassavica* for that matter) and *E. fulgens* were found in the present study. Furthermore, *E. fulgens* presents different morphs as to flower color, with some individuals presenting exclusively yellow inflorescences, while others, orange. It is obvious, then, that if *Epidendrum* is independent of *Lantana* for its survival and reproduction, the idea of a mimicry system at Parque Estadual de Itapeva becomes weakened. Moreover, the analysis of its reproductive system showed that induced self-pollination, by pollination between flowers of different inflorescences of the same individual, and between different individuals, in all cases produced fruits. Finally, data obtained in the present study suggest that the occurrence of mimicry among these plants although possible, has not been showed, which is consistent with the data reported by Boyden (1980) and Bierzychudek (1981).

To our knowledge this is the first study in Brazil which investigated some ecological relations between a group of three species of plants which constitute a presumable mimicry system, and their potential pollinators (butterflies).

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