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Specialized use of pollen vectors by *Caesalpinia gilliesii*, a legume species with brush-type flowers

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The pollination of *Caesalpinia gilliesii* (Fabaceae), a legume species with long, brush-type flowers, was studied in wild populations in Argentina. A total of 341 hawkmoths (Sphingidae), belonging to 10 species, with tongues ranging from 1.5 to 13.5 cm in length, were captured by means of light traps. Hawkmoths could be classified in four significantly different tongue-length classes or guilds: short (15.35 ± 1.11 mm), medium (30.23 ± 2.24 mm), long (55.85 ± 4.98 mm) and very long (95.61 ± 13.63 mm). A total of 133 of the hawkmoths, belonging to seven species, carried pollen of *Cae. gilliesii*, mainly on their venter. Successful contact with anthers while drinking nectar depended upon hawkmoth tongue length. The relative frequency of pollen-carriage and the mean tongue length of each species were positively and significantly correlated. Considering a null hypothesis of nonspecialization, in which hawkmoths carrying pollen are distributed at random among individuals of the four guilds, long-tongued hawkmoths carried *Cae. gilliesii* pollen more frequently than would be expected by chance. In contrast, short- and medium-tongued guilds carried pollen less frequently than is predicted by random expectation. Individuals with short tongues accessed nectar from below without touching the anthers, whereas very long-tongued hawkmoths, with tongues longer than the length range of the flower reproductive organs, can probably reach nectar without touching the fertile organs. Results show that a pterotribic pattern of pollen deposition on the body of long-tongued hawkmoths is operating in this species. This suggests that brush-type blossoms are not necessarily unspecialized, despite popular belief. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **88**, 579–592.

ADDITIONAL KEYWORDS: Fabaceae – long-tongued hawkmoth pollination – pollinator guild – pterotribic pollen deposition – Sphingidae.

INTRODUCTION

Brush-type blossoms are distinct in their architecture for having greatly exserted stamens and styles, and a tubular container or other structure concealing nectar in deep parts often being reduced or completely lacking (Endress, 1994). Since the perianth does not provide a landing surface for pollinators, it is either reduced, if it is calyx-like, or horizontally spreading or folded back, if it is petal-like. The stamens, which may be free or united, and the style are protruding and often divergent. This blossom type is widespread in flowering plants; it may be represented by single flowers (*Ceiba*, *Capparis*) or inflorescences (*Albizzia*, *Calliandra*), it may range from small heads (*Acacia*) to large brushes (*Pachyra*), and it may be diurnal or night blooming. Details of the most conspicuous examples of brush-type flowers are given in Appendix 1.

Brush-type blossoms evolved in basal eucotyledoneous lineages in which fused tubular flower structures are seldom produced, probably as a result of phylogenetic or developmental constraints (Endress, 1994). It has been suggested that this blossom type is structurally unspecialized because of the lack of a tube protecting the nectar and the wide array of visitors (bats, nonflying mammals, hummingbirds, hawkmoths, skippers, settling moths, stingless bees, bees, flies, butterflies and beetles) that have been recorded as effective pollinators of species such as *Adansonia, Capparis*, *Inga* and *Luehea* (Haber & Frankie, 1982; Koptur, 1983; Eisikowitch, Ivri & Dafni, 1986; Dafni,

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Eisikowitch & Ivri, 1987; Baum, 1995). If brush-type flowers are open to pollinators of many kinds, which show considerable variation in the length of their mouthparts, and if these are all equally effective pollen vectors, the plant population should evolve diffusely to match in length the more frequent pollinators. Thus, evolution of extremely long flowers, as found in long tubular or spurred flowers, should be less likely in brush flowers (Darwin, 1862; Nilsson, 1988). Indeed, hawkmoth-pollinated brush-type flowers have been found to filter pollinators less effectively than do tubular flowers. For example, even relatively long brush-type flowers (6 cm) in a Costa Rican community may be pollinated by 18 hawkmoth species, ranging in tongue length from 1.5 to 10.6 cm (Haber & Frankie, 1989). However, contradicting this hypothesis, very long brush-type flowers do exist, such as *Cleome gigantea* L. (11.1 cm, pers. observ.) and *Pseudobombax longiflorum* (C. Martius & Zucc.) Robyns (13 cm), and extremely long examples are known, such as the 31-cm long flowers of *Pachira aquatica* (Jacq.) W. S. Alverson (Killeen, García & Beck, 1993; Cascante-Marín, 1997). However, other than the work of Baum (1995) on pollination of *Adansonia* species, almost no attempt has been made to determine whether all pollinators of brush-type blossoms are indeed equally effective.

To elucidate this apparent contradiction, we selected the legume *Caesalpinia gilliesii* (Wall. ex Hook.) Dietr., which has relatively long, brush-type flowers (up to 12.3 cm), to test whether or not available visitors transport pollen with different effectiveness according to the length of their tongues, and whether flower length matches a specific group of pollinators that can be defined by a narrow or wide range of tongue length. If long-tongued pollinators transported pollen differentially, pollinators could exert selective pressure favouring long flowers even if nectar were widely available to visitors.

Cae. gilliesii is considered endemic to Argentina (Burkart, 1936). Plants are andromonoecious and show variability in the production of staminate and perfect flowers in relation to plant and inflorescence size (Cocucci, Galetto & Sérsic, 1992; Calviño & Carrizo García, 2005). The fragrant flowers have dark-red, exserted styles and stamens that contrast with the light-yellow, highly reflective petals (Moré *et al.*, 2003). Effective pollination in this species by nocturnal hawkmoths, first recorded by Cocucci *et al.* (1992), is probably the only instance of hawkmoth pollination in this large and otherwise mainly bee-pollinated genus (Cocucci *et al.*, 1992; Endress, 1994; Simpson & Miao, 1997). Brush-type flowers are exceptional in *Caesalpinia*, a genus in which the majority of species have short, sternotribic stamen fascicles. Besides *Cae. gilliesii*, only *Cae. pulcherrima* has a conspicuous brush, but it has a tubular median petal and is pollinated by butterflies (Vogel, 1954; Cruden & Hermann-Parker, 1979).

Diurnal visitors to *Cae. gilliesii,* such as *Apis mellifera* L., *Bombus morio* (Swederus 1787) and *Xylocopa* sp., have been recorded in the early morning, foraging for pollen before the flowers wilt, but they rarely touched the stigmas. The hummingbird *Chlorostilbon aureoventris* (Orbigny & Lafresnaye 1838) has also been recorded drinking nectar from *Cae. gilliesii*, but because of its short bill it accessed flowers from below, without touching the fertile parts (A. Calviño, pers. comm.; Cocucci *et al.*, 1992).

Reported hawkmoth pollinators of *Cae. gilliesii* had tongues ranging from 5.2 to 11.5 cm in length (Cocucci *et al.*, 1992). The hawkmoth fauna of Argentina is diverse (Moré, Kitching & Cocucci, 2005) and varies considerably throughout the distributional range of *Cae. gilliesii*. Thus, we expected to find heterogeneous pollinator assemblages between and within populations of *Cae. gilliesii*, with a wide range of tongue lengths.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in ten sites in Argentina where *Cae. gilliesii* grows naturally (Appendix 2). Populations were located in open forest and savannas in the Chaco region and one, Reserva Luro, in the Espinal region (Cabrera, 1976). Observations were made during the flowering season (November to February), between November 2000 and November 2002.

FLOWERS

Style and stamen lengths were measured with a digital calliper to the nearest 0.01 mm in six populations (Appendix 2). Measurements were taken from all individuals in small populations (fewer than six individuals) or from seven to 19 individuals, chosen randomly, in larger populations (Fig. 1A). A Shapiro–Wilks test showed non-normal distribution of both raw and transformed data, so a Kruskal–Wallis analysis was performed to test if the length of fertile parts showed variation at the interpopulation level (Sokal & Rohlf, 1995).

HAWKMOTHS

Seven populations of hawkmoth were sampled with a vertical sheet light trap (Fry & Waring, 2001) on a total of 12 nights (Appendix 3). Each trapping lasted 4 h (20 : 00–24 : 00 h) and used two light traps set 60 m apart. Hawkmoths that settled on the sheets

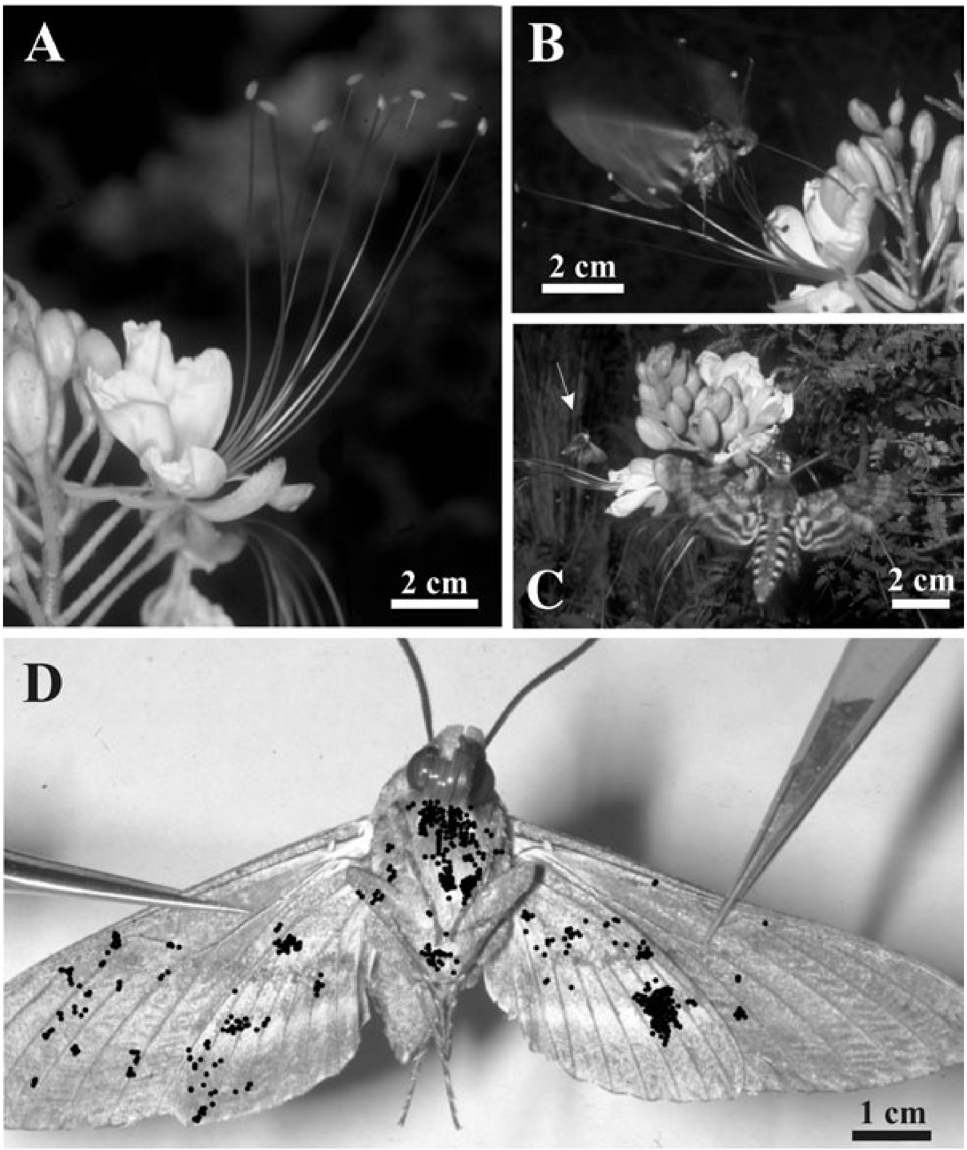

Figure 1. A, *Caesalpinia gilliesii* freshly opened flower, lateral view, and an older one with wilted stamens and petals behind. B, front view of a hawkmoth (presumably *Sphinx maura*) taking nectar from the base of the middle petal and striking the anthers with its wings. C, abdominal view of *Agrius cingulata* and a quadrifine noctuid moth (arrow) taking nectar from flowers. D, *Manduca sexta* ventral face onto which pollen clumps are mapped out as dots.

were immobilized immediately in clean jars containing chloroform vapour and kept in individual entomological envelopes for identification later. The species, sex, and tongue length of each specimen were recorded shortly after capture.

POLLINATION MECHANISM

Mechanical interactions between flowers and pollinators were studied from direct observations and photographs taken with a 35-mm Nikon camera and a Metz 45 CL flashlight. To determine the presence of *Cae. gilliesii* pollen and its location on captured hawkmoth body parts (tongue, antennae, legs, wings, thorax and abdomen), specimens were inspected in the field under a binocular microscope (magnification 35×). Pollen samples were taken from hawkmoth bodies and mounted in glycerine jelly for microscopic analysis later (Kislev, Kraviz & Lorch, 1972; Kearns & Inouye, 1993). Pollen grains were identified using reference samples taken at each site from *Cae. gilliesii* and other plants likely to be visited by hawkmoths. The large size of the pollen grains of *Cae. gilliesii* allowed us to identify them individually on highresolution photographs. Thus, the pattern of pollen deposition could be mapped on captured hawkmoths.

SPECIFICITY IN THE USE OF POLLEN VECTORS

Interspecific differences in tongue length were tested using a Kruskal–Wallis analysis for the merged dataset; an ANOVA was used only for the largest and normally distributed Cuesta Blanca dataset. For each body part, a Williams adjusted *G*-test of goodness of fit was performed with the merged dataset to determine if hawkmoths carrying pollen were distributed randomly between two tongue-length classes: short plus medium, and long plus very long (Sokal & Rohlf, 1995).

The existence of tongue-length classes in the captured hawkmoths (irrespective of their taxonomic assignment) was assessed by calculating the difference on a $\log_{10}$ scale between the tongue length of each individual and that of the next shortest. The greatest difference was used to split the data into two classes ,and a Kruskal–Wallis test was performed to determine if there was a significant difference between these classes. This procedure was then performed with the next greatest difference and the procedure repeated until no more new significantly different groups were found. Groups were then tested for normality with the Shapiro–Wilks test.

To test for differential transport of *Cae. gilliesii* pollen by hawkmoths according to species or tongue-length class, the *G*-tests of independence were performed for the Cuesta Blanca dataset (Sokal & Rohlf, 1995). This tested the null hypothesis that pollen is distributed randomly among individuals of all species or classes. Species and classes were tested for homogeneity with the unplanned comparison procedure (Sokal & Rohlf, 1995). To test if the frequency of individuals carrying *Cae. gilliesii* pollen in a hawkmoth species was correlated with species mean tongue length, a product moment correlation was performed.

RESULTS

FLOWERS

Intrapopulation variation in flower length

Styles and stamens showed variation in length between the six populations studied (Kruskal–Wallis test: $H_{\text{stamens}} = 222.44$; $H_{\text{stigma}} = 146.76$; $P < 0.0001$). El Arenal and Ampimpa populations had the shortest styles and stamens, while El Carmen I and Reserva Luro had the longest styles and stamens, respectively. Cuesta Blanca and El Carmen II had intermediate lengths (Table 1).

Flower visitation

Flowers were visited mainly by hawkmoths, but also by noctuid moths at dusk and after dark. Hawkmoths were never seen to settle on the flowers, but always took nectar in hovering flight, mainly reaching from above the anther level (Fig. 1B, C). The anthers and stigmas of visited or neighbouring flowers were impacted by body thrust and wing beating (Fig. 1D). Individuals of a short-tongued hawkmoth, *Callionima grisescens*, and a quadrifine noctuid moth that could not be captured, accessed the flowers from below without touching the anthers and stigma (Fig. 1C).

HAWKMOTHS

Species and variations in tongue length

A total of 341 hawkmoths of 10 species were captured by light trap (Appendix 3). Individuals of an additional species, *Agrius cingulata*, were seen and photographed in the Alta Gracia and San Nicolás

Table 1. Style and stamen lengths of six populations of *Caesalpinia gilliesii* growing in Argentina

	Stamen length		Style length	
Locality	*N*	mm, mean ± SD	*N*	mm, mean ± SD
El Arenal	51	76.88 ± 6.04 A	47	84.40 ± 9.08 A
Ampimpa	33	80.26 ± 4.20 A	28	85.86 ± 5.93 AB
Cuesta Blanca	88	81.68 ± 7.74 B	57	95.01 ± 7.79 B
El Carmen (pop. 1)	59	88.61 ± 6.09 C	58	102.09 ± 7.74 C
El Carmen (pop. 2)	45	91.65 ± 3.03 D	42	106.23 ± 6.68 C
Reserva Luro	111	98.47 ± 5.75 D	70	106.00 ± 7.19 D
Total	387		302	

Different letters show significant differences between means according to Kruskal–Wallis nonparametric test ($P < 0.001$). See text and Appendix 2 for further explanations.
pop, population.

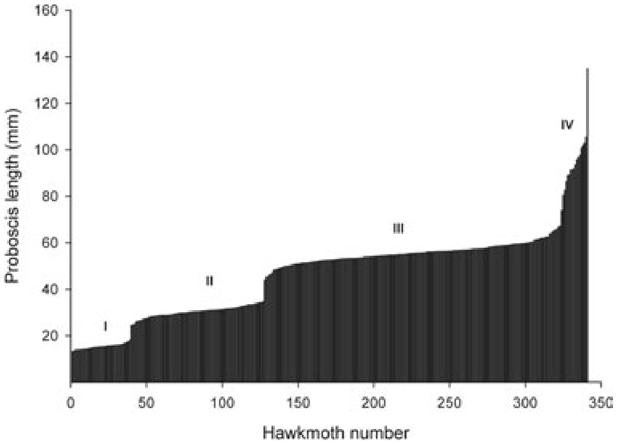

Figure 2. Tongue length of all hawkmoths captured arranged in order of increasing length. Species were sorted into four groups according to tongue length. I, *Callionima grisescens* (15.35 ± 1.11 mm, $N = 39$); II, *Hyles euphorbiarum, H. lineata, Xylophanes tersa*, and one individual of *Manduca diffissa* (30.33 ± 2.29 mm, $N = 88$); III, *Man. florestan, Sphinx maura, Man. bergi, Man. diffissa* and one individual of *Man. sexta* (55.52 ± 4.12 mm, $N = 196$); IV, *Man. sexta* and *Man. rustica* (94.78 ± 12.92 mm, $N = 18$).

populations, but no individuals were attracted to the lights. Of 30 photographs of this species hovering in front of flowers, contact was made with the stamens and stigmas in eight cases (Fig. 1C). There was a wide range of tongue lengths among the captured hawkmoths, from 15.35 mm in *Cal. grisescens* to 134.90 mm in *Manduca rustica*. Tongues differed significantly in length at the interspecific level ($H = 258.10$, $P < 0.001$).

Tongue-length classes

Individuals could be separated, irrespective of their taxonomic assignment, according to the length of their tongues into a maximum of four significantly different groups or guilds: I, short; II, medium; III, long; IV, very long ($F = 1510.20$; $P < 0.0001$) (Fig. 2). Within these guilds, tongue length was distributed normally (Shapiro–Wilks test, not significant). The longest-tongued individual, the single *Man. rustica* captured, was not assigned by the analysis to any of these guilds and had a proboscis significantly longer than guild IV ($t = 4.80$; d.f. = 16; $P < 0.001$).

Interpopulation variation in hawkmoth assemblages

Hawkmoths with long (Guild III) tongue were present in all populations sampled, with the exception of Reserva Luro, where only the guild with very long (Guild IV) tongues was present. The guilds with short and/or medium tongues (Guilds I and II) were present at Cuesta Blanca, La Quebrada and San Nicolás (Appendix 3).

Hawkmoths carrying pollen

More than 39% of captured hawkmoths (133 individuals) carried *Cae. gilliesii* pollen. The proportion of hawkmoths carrying pollen varied considerably among sites ($G = 28.36$, $P < 0.0001$) and among samples for the same site ($G = 114.20$, $P < 0.0001$). Either hawkmoths did not carry *Cae. gilliesii* pollen (Cuesta Blanca, February 25, 2001), or the number of specimens carrying pollen of *Cae. gilliesii* was lower (Cuesta Blanca, November 8, 2001), not different (Cuesta Blanca, November 2, 3 and 21, 2000; La Quebrada, October 17, 2002; Cachi Adentro, November 11, 2002; Reserva Luro, December 13, 2000) or greater (Cuesta Blanca, October 24, 2002; San Nicolás, November 27, 2002; Alta Gracia, October 31, 2002) compared with the number of specimens not carrying this pollen type (Appendix 3).

Seven of the 10 species captured carried *Cae. gilliesii* pollen; no individuals of *Hyles lineata, Man. florestan,* or *Man. rustica* carried pollen of this species. Across species, the proportion of individuals carrying pollen of *Cae. gilliesii* was positively correlated with the mean length of the tongue in the species ($r = 0.90$; $P < 0.001$) (Fig. 3A).

Taking all captured hawkmoths into account, the percentage of those carrying pollen of *Cae. gilliesii* differed between guilds. Of the 133 hawkmoths carrying pollen, 109 individuals had tongues longer than 43 mm (Guilds III and IV) and only 24 individuals had shorter tongues (Guilds I and II); most ($N = 97$) belonged to Guild III (Fig. 3B). Guild IV had the highest percentage of individuals carrying *Cae. gilliesii* pollen (Fig. 3B).

Man. diffissa and *Man. sexta*, most of whose individuals belonged to Guilds III or IV, respectively, either together or alone were the only very long- and long-tongued species found carrying *Cae. gilliesii* pollen in all populations. The guilds of short- and medium-tongued hawkmoths (Guilds I and II) carrying *Cae. gilliesii* pollen varied in species composition between populations, or else were not present, as in the Reserva Luro population (Appendix 3).

Patterns of pollen deposition

Pollen of *Cae. gilliesii* was found on antennae, palps, tongue, eyes, thorax, wings, legs and abdomen of captured hawkmoths. Pollen was more frequently deposited on the wings (72.2%) and tongue (70.6%), while legs (12.0%), antennae plus eyes (4.5%) rarely carried pollen. The frequency of pollen deposition on palps (29.3%), abdomen (28.6%) and thorax (31.6%) was intermediate.

The pattern of *Cae. gilliesii* pollen deposition on the hawkmoths' bodies differed according to hawkmoth

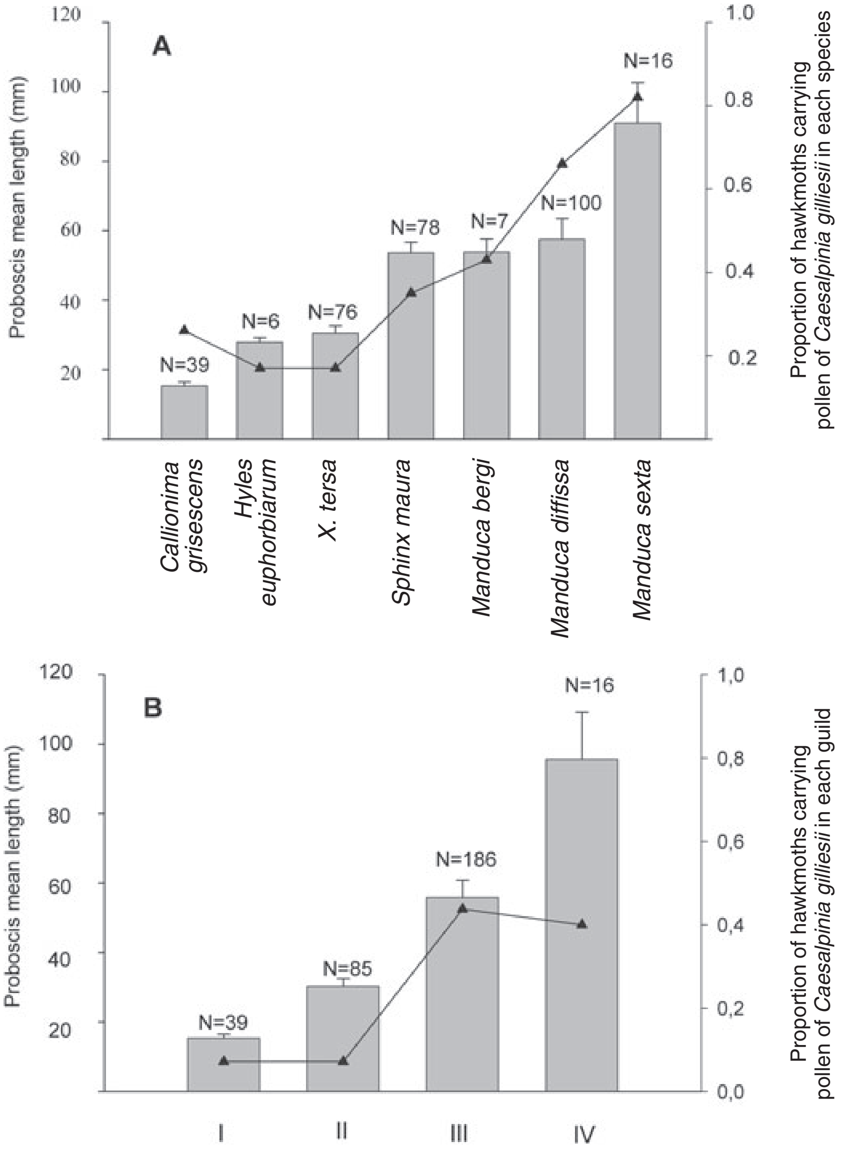

Figure 3. Species (A) and guilds (B) of hawkmoths carrying *Caesalpinia gilliesii* pollen sorted in order of increasing mean tongue length (grey bars). The lineplot shows the proportion of hawkmoths carrying pollen of each species calculated as number of individuals carrying pollen/total number of individuals captured (Pearson's $r = 0.90$; $P < 0.01$).

tongue length. Short-tongued species (*Cal. grisescens*, *H. euphorbiarum* and *Xylophanes tersa*) carried pollen principally on the tongue and less frequently on the wings and thorax, palps, antennae or eyes (Fig. 4). Long-tongued species (*Man. diffissa*, *Sphinx maura* and *Man. sexta*) carried pollen instead mainly on wings and tongue, and in a lower proportion of cases on thorax, palps, abdomen, legs, and antennae (Figs 1D, 4).

Among short and medium tongue-length guilds (Guilds I and II) only a few individuals carried *Cae. gilliesii* pollen on the wings. In contrast, nearly all hawkmoths with long and very long tongue (Guilds III and IV) carried *Cae. gilliesii* pollen on the wings (Fig. 3B).

In the Cuesta Blanca population, the proportion of hawkmoths carrying *Cae. gilliesii* pollen on the wings was 0.27. This ratio represents the probability that one individual was carrying pollen in this population. The observed frequencies of individuals carrying *Cae. gilliesii* pollen on the wings depended significantly on species and guild (Table 2). *Cal. grisescens* and *X. tersa* formed a homogeneous group in which the ratio of individuals carrying *Cae. gilliesii* pollen on the wings was less than the 0.27 ratio expected by chance alone (Table 2).

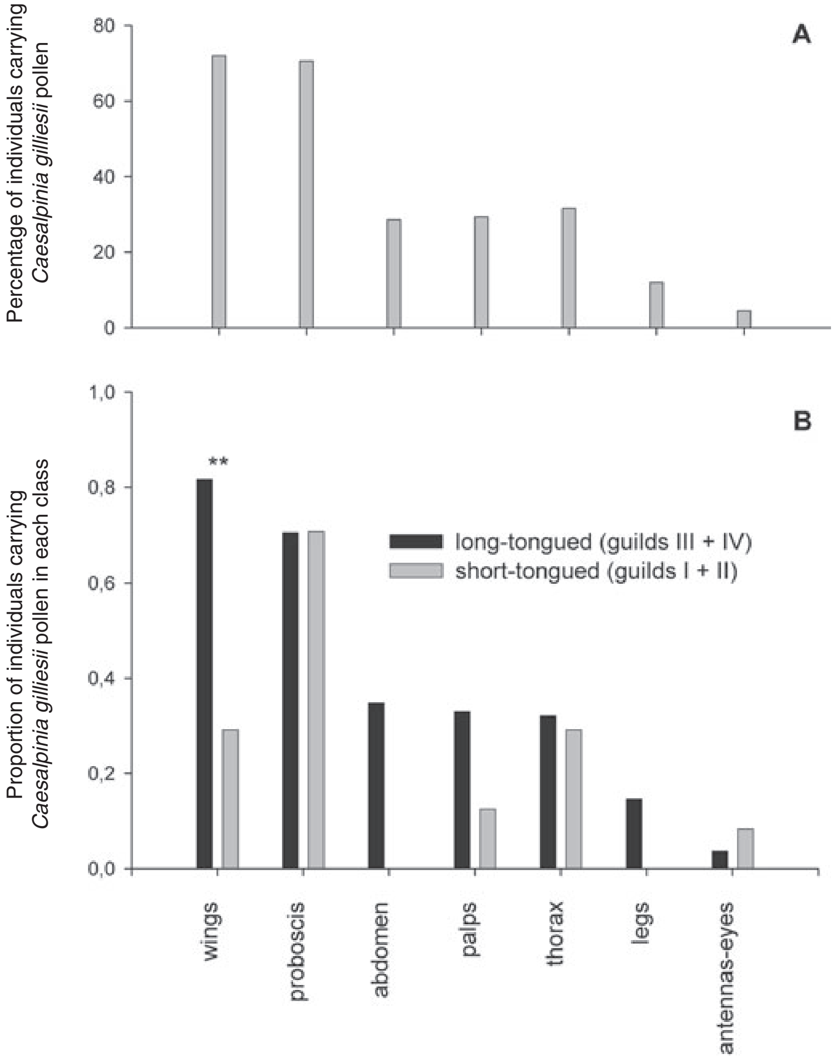

Figure 4. Pollen deposition on different body parts among the hawkmoths carrying *Caesalpinia gilliesii* pollen. A, percentage of hawkmoths carrying pollen on each body part. B, proportion of captured hawkmoths of two tongue-length classes carrying pollen. Short-tongued species: *Callionima grisescens*, *Hyles euphorbiarum* and *Xylophanes tersa*. Long-tongued species: *Manduca diffissa*, *Sphinx maura* and *Man. sexta*. **Significant differences between proportions at $P < 0.01$ (Adjusted $G = 9.21$).

Man. difissa, Man. sexta, and *S. maura* formed a second homogeneous group in which this ratio was greater than that expected from random (Table 2). The guilds of short and medium tongue length (Guilds I and II) constituted a homogeneous group where the ratio of hawkmoths carrying *Cae. gilliesii* pollen on the wings was much less than expected from random. Finally, the guilds of long and very long tongue lengths belonged to a second homogeneous group where this ratio was greater than expected from random (Table 2). Although the amount of pollen carried by hawkmoths was not measured we observed that pollen quantity on wings was much greater than that found on the tongues. Wings of some specimens were heavily dusted with *Cae. gilliesii* pollen (Fig. 1D). In addition to *Cae. gilliesii*, pollen of several other plant species was found on hawkmoth bodies. However, only one additional pollen type was transported on the wings of hawkmoths, *Lonicera japonica* Thunb. ex Murray, an exotic ornamental plant cultivated about one km from trapping site about 1 km from trapping sites (Fig. 5B). Other pollen included *Mirabilis jalapa* L. (Nyctaginaceae), *Macrosiphonia petraea* (A. St.-Hil.) K. Schum. (Apocynaceae), *Cestrum parqui* L'Hér., *Petunia axillaris* (Lam.) Britton, Stern & Poggenb. (Solanaceae), *Oenothera affinnis* Cambess. (Onagraceae) and seven unidentified types.

Table 2. Species and tongue-length guilds of hawkmoths carrying or not carrying *Caesalpinia gilliesii* pollen on their wings in Cuesta Blanca population

Species/guild	*N*	W = with pollen	Ratio of W/*N*†	Homogenous groups	Williams adjusted G-value
Species					
Manduca sexta	10	5	0.50	A	
Man. diffissa	53	23	0.43	A	
Sphinx maura	43	18	0.42	A	
Hyles lineata + *H. euphorbiarum*	5	1	0.20	A B	$G_{\text{group A}} = 1.38$ NS
Xylophanes tersa	65	4	0.06	B	
Callionima grisescens	14	1	0.07	B	$G_{\text{group B}} = 0.97$ NS
Total	190	52	0.27		$G_{\text{total}} = 35.88$***
Guild					
I	14	1	0.07	A	
II	70	5	0.07	A	$G_{\text{group A}} < 0.01$ NS
III	96	42	0.44	B	
IV	10	4	0.40	B	$G_{\text{group B}} = 0.05$ NS
Total	190	52	0.27		$G_{\text{total}} = 34.75$***

†The ratio between hawkmoths carrying *Cae. gilliesii* pollen on the wings and the number of hawkmoths captured, i.e. the probability that one individual was carrying pollen of *Cae. gilliesii* in the population, which was equal to 0.27 for the whole sample. See text for further explanation.

***$P < 0.0001$.

N, number of hawkmoths captured.

W, number of hawkmoths carrying *Cae. gilliesii* pollen on the wings.

NS, not significant.

RELATION BETWEEN FLOWER AND TONGUE LENGTHS

The mean tongue length of all hawkmoths and of hawkmoths carrying *Cae. gilliesii* pollen was shorter than the mean stamen and style length of *Cae. gilliesii*. This relation also held for each population (Fig. 6). Guilds I, II and III always had mean tongue lengths shorter than the lengths of the flower fertile parts. Hawkmoths of Guild IV had tongues nearly as long as, or longer than, the flower fertile parts at each site. There were no significant correlations between mean tongue length of hawkmoths carrying pollen and the length of fertile flower parts at each site.

DISCUSSION

INTER-POPULATION VARIATION IN FLOWER LENGTH

The differences in style and stamen lengths observed between *Cae. gilliesii* populations could have resulted from selection pressure exerted by different hawkmoth assemblages in geographically isolated populations (Thompson, 1999). Although we did not observe a significant correlation between the mean tongue length of hawkmoths carrying *Cae. gilliesii* pollen and the length of floral fertile parts, the mean tongue length was slightly shorter than stigma and stamen lengths in all populations (Fig. 6). If the tongue was too short, as in *Cal. grisescens,* or too long, as in *Man. rustica*, visitors did not carry pollen. The existence of an optimum range of pollinator tongue length adjusted to flower length suggests that stabilizing selection mediated by pollinators could be operating in *Cae. gilliesii*. In contrast, other authors have found that in hawkmoth-pollinated plants of Iridaceae and Orchidaceae, directional selection to longer floral tubes or spurs is operating (Nilsson, 1988; Johnson & Steiner, 1997; Maad, 2000; Alexandersson & Johnson, 2002), as first suggested by Darwin (1862) for the Malagasy orchid *Angraecum sesquipedale*.

In Reserva Luro, where we recorded the longest styles and stamens, only the very long-tongued hawkmoth, *Man. sexta,* was present. This could indicate a local adjustment of floral dimensions to match the length of pollinator's tongue to assure both removal of pollen from anthers and its deposition on stigma. Further studies involving a much broader temporal and geographical sampling should help to elucidate whether flower length is under pollinator-mediated stabilizing selection in *Cae. gilliesii*.

INTRA- AND INTERPOPULATION VARIATION IN HAWKMOTH TONGUE LENGTHS AND PATTERNS OF POLLEN DEPOSITION

The answer to the question we posed in this study is that, contrary to the implications of the hypothesis of

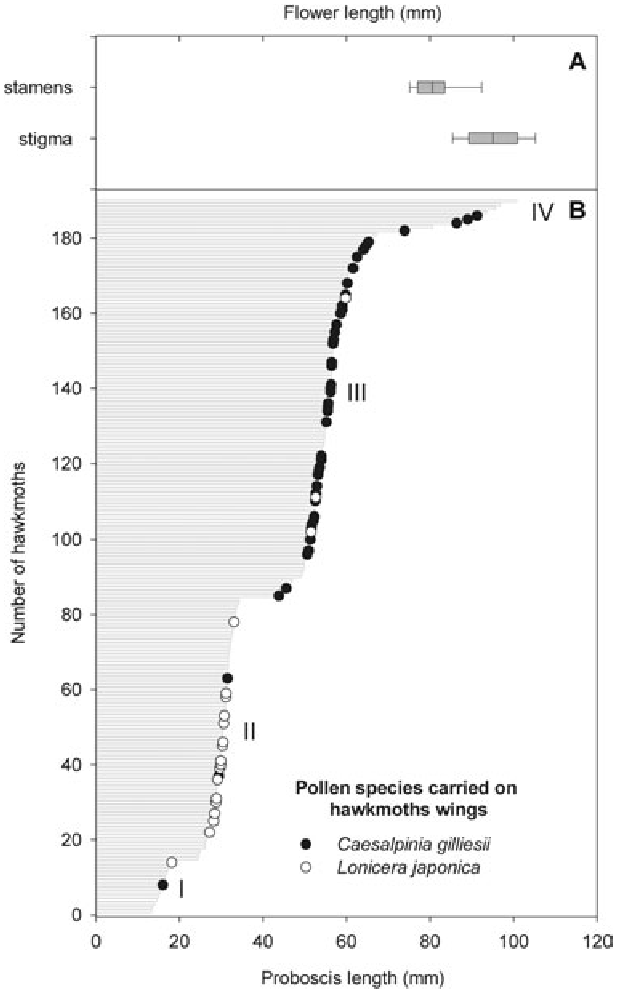

Figure 5. Comparison between *Caesalpinia gilliesii* flower and tongue lengths in Cuesta Blanca population. A, stamen ($N = 387$) and stigma ($N = 302$) lengths. B, tongue length of 190 hawkmoths captured carrying pollen on the wings of *Cae. gilliesii* and *Lonicera japonica*. Individuals were sorted into four categories significantly different in their mean tongue length ($F = 1809.86$; $P < 0.001$). I, *Callionima grisescens*; II, *Hyles euphorbiarum*, *H. lineata*, *Xylophanes tersa*; III, *Manduca diffissa, Sphinx maura*; IV, *Man. sexta*.

unspecialized flower morphology, the brush-type flowers of *Cae. gilliesii* are pollinated more frequently by hawkmoths with tongues ranging from 43.77 to 105.48 mm in length than expected by chance alone. This group included four species: *Man. bergi, Man. diffissa, Man. sexta* and *S. maura*. Hawkmoths with shorter or longer tongues can also be pollinators, but at a frequency not different from or below that expected for hawkmoth guilds or species in a given site. In other studies on brush-type flowers visited by animals with drinking apparatus varying widely in length, the relative frequencies of different pollinator types carrying pollen were usually not reported, so we do not know if all are equally important pollen vectors (Koptur, 1983; Eisikowitch *et al.*, 1986; Dafni *et al.*, 1987).

We found that *Cae. gilliesii* pollen was transported principally on the wings of the long-tongued hawkmoths mentioned above. These results, which show that the brush-type flowers of *Cae. gilliesii* make selective use of pollen vectors, strongly suggest functional specialization. A significantly higher proportion of hawkmoths carrying pollen on the underside of the wings indicates that these flowers have a mechanism of ventral pollen deposition. That nectar is accessible to hawkmoths across the range of tongue length is evident from the wide distribution of *Cae. gilliesii* pollen among captured hawkmoths. Also, nectar is accessible from below the flower, without touching the anthers, so the low frequency of pollen-carrying short-tongued hawkmoths recorded will be an underestimate of their actual visitation frequency. Thus, flowers do not limit access to nectar but rather ensure that pollen covers a greater area on the pollinator's body. Nectar robbing, performed by short-tongued lepidopterans is apparently 'tolerated' in order to maintain this pollen deposition strategy. It is one of several strategies competing to utilize different parts of the hawkmoth's body to place pollen. In the community studied here, pollen of other plant species also get attached to the bodies of long-tongued hawkmoths. For example, pollinia of *Habenaria gourlieana* Gillies ex Lindl. (Orchidaceae) get attached to the eyes (Singer & Cocucci, 1997), pollen clumps of *Mac. petraea* (Apocynaceae) are stuck to the tongue, pollen chains of *Oenothera* sp. are entangled on the legs, and pollen of *Nicotiana longiflora* Cav. and *P. axilaris* are deposited along the whole tongue (Roqueiro *et al.*, 2001a; Roqueiro, Sérsic & Cocucci, 2001b). That only a few hawkmoth species with long tongues pollinate many plant species is known not only for this but also for other hawkmoth-pollinated communities (Nilsson *et al.*, 1987; Haber & Frankie, 1989).

We can define our observed pattern of pollen deposition on hawkmoth wings as being vertically precise, because pollen is carried by a guild of hawkmoths whose tongue lengths nearly match the flower length of *Cae. gilliesii*, but being horizontally diffuse, because pollen is deposited over a wide area of the hawkmoth body. The mechanism used by *Cae. gilliesii* is no less adjusted for its purpose than are the mechanisms of pollen deposition in tubular flowers (Nilsson, 1988). Less economical use of pollen does not necessarily mean that the mechanism is not well suited to its pollinators. Though some short-tongued hawkmoths were carrying *Cae. gilliesii* pollen, they can be considered inefficient pollinators because we observed them touching the fertile flower parts only infrequently while drinking nectar. Rather, they act as nectar robbers. Hawkmoths with tongues longer than the flower

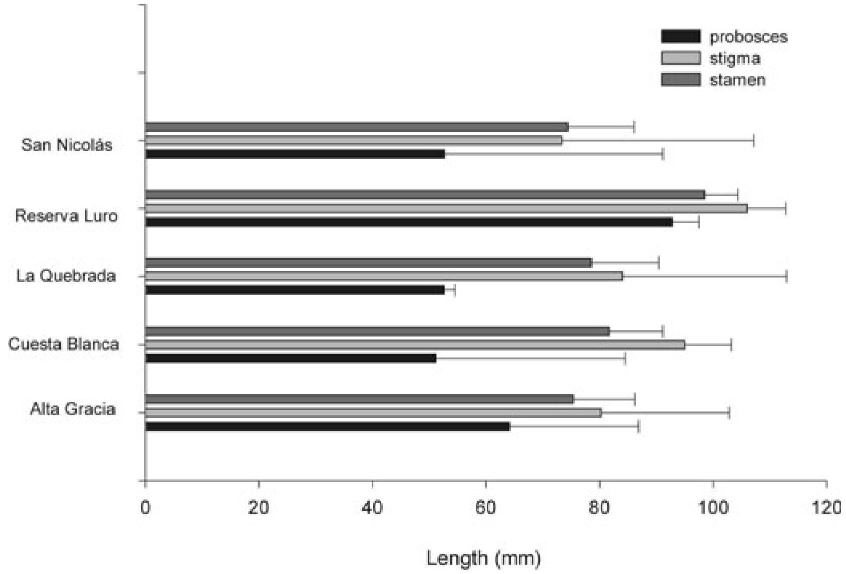

Figure 6. Stamens and stigma length (mm) of *Caesalpinia gilliesii* and the tongue mean length (mm) of hawkmoths carrying its pollen in five different populations. Error bars correspond to variation coefficient.

length, such as *Man. rustica* (134.9 mm), could also be considered nectar robbers, as pollen is unlikely to be deposited on their bodies while they drink nectar from the flowers above the level of the anthers.

That brush-type flowers have evolved twice in *Caesalpinia* is evident from the positions of *Cae. gilliesii* and *Cae. pulcherrima* on morphological and cpDNA sequence-generated phylogenetic trees of *Caesalpinieae* (Simpson & Miao, 1997). Both species are sister to clades dominated by bee-pollinated species with sternotribic-type flowers (Cocucci *et al.*, 1992). In these bee-pollinated species, pollen deposition is on the ventral parts of the pollinator's body. A shift in the mechanism of pollen deposition must have taken place, with selection leading to pollination by lepidopterans, involving an increase in stamen and style lengths. This increase in length is evident in *Cae. pulcherrima*, which has stamens and styles about twice as long as its petals, and is much more pronounced in *Cae. gilliesii*, which has stamens and styles about three times as long as its petals. The shorter stamens and styles of *Cae. pulcherrima* are adjusted to the shorter tongue lengths of the pollinating butterflies (Cruden & Hermann-Parker, 1979). Additional traits that can be associated in *Cae. gilliesii* and *Cae. pulcherrima* to a mechanism of wing specialization include pollen with threads and versatile anthers (Cruden & Hermann-Parker, 1979; Cocucci *et al.*, 1992).

On the basis of these results for *Cae. gilliesii*, we should expect that other long-flower brush-type blossoms might also demonstrate cryptic pollinator specialization by long-tongued animals.

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APPENDIX 1

Most conspicuous examples of brush-type flowers and inflorescences in several plant families

Family	Species	Stamen length (mm)
Flowers		
Bombacaceae Section Adansonia	*Adansonia digitata* L.	60–100[1]
Bombacaceae Section Brevitubae	*Adansonia grandidieri* Baill.	43–75[1]
	Adansonia suarezensis H. Perr.	59–87[1]
Bombacaceae Section Longitubae	*Adansonia gibbosa* (A. Cunn.) Baum ex Guymer	45–130[1]
	Adansonia magadascariensis Baill.	100–200[1]
	Adansonia perrieri Capuron	140–210[1]
	Adansonia rubrostipa Jumm. & H. Perr.	130–230[1]
	Adansonia za Baill.	100–200[1]
	Bombacopsis quinatum (Jacq.) Dugand	60[2]
	Pachira sessilis Benth.	150[3]
	Pachira aquatica (Jacq.) W. S. Alverson	160–310[3]
	Pseudobombax argentinum (R. E. Fr.) A. Robyns	50–70[4]
	Pseudobombax ellipticum (H.B.K.) Dugand	120–132[5]
	Pseudobombax longiflorum (C. Martius & Zucc.) Robyns	130[6]
	Pseudobombax septenatum (Jacq.) Dugand	80[6]
Capparaceae	*Capparis cynophallophora* L.	40[7]
	Capparis retusa Gris.	30[7]
	Capparis salicifolia Gris.	10[8]
	Capparis speciosa Gris.	25–30[7]
	Capparis spinosa L.	30[8]
	Capparis tweediana Eichler	25[8]
	Cleome flexuosa Gris.	210[8]
	Cleome gigantea L.	100[8]
	Cleome hassleriana Chodat	16–35[9]
	Cleome lilloi Gómez	100[7]
	Cleome paludosa Willd. Ex Eichl	9–35[8]
	Cleome rosea Vahl ex DD	20[8]
	Cleome spinosa Jacq.	15–65[8]
	Cleome titubans Speg.	14–25[9]
	Cleome trachycarpa Klotzch ex Eichler	40–50[7]
	Cleome viridiflora Schreb.	50–100[10]
	Crataeva tapia L.	20–25[7]
Caryocaraceae	*Caryocar amydaliferum* Mutis	40–50[11]
	*Caryocar amygdaliforme*G. Don	40–65[12]
	Caryocar brasiliense Cambessèdes	35–50[12]
	Caryocar coriaceum Wittmack	32–40[12]
	Caryocar costaricense Doell Smith	40–50[12]
	*Caryocar cuneatum*Wittmack	40–60[12]
	Caryocar dentatum Gleason	60[12]
	Caryocar glabrum (Aublet) Persoon	30–60[12]
	Caryocar gracile Wittmack	22[12]
	Caryocar microcarpon Ducke	50–70[12]

APPENDIX 1. *Continued*

Family	Species	Stamen length (mm)
	Caryocar montanum Prance	40–55[12]
	Caryocar nuciferum L.	70–85[12]
	Caryocar pallidum A. C. Smith	20–30[12]
	Caryocar villosum (Aublet)	65–70[12]
Chrysobalanaceae	*Couepia grandiflora* (Mart. & Zucc.) Benth. ex Hook. f.	35[13]
Fabaceae (Caesalpinioideae)	*Bauhinia argentinensis* Burkart var *argentinensis*	25–40[14]
	Bauhinia argentinensis Burkart var *megasiphon*	70–130[14]
	Bauhinia bauhiniodes (Martius) Macbride	35–50[14]
	Bauhinia forficata Link	80–110[14]
	Bauhinia microstachya (Raddi) Macbride	5–10[14]
	Bauhinia mollis (Bongard) Dietrich	70–90[14]
	Bauhinia uruguayensis Fort. et Wund.	30–40[14]
Fabaceae (Mimosoideae)	*Afzelia bracteata* T. Vogel ex Benth.	27[15]
	Berlinia grandiflora (Vahl) Hutch.	50[15]
	Hymenostegia aubrevillei Pellegr.	18[15]
	Inga brenesii Standl.	43.5[16]
	Inga densiflora Benth.	15[16]
	Inga longispica Standl.	16[16]
	Inga mortoniana Jorge León	20[16]
	Inga oerstediana Benth.	35–40[16]
	Inga punctata Willd.	14–15[16]
	Inga thibaudiana DC.	45[13]
	Inga vera Willd.	45–50[2]
Lechytidaceae	*Barringtonia asiatica* Koord. & Val.	40–70[17]
	Barringtonia gigantostachya Koord. & Val.	40–70[17]
	Barringtonia lanceolata (Ridl.)	35–50[17]
	Barringtonia papuana Laut.	35–45[17]
	Barringtonia petiolata A. C. Smith	35[17]
	Barringtonia revoluta Merr.	30[17]
Lythraceae	*Lafoensia pacari* St. Hil.	65[13]
	Lafoensia densiflora Pohl.	64[13]
	Lafoensia replicata Pohl.	97[13]
Loasaceae	*Mentzelia conspicua* Todsen	30[18]
Tiliaceae	*Luehea seemannii* Triana & Planch	15[19]
Inflorescences		
Fabaceae (Mimosoideae)	*Acacia baileyana* F. Muell.	10[20]
	Albizia longepedata (Pittier) Britton & Rose ex Record	40–50[2]
	Albizia julibrissin Duraz	30–40[20]
	Calliandra boliviana Britton	40[6]
	Calliandra parvifolia (Hook. f. et Arn.) Speg.	35–60[20]
	Calliandra tapirorum Standl.	25–30[2]
	Calliandra tonduzzi (Britton & Rose) Standl.	30[2]
	Calliandra tweedii Benth.	25–50[20]
	Pithecellobium longifolium (Humb. & Bonpl. ex Willd.) Standl.	
	Pithecellobium saman (Jacq.) Benth.	28.5–31.5[2]
Gentianaceae	*Lisianthius skinneri* (Hemsl.) Kuntze	20–50[10]
Myrtaceae	*Callistemon viminalis* (Sol. ex Gaertn.) G. Don ex Loudon	60[10]
	Melaleuca huegelii Endl.	50–75[21]

References: [1]Baum, 1995; [2]Haber & Frankie (1989); [3]Cascante-Marín (1997); [4]Meyer (1969); [5]Eguiarte, Martínez del Río & Arita (1987); [6]Killeen *et al*. (1993); [7]Legname (1972); [8]Gómez (1953); [9]Troncoso (1987); [10]Stevens *et al*. 2001; [11]Prance (1976); [12]Prance & Silva (1973); [13]Silberbauer-Gottsberger & Gottsberger, 1975; [14]Fortunato (1986); [15]Breteler (1995); [16]Koptur (1983); [17]Payens (1967); [18]Todsen (1999); [19]Haber & Frankie (1982); [20]Ulibarri *et al*. 2002; [21]Quinn *et al*. (1992).

APPENDIX 2

Populations of *Caesalpinia gilliesii* where flower measurements (F) and hawkmoths capture (H) were performed

Locality	Province	Latitude south	Longitude west	Altitude (m)
Alta Gracia (F* & H)	Córdoba	31°39′09.6″	64°19′48.4″	577
Cuesta Blanca (F & H)	Córdoba	31°24′21.6″	64°34′0.5″	820
Reserva La Quebrada (F* & H)	Córdoba	31°10′00″	64°17′30″	823
San Nicolás (F* & H)	Córdoba	31°26′58.6″	64°25′40.1″	694
Reserva Parque Luro (F & H)	La Pampa	36°54′35.52″	64°10′29″	256
Cachi Adentro (H)	Salta	25°06′17.4″	66°11′44.5″	2477
El Arenal (F)	Salta	25°5′58.9″	66°12′31.9″	2463
El Carmen (F)	Salta	25°26′43.9″	65°33′37.0″	1211
La Viña (H)	Salta	25°27′93.0″	65°33′43.8″	1207
Ampimpa (F)	Tucumán	26°35′18″	65°51′48″	2320

*Flower measurements for three populations were provided by Ana Calviño.

APPENDIX 3

List of hawkmoth species captured or sighted (*) in different Argentinian populations

Locality and sampling date	Species	Hawkmoths (*N*) Captured	Hawkmoths (*N*) Carrying *C. g.* pollen	Tongue mean length (mm)	SD (mm)
Alta Gracia October 31, 2002	*Agrius cingulata* (Fabricius, 1775)*				
	Manduca diffissa (Butler, 1871)	8	8	59.31	1.45
	Manduca sexta (Linnaeus, 1763)	1	1	102.92	
Cachi adentro November 11, 2002	*Manduca diffissa* (Butler, 1871)	1	1	67.26	
Cuesta Blanca					
November 2, 2000	*Callionima grisescens* (Rothschild, 1894)	27	14	15.49	1.24
November 3 & 21, 2000	*Hyles euphorbiarum* (Guérin-Méneville & Percheron, 1835)	6	2	27.87	1.34
November 8, 2001	*Hyles lineata* (Fabricius, 1775)	3	3	29.63	3.84
February 25, 2002	*Manduca diffissa* (Butler, 1871)	71	54	56.91	5.15
October 24, 2002	*Manduca sexta* (Linnaeus, 1763)	11	10	86.45	11.70
	Sphinx maura Burmeister, 1879	77	53	53.48	3.15
	Xylophanes tersa (Linnaeus, 1771)	78	67	30.50	2.17
La Quebrada October 17, 2002	*Callionima grisescens* (Rothschild, 1894)	4	4	15.32	0.73
	Manduca diffissa (Butler, 1871)	5	5	56.87	4.15
	Sphinx maura Burmeister, 1879	1	1	54.47	
La Viña November 8, 2002	*Manduca bergi* (Rothschild & Jordan, 1903)	7	7	53.81	3.80
	Manduca florestan (Stoll, 1782)	1	1	51.21	
	Manduca rustica (Fabricius, 1775)	1	0	134.90	
	Manduca sexta (Linnaeus, 1763)	1	1	101.81	
Reserva Luro December 13, 2000	*Manduca sexta* (Linnaeus, 1763)	3	3	92.78	4.37
San Nicolás November 27, 2002	*Agrius cingulata* (Fabricius, 1775)*				
	Callionima grisescens (Rothschild, 1894)	8	8	14.90	0.65
	Manduca diffissa (Butler, 1871)	15	14	56.24	2.93
	Manduca sexta (Linnaeus, 1763)	2	2	98.65	9.66
	Sphinx maura Burmeister, 1879	10	10	54.44	2.65
TOTAL		341			

C.g., *Caesalpinia gilliesii*.