Composition and Activity of Ant Visitors to Inflorescences of *Heliconia Hirsuta* (Heliconiaceae)

by

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ABSTRACT

The neotropical understory plant *Heliconia hirsuta* is notable for the conspicuous presence of ants on its inflorescences. We recorded 17 ant species on inflorescences in a lowland forest in Trinidad, West Indies. The commonest of these in descending order were *Ectatomma tuberculatum*, *Crematogaster* sp., *Solenopsis altinodis* and *Dolichoderus bispinosus*. The ants collected exudate from the bracts, tended treehoppers (Membracidae), and nested on late-stage inflorescences, in addition to minor activities. Activity showed a distinct correlation with age of the inflorescence, with peak attendance in the middle developmental stages. The level of attendance by ants varied throughout the day. *E. tuberculatum*'s alert responses to disturbance suggest that it may serve as an effective defender of *Heliconia* inflorescences against herbivores.

KEY WORDS: extra-floral nectary, Formicidae, *Heliconia*, mutualism

INTRODUCTION

Some of the great many interactions between ants and plants are known or believed to be mutualistic (Huxley 1991). Ant-plant mutualisms seem especially common in tropical habitats, where some associations involve plants with special structures to provide housing (domatia) and/or food to their ant partners (Bronstein 1998, Hölldobler & Wilson 1990:Ch. 14, Rico-Gray & Oliveira 2007, Schupp & Feener 1991, Whitman 1994). Few such mutualisms are species-specific. Ant visitors can benefit their plant hosts as protectors against natural enemies, as seed dispersers, and/or occasionally as pollinators (Beattie 1985, Rico-Gray & Oliveira 2007, Whitman 1994).

Apparent adaptations for rewarding or attracting ant visitors provide good evidence of a mutualistic relationship (Bronstein 1998). One such widespread adaptation is extrafloral nectaries, known from a variety of plants as a source

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of reward for defense of both reproductive and non-reproductive tissue (Rico-Gray & Oliveira 2007: Ch. 6, and references therein). Ant visitors attracted to the nectar may decrease herbivore damage simply by their presence, apart from any active response to other animals (Bentley 1976).

Other common insect visitors include treehoppers (Membracidae) and other homopterans. It has been suggested that extrafloral nectar may function to turn ants away from mutualisms with homopterans (Becerra 1989).

Several studies indicate that the pattern of ant attendance changes in direct relation to the level of nectar production, which in turn depends on the nectary's age, with peak attendance coïnciding with maximum nectar production (Bentley 1977a, Inouye & Taylor 1979, Keeler 1977, O'Dowd 1979, Schemske 1980).

Heliconia (Heliconiaceae) is a genus of about 200-225 species of neotropical herbaceous plants (Kress 1994). *H. hirsuta* L.f. is common throughout the lowland forests of Trinidad, West Indies. It occurs in small clumps to substantial stands in micro-habitats ranging from forest edge to closed-canopy forest. It flowers in all seasons (Dobkin 1984), although our observations suggest a flowering peak during the January-April dry season.

Flowers are borne in long-lasting inflorescences, each flower subtended by a leaf-like cincinnal bract (Berry & Kress 1991; Fig. 1). Bracts decrease in size from the base to the tip of the inflorescence. The invertebrate fauna of several *Heliconia* spp. has been investigated (Seifert 1975, 1982), but most studies treat species with deep, boat-like bracts that hold abundant water. Bracts of *H. hirsuta* are termed "closed", the lips remaining less than 5 mm apart, and hold little or no water. It is now demonstrated that bracts have extrafloral nectaries during part of their life (Ballah 2004).

This paper was prompted by preliminary observations that inflorescences of *H. hirsuta* very commonly have large numbers of ants on them (Fig. 2). It was our observation that ants were almost always present on all but quite old inflorescences. Our purpose here is to investigate this relationship, with attention to the composition of ant visitors, their activities on inflorescences, and the relation between ant attendance and inflorescence age.

The developmental stages of the *H. hirsuta* inflorescence are described in an appendix.

MATERIALS AND METHODS

This study was carried out in the Arena Forest Reserve (10°34N 61°14W), Trinidad, West Indies. The area is low and undulating, with well-drained sandy soil. It is covered by evergreen seasonal forest that was logged until the 1970s. It has a closed canopy, with little to moderate understory vegetation (Beard 1946). Four of Trinidad's five native species of *Heliconia* are found here.

The vegetative form of *H. hirsuta* is zingerberoid in growth with an erect terminal inflorescence (Fig. 1). Flowers are hummingbird pollinated, and inflorescences last for some months (Dobkin 1984; Table 4).

After selecting study trails with a summed length of roughly 500 m, we tagged all *H. hirsuta* plants within about 20 m on either side of each trail, more than 350 in all. Because of its rhizomatous growth pattern, *H. hirsuta* can form extensive clonal clumps, which can separate into distinct patches as they expand. For present purposes, clumps separated by a distance of at least one meter are considered distinct plants. In some instances an individual plant bore two or more inflorescences on separate stems, in which case we

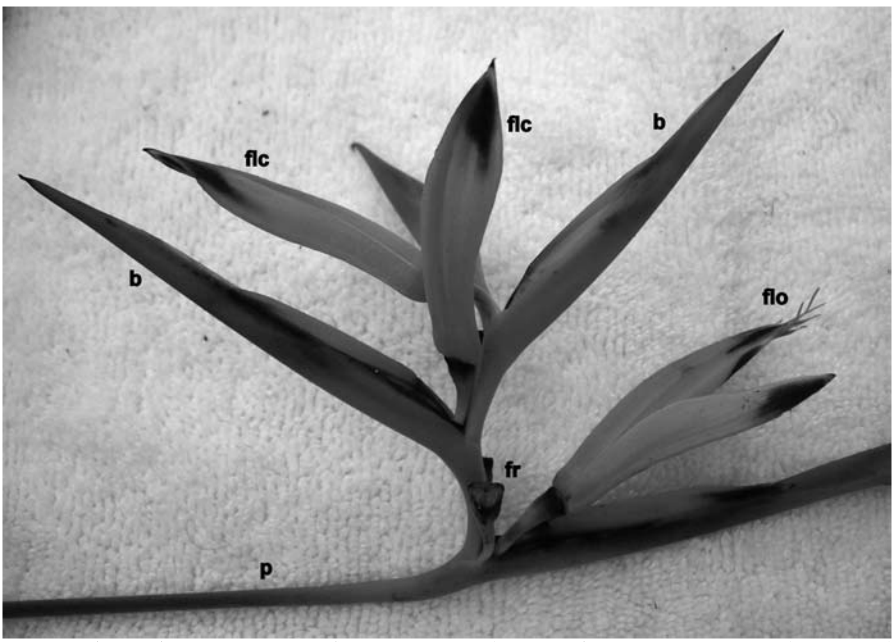

Fig. 1. *Heliconia hirsuta* Stage-3B inflorescence, near the time of maximum nectar production and ant visitation. b = bract. flc = closed flower. flo = open flower. fr = fruit. p = peduncle.

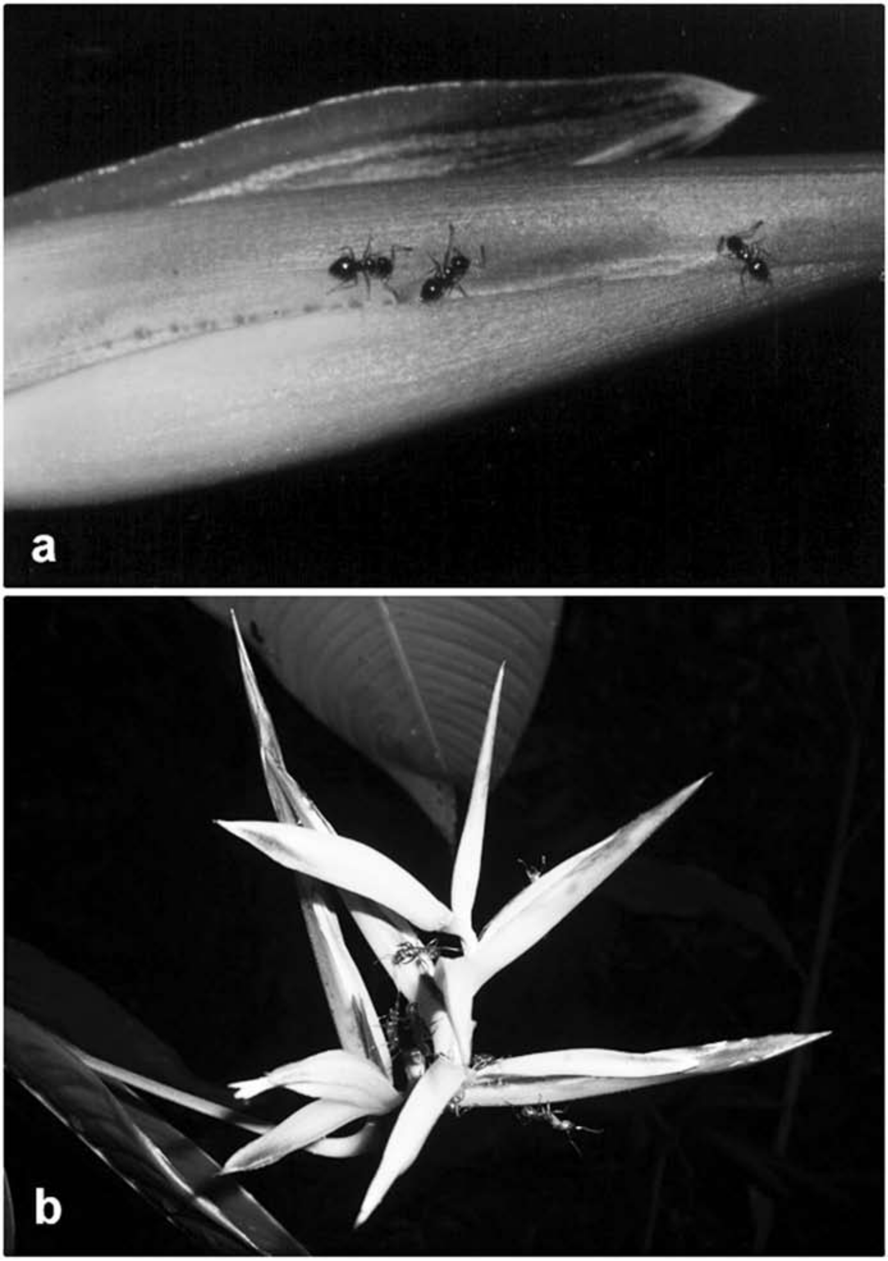

Fig. 2. Ants collecting nectar from *Heliconia hirsuta* extrafloral nectaries on Stage-2 inflorescences. a. *Crematogaster* sp. A. b. *Ectatomma tuberculatum*.

treated each inflorescence separately, for a total of 368 inflorescences. We characterized all inflorescences according to a six-stage scheme of development (see Appendix).

One of us (STB) visited each plant daily over a fortnight in September 1998, recording all insect visitors on its three above-ground parts: stem, leaf and inflorescence (if any). In order to assess the prevalence of ants on *H. hirsuta* inflorescences, we compared these with *H. hirsuta* without inflorescences and five other common understory plants (background plants) in the study area. In a single survey, STB recorded the presence or absence of ants on hapharzardly chosen individuals of each background-plant species.

Ant behavior was monitored in five-minute periods at selected *H. hirsuta* inflorescences representative of each of the six stages. The activity observed was defined based on behavior of the two most frequently encountered ants: *Ectatomma tuberculatum* Olivier and *Crematogaster* sp. A. The response of each ant species when confronted with an approaching object (the tip of a pencil) was rated on a scale of 0-3:

0. No evident response
1. Retreat
2. Approach, with at most mild aggression
3. Vigorous aggressive response.

Preliminary observations indicated maximum presence of ants on Stage-3 inflorescences. In order to establish the pattern of activity of ant visitors, 20 Stage-3 inflorescences were selected, and ant abundance and activity monitored at three hour intervals from 06:00 to 18:00.

Preliminary observations indicated that ant activity is highest from 06:00 to 12:00. In order to determine the relationship between ant activity and inflorescence age, STB monitored the 368 tagged inflorescences from about 06:00 to about 14:10 in three replicate sessions. All ants encountered on the plants were identified and counted, and the region of the plant where they were found was recorded.

Ants collected by S.T. Ballah & C.K. Starr from the Arena Forest Reserve during 1998 and deposited in the Land Arthropod Collection of the University of the West Indies will serve as vouchers.

RESULTS

Ants were the predominant insect visitors to *H. hirsuta*. Others included wasps (Hymenoptera), flies and mosquitoes (Diptera), cockroaches (Blattodea) and treehoppers (Hemiptera: Membracidae). We recorded ants on all above-ground regions of the plant, with the highest number on inflorescences. Of the 21 ant species recorded on *H. hirsuta,* 17 were clearly associated with inflorescences (Table 1). With few exceptions, Stage-2 through Stage-4 inflorescences had ants. In 139 of 145 cases (96%), only one ant species was present at any time, and in each of the exceptions one species was in clear "possession".

Where we observed ants at leaf bases, these were mainly the young, furled leaves of developing shoots. We did not confirm the presence of nectaries at this type of site.

While we recorded ants on all types of background plants (Table 2), they were present at much lower levels than on *H. hirsuta* with inflorescences. Only seven of the ants associated with *H. hirsuta* were also found on our sample of background plants.

The behavior patterns of ants on inflorescences are conveniently grouped into four general activities:

1. Collection of bract exudate. This was the most commonly observed activity. Some ants stood motionless with forelegs raised at the site of nectaries. Others had their mouthparts applied to the site of the nectary, which they also antennated.

2. Tending treehoppers. When treehoppers were present on an inflorescence, ants were commonly found in close attendance. We recorded this in three species of ants: *Crematogaster* sp. A, *E. tuberculatum* and one unidientified species. Some ants stood motionless with forelegs raised in apparently the same posture noted above. Others had their mouthparts applied to the treehopper's anus, evidently collecting honeydew.

3. Patrolling. In this activity, ants walked about on the inflorescence as if on a tour of inspection.

4. Nesting. We observed colonies of *Crematogaster* sp. B, *Solenopsis altinodis* and *Dolichoderus bispinosus* nesting on inflorescences. Individual ants engaged in nest construction and standing at the nest edge, apparently guarding.

Table 1. Composition of ant visitors to 368 *Heliconia hirsuta* inflorescences at differing developmental stages (see Appendix). Response level is the mode according to the 0-3 scale in the text.

Subfamily	Species	Inflorescence stage						Total	Response level
		1	2	3	4	5	6		
Dolichoderinae	*Dolichoderus bispinosus*	0	3	7	2	1	0	13	1
Dolichoderinae	*Dolichoderus decollatus*	0	1	5	1	1	0	8	1
Dolichoderinae	*Azteca* sp.	0	0	3	0	0	0	3	2
Ectatomminae	*Ectatomma tuberculatum*	0	16	14	7	13	0	50	3
Myrmicinae	*Crematogaster* sp. A	0	12	6	2	6	3	29	2
Myrmicinae	*Crematogaster* sp. B	0	1	2	0	0	0	3	0
Myrmicinae	*Solenopsis altinodis*	0	9	8	2	1	0	20	0
Ponerinae	*Pachycondyla crassinoda*	0	0	1	1	1	0	3	0
Ponerinae	*Pachycondyla laevigata*	0	2	1	1	0	0	4	0
Pseudomyrmecinae	*Pseudomyrmex* sp. A	0	0	2	1	0	0	3	0
Pseudomyrmecinae	*Pseudomyrmex* sp. B	0	0	1	0	0	0	1	0
Pseudomyrmecinae	*Pseudomyrmex* sp. C	0	1	0	0	0	0	1	0
Pseudomyrmecinae	*Pseudomyrmex* sp. D	0	0	1	0	0	0	1	0
Unidentified sp.1		0	0	0	0	2	1	3	0
Unidentified sp.2		0	0	1	0	0	0	1	0
Unidentified sp.3		0	0	1	0	0	0	1	0
Unidentified sp.4		0	0	0	1	0	0	1	0
Number with ants		0	45	53	18	25	3	145	
Number without ants		20	29	10	5	33	126	223	
Total		20	74	63	23	58	130	368	

Table 2. Occurrence of ants on background plants in the Arena Forest Reserve understory, for comparison with flowering *Heliconia hirsuta*. The *H. hirsuta* in this table lack inflorescences. The *Pentraclethra macroloba* are seedlings.

Species	Total plants	Plants with ants
Attalea maripa (Aubl.) Mart. (Palmae)	27	11 (41%)
Costus scaber (Ruiz & Pav.) (Zingiberaceae)	6	3 (50%)
Heliconia hirsuta L.f. (Heliconiaceae)	68	50 (73%)
Heliconia spathocircinata Aristeg. (Heliconiaceae)	31	8 (26%)
Ischnosiphon arouma (Aubl.) Körn. (Marantaceae)	25	7 (28%)
Pentaclethra macroloba (Wild.) O. Kuntz (Leguminosae)	36	8 (22%)
Total	193	97 (50%)

Table 3. Relative frequency of activity types of ant visitors to *Heliconia hirsuta* according to development stage of the inflorescence (see Appendix). Ce = collection of bract exudate. Tt = tending treehoppers. P = patrolling. N = nesting.

	Stage 2				Stage 3				Stage 4				Stage 5				Stage 6			
	Ce	Tt	P	N	Ce	Tt	P	N	Ce	Tt	P	N	Ce	Tt	P	N	Ce	Tt	P	N
Ectatomma tuberculatum	16	2			14	5			6	2				12	1					
Crematogaster sp. A	12	1			6				1		1			1	2	3				3
Solenopsis altinodis	8		1		8				2							1				
Dolichoderus bispinosus	3				6	1					1	1								
Others	5		1		16	2	1		3	2				1	2			1	1	2
Total	44	3	2	0	50	8	1	0	12	4	2	1	0	14	5	4	0	1	1	5

Only four of the 17 ant species showed a clear aggressive response to our disturbance during any of these activities: *Azteca* sp., *D. bispinosus*, *E. tuberculatum* and *Paratechina crassinoda*. Of these, *E. tuberculatum* showed the strongest, most consistent response (Table 1). In some instances workers were observed chasing individuals of other ant species encountered on leaves and stems.

As seen in Table 1, attendance of ants varies strongly according to age of the inflorescence. Pattern of activities according to inflorescence age is shown in Table 3. Except in old inflorescences, collection of bract exudate is by far the predominant activity. For *E. tuberculatum* on Stage-5 inflorescences, this is replaced by tending of treehoppers.

The daily pattern of activity is shown for *E. tuberculatum* and *Crematogaster* sp. A on Stage-3 inflorescences (Fig. 3). While *E. tuberculatum* showed fairly constant activity throughout the daytime, *Crematogaster* sp. A had a decided peak around mid-day.

DISCUSSION

The results confirm our impression of an inordinately high presence of ants on *H. hirsuta* inflorescences. The ants most often found on inflorescences can be characterized as generalist feeders. It is our experience that the commonest visitor, *E. tuberculatum*, is the most conspicuous ant on understory vegetation in Arena. This relatively large ant is also conspicuous for its aggressive response to disturbance (Bentley 1977b). We have very often seen it standing poised with mandibles open, as if ready to repel any intruder. The much smaller *Crematogaster* sp. A and *S. altinodis*, in contrast, are often present in much larger numbers than *E. tuberculatum*. At least two of the criteria proposed by Bentley (1977b) for ants to be deemed plant protectors are seen in *E. tuberculatum*, *Crematogaster* sp. A and, to a lesser extent, *S. altinodis*: abundance of workers at the reward source, aggressive response to disturbance, and a daily pattern of activity.

At the same time, we have not observed any ant directly deterring herbivorous insects from the inflorescences, and an exclusion experiment failed to show unequivocally that ant visitors confer a fitness advantage (Ballah 2004).

The exudate from bract nectaries is evidently the primary attractant for ant visitors. Ant activity appears to be correlated with exudate production over the life of the inflorescence and, in the case of *E. tuberculatum*, on a daily basis.

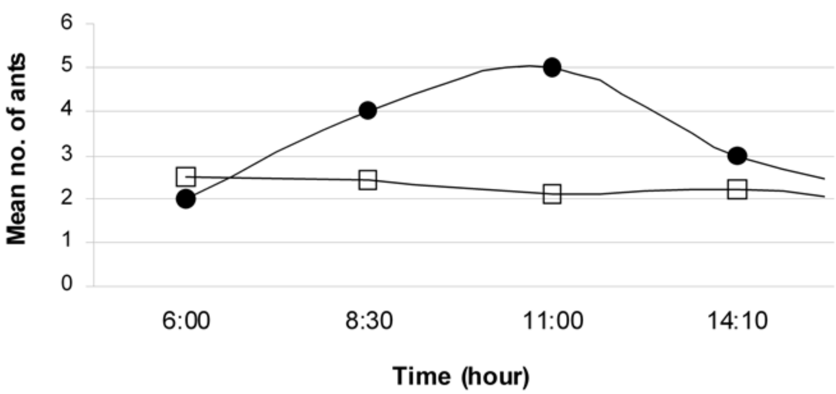

Fig. 3. Activity levels of *Ectatomma tuberculatum* (black circles) and *Crematogaster* sp. A (white squares) on Stage-3 inflorescences over an eight-hour daytime period.

That is, peak *E. tubercularum* activity in the middle part of the day coincides with peak extrafloral nectar production (Ballah 2004).

The ants on a given inflorescence are presumably typically nestmates. The pattern in the *H. hirsuta* population can be characterized as an ant mosaic (Hölldobler & Wilson 1990: Ch. 11, Leston 1973) in the limited sense that each inflorescence is under the control of a single colony. What is not known is whether a given colony typically retains possession for the life of the inflorescence.

The presence of the membracid introduces a third party to the ant-plant association. The switch by ants to tending membracids may be due to unavailability of exudate in older inflorescences. Alternatively, the honeydew secreted by the membracid may be preferred over late-inflorescence exudate. Membracids were also observed in younger inflorescences during this study, and ants showed a preference for plant-secreted exudate over membracid-produced honeydew.

Ant-plant-homopteran relationships have been studied extensively by some authors (Buckley 1987). For the most part, homopterans have a detrimental effect on the plants they inhabit. The plants concerned develop both physical and chemical defences against them. In this regard, ants, by tending and protecting homoptera, may prove deleterious to the plants.

For the plant's part it would appear beneficial to solicit the help of ants to protect the inflorescence, one of its most vulnerable regions. Despite a lack of experimental corroboration, it remains our working hypothesis that ant visitors to *H. hirsuta* serve to deter potential herbivores and that the provision of extrafloral nectar serves to keep them in place during the critical stages of development. In older inflorescences, the production of honeydew by the treehoppers would appear to keep ants in place, although it is by no means evident that this confers a net advantage to the plant.

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APPENDIX: DEVELOPMENTAL STAGES OF THE *HELICONIA HIRSUTA* INFLORESCENCE.

Differences in appearance of inflorescences in this and other Heliconiaceae are useful in distinguishing individual plants. The long-lived inflorescences undergo a regular developmental pattern (Stiles 1975, Dobkin 1984). We found it difficult to apply to *H. hirsuta* Stiles's (1975) seven-stage developmental classification for nine *Heliconia* spp. Accordingly, we examined more than 100 inflorescences of *H. hirsuta* in the field and laboratory in order to identify characters that change fairly consistently over time and can be unambiguously expressed. Three physical and one physiological character proved to be acceptably reliable:

1. Number of open bracts.

A bract is considered open when it has extended itself from the main axis of the inflorescence. The basal bract is visible in all stages and is identified as bract 1 even while unopened (Fig. 4a). The majority of inflorescences observed reached a maximum number of open bracts (mode = 6) in Stage 4.

2. Number of flowers per inflorescence

This is determined by summing the number of pedicels observed within each cincinnial bract of the inflorescence.

3. Color (hue and intensity) of bracts

Color, although somewhat subjective, is a useful criterion, as an inflorescence's predominant color gradually changes with age. Younger inflorescences tend to be more brightly colored, presumably related to the attraction of hummingbird pollinators. The darkening of older bracts is also due to fungus growth.

4. Secretion of extrafloral nectar

For a part of its development, a bract secretes a sticky, clear, sweet substance. Nectar production is visible during specific stages in inflorescence growth.

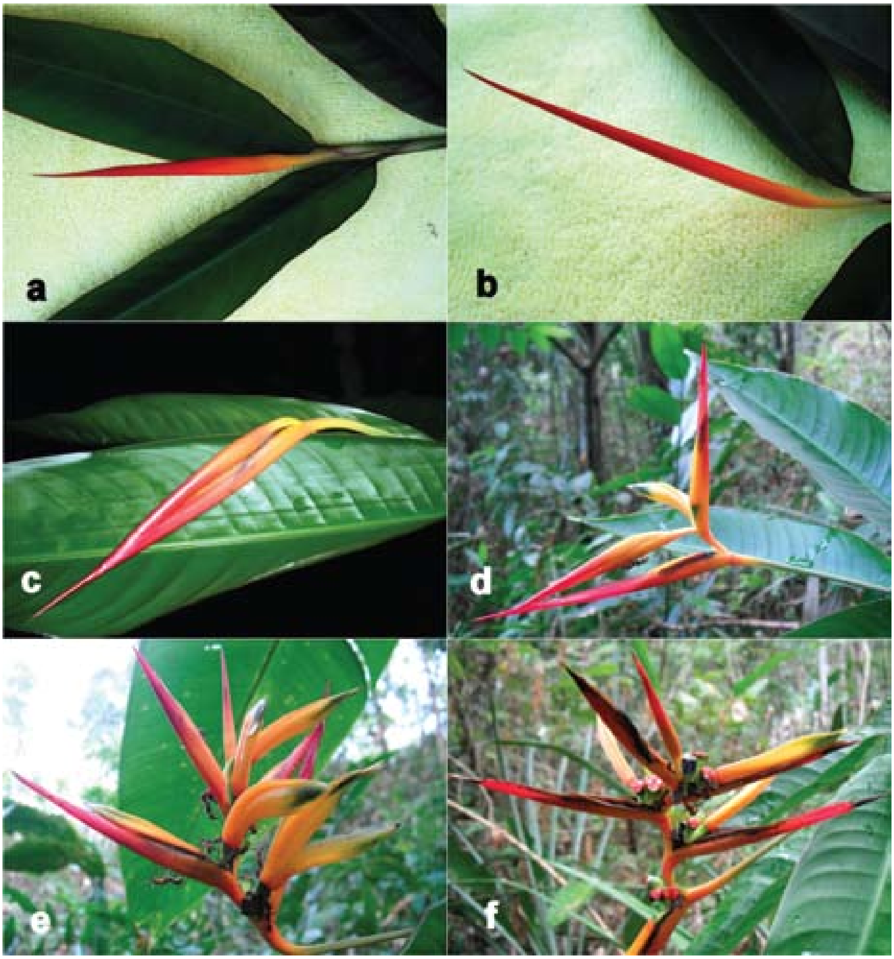

Fig. 4. Development stages of *Heliconia hirsuta* inflorescence. a. Stage 1B, with bract 1 emerging. b. Stage 2A, with bract 1 bending away from axis of stem. c. Stage 2B, with bract 2 emerging. d. Stage 3A. e. Stage 4A, with many flowers flowers and the first fruit; the abundance of ants (*Ectatomma tuberculatum* in this case) is typical of Stage-3 and -4 inflorescences. f. Stage 5B, with mature fruit and the first signs of decay.

No one character by itself is sufficiently reliable, in our experience, so that it is best to use them in combination. These characters allow us to identify six stages of inflorescence development (Fig. 4). Each of these can be further subdivided into two sub-stages, which vary in their distinctness among stages. The stages and their substages are described below and summarized in Table 4.

Stage 1. Emergence (Fig. 4a). Inflorescence emerges from terminal end of pseudostem. Peduncle not visible, bracts still closed, no nectar secretion. Inflorescence reddish-orange.

1A. Tip of bract 1 visible.

1B. Bract 1 fully emerged.

Stage 2. Elongation. Peduncle emerges and elongates. Inflorescence rotates relative to axis of pseudostem. Bracts remain closed, bright reddish-orange. Nectar droplets appear on cheek of basal bract.

2A. Peduncle begins to appear and elongate, elevating inflorescence away from pseudostem (Fig. 4b). Inflorescence oriented parallel to axis of peduncle.

2B. Inflorescence rotates to angle of 45-90° from axis of peduncle. Bract 2 starts to emerge (Fig. 4c).

Stage 3. Opening of first bracts. Nectar droplets appear on all bracts. Flowers and fruits appear. Inflorescence bright reddish-orange with some yellow (Fig. 4d).

3A. Bracts begin to open, bracts 1-2 unfurl, each with droplets of nectar. At least one flower may be present in either or both of these bracts. Immature fruit may be present in bract 1 only.

3B. Bracts 3-4 unfurl, with nectar droplets. Flowers may be present in all bracts with immature fruit. Mature fruit in bracts 1-2 only.

Stage 4. Complete opening of inflorescence (Fig. 4e). Flowers and fruits visible in all bracts, with dried pedicels in bracts 1-4. No nectar secretion on bracts 1-2. Bracts brick red-orange.

4A. Bracts 5-6 unfurling. Flowers visible in all bracts, with fruits at all stages of maturity. Pedicels only in bracts 1-4. Nectar droplets in bracts 3-6.

4B. All bracts fully unfurled.

Stage 5. Early senescence (Fig. 4f). New-flower production reduced, darkening of bracts and cessation of nectar secretion.

5A. Reduced rate of flower production. Bracts darken, immature and mature fruit present in all bracts together with dried pedicels.

5B. Further darkening of bracts to dull red to pale orange in parts. Increased ratio of dried pedicels to flowers and fruits.

Stage 6. Full senescence. Flower production stops entirely, with clear decay in all parts of inflorescence. Distinct loss of color, with bracts going from dark red to blackish.

6A. Only mature fruit present in some bracts.

6B. Inflorescence dry and lifeless, its parts disintegrating.

Table 4. Characters of developmental stages of the *Heliconia hirsuta* inflorescence. Codes at the top refer to substages described in the text. Bract color refers to the predominant hue: 1 = yellow to light orange, 2 = medium orange to medium red, 3 = deep red to dark brown.

	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	6A	6B
Number of open bracts	0	0	0	0	1-2	3-4	4-6	4-6	4-6	4-6	4-6	4-6
Mean flowers per inflorescence	0	0	0	0	5	24	38	60	65	71	84	123
Presence of nectar droplets	-	-	+	+	+	+	+	+	-	-	-	-
Bract color	2	2	1	1	1	1	2	2	2	2	3	3
Duration (days)	1-2	1-2	2-4	1-3	7-9	5-14	12-20	14-18	14-20	14-20	>30	>10

In order to estimate the typical duration of each stage, we chose five inflorescences of each of the pre-identified stages and monitored their development in the field. These data were supplemented by monitoring some plants under controlled conditions. We tagged 10 additional plants with early-stage inflorescences and monitored them through to senescence, except for three individuals that suffered severe unnatural damage long before senescence. There is moderate variation in the duration of individual stages, with a total duration of about four months (Table 4).