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Natural history of *Belonuchus* Nordmann spp. and allies
(Coleoptera: Staphylinidae) in *Heliconia* L. (Zingiberales:
Heliconiaceae) flower bracts

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Abstract. Adults, and in some species larvae, of several members of *Belonuchus* Nordmann (Coleoptera: Staphylinidae: Staphylininae) and a few related genera seem to be to various degrees consistently associated with flower bracts of the genus *Heliconia* (Zingiberales: Heliconiaceae). They are predators and eat various dipterous and lepidopterous larvae in that habitat. Adults of at least *Belonuchus cephalotes* (Sharp) and *Odontolinus fasciatus* Sharp are able to immerse completely in water to capture larvae and/or pupae of mosquitoes (Culicidae).

Adults and larvae of *Belonuchus satyrus* Erichson, and adults of *B. cacao* Blackwelder and *B. rufipennis* (F.) were found in water-filled flower bracts of *Heliconia bihai* (L.) L. in northern, lowland Venezuela. The bracts also contained mosquito larvae and semiaquatic coleopterous (Chrysomelidae: Hispinae), lepidopterous (Crambidae: Pyraustinae) and dipterous (Syrphidae, Stratiomyidae, Psychodidae, Richardiidae) larvae, and Annelida. In feeding trials, *B. satyrus* adults and larvae did not feed on hispine larvae or annelids, but did feed on all the lepidopterous and dipterous larvae available to them; adults dragged larvae and pupae of the mosquito genus *Toxorhynchites* Theobald from shallow water and thus seemed to be the top predators of the food pyramid within bracts. Records are compiled of association of *Belonuchus* and relatives with *Heliconia* bracts in the neotropics.

We correct the names used for *Heliconia* spp. by earlier entomological authors working in Venezuela. Their '*Heliconia caribaea* Lamarck' is *H. bihai* (L.) L. and their '*H. aurea* Rodríguez' is *H. bihai* cv. Aurea.

Resumen. Los adultos y en algunos casos también las larvas de varias especies de *Belonuchus* spp. (Coleoptera: Staphylinidae: Staphylininae) y algunos géneros relacionados están consistentemente asociados con las espaldas florales del género *Heliconia* (Zingiberales: Heliconiaceae). Estos coleópteros son depredadores y comen larvas de varios tipos de dípteros y lepidópteros en ese hábitat. Los adultos de *Belonuchus cephalotes* (Sharp) y *Odontolinus fasciatus* Sharp pueden sumergirse completamente en el agua para capturar las larvas y pupas de mosquitos (Culicidae).

Larvas y adultos de *Belonuchus satyrus* Erichson, así como adultos de *B. cacao* Blackwelder y *B. rufipennis* (F.) fueron encontrados en las brácteas florales de *Heliconia bihai* (L.) L. de las partes bajas del norte de Venezuela. Las brácteas también contenían larvas de mosquitos y coleópteros semi-acuáticos (Chrysomelidae: Hispinae), larvas de lepidópteros (Crambidae: Pyraustinae) y de dípteros (Syrphidae, Stratiomyidae, Psychodidae, Richardiidae), y anélidos. En experimentos de alimentación, las larvas y los adultos de *B. satyrus* no se alimentaron de larvas de Hispinae ni de anélidos, sin embargo todas las larvas de lepidópteros y de dípteros que se les ofrecieron fueron ingeridas; los adultos de *B. satyrus* también extraen larvas de mosquitos del género *Toxorhynchites* Theobald del agua, por lo cual parecen ser los depredadores del tope de la pirámide alimentaria en las brácteas. Los registros de asociaciones de *Belonuchus* y géneros afines con las brácteas de *Heliconia* en el Neotrópico fueron recopiladas.

Corregimos los nombres de *Heliconia* spp. utilizados anteriormente por entomólogos que trabajaron en Venezuela. Su '*Heliconia caribaea* Lamarck' corresponde a *H. bihai* (L.) L. y su '*H. aurea* Rodríguez' corresponde a *H. bihai* cv. Aurea.

Key words. Culicidae, mosquito larva, mosquito pupa, predation, predator, immersion in water, insect communities

Introduction

Belonuchus Nordmann contains more than 100 described species, mostly neotropical, and its adults may be conspicuously colored and quite large (up to about 15 mm). It is related to *Odontolinus* Sharp, *Paederomimus* Sharp and *Philonthus* Stephens within the subtribe Philonthina of the subfamily Staphylininae, but its limits are poorly defined taxonomically. Not only are specimens often difficult to identify specifically because of lack of illustrations, keys, and adequate descriptions, but some are difficult to place even to genus. Published ecological and ethological information on the genus is scant. Staphylinidae are the largest family of insects, and many of them are predacious as adults and larvae; some of them are known to prey on mosquito eggs, larvae, and adults, but ethological and ecological research on predator-prey relationships has been hindered by difficulty of identification of staphylinid specimens; extremely few of them are reported as habitually associated with individual plant genera (Frank and Thomas 1999). The most complete identification key to adults of the species mentioned below is that by Blackwelder (1943), although it was designed just for the species that occur in the West Indies.

Insect communities associated with plants of the mainly neotropical genus *Heliconia* L. (order Zingiberales, family Heliconiaceae) have received considerable attention during recent decades. The aquatic insect communities in water-filled flower bracts, and the herbivorous insect communities of the leaves, have been emphasized (Seifert 1982). Preimaginal stages of mosquitoes are often abundant in the flower bracts and have been studied in Costa Rica (Seifert and Seifert 1976a) and at two localities in Venezuela (Seifert 1982, Machado-Allison et al. 1983). Interactions occur not only between preimaginal mosquitoes and other aquatic organisms, but also between preimaginal mosquitoes and terrestrial Coleoptera of the family Staphylinidae.

Predatory adult staphylinids of the genus *Odontolinus* were found to enter the water in *Heliconia* bracts in Costa Rica to catch mosquito larvae (Seifert and Seifert 1976a). *Odontolinus* is a monotypic genus. We report on the behavior of species of *Belonuchus* associated with *Heliconia* at Panaquire, estado Miranda, and Rancho Grande, estado Aragua in Venezuela, and we record associations of additional species of Philonthina with several *Heliconia* species in Antigua, Costa Rica, the Dominican Republic, Jamaica, Panama, and Venezuela.

More is now known about the genus *Heliconia* than when some of the reported studies were conducted. Identification of *H. caribaea* Lamarck and *H. aurea* Rodríguez by Machado-Allison et al. (1983) and other authors working in Venezuela was based upon Aristeguieta (1961). Berry and Kress (1991) revised species concepts in *Heliconia*, and subsequently these two taxa must be known as *H. bihai* (L.) L. (Fig. 1) and *H. bihai* cv. Aurea. The nomenclature in several entomological papers reporting work in Venezuela (Seifert and Seifert 1976a, b, 1979a, b, Seifert 1980, 1982, Seifert and Barrera 1981, Machado-Allison et al. 1983, 1985, 1988, Lounibos et al. 1987, Lounibos and Machado-Allison 1993, and Navarro 1998) must be corrected. We note that bracts of *H. bihai* cv. Aurea are typically considerably more colorful and are larger and hold more water than those of the nominal species.

Materials and methods

Study sites. The Venezuelan study sites were at Panaquire, estado Miranda (a locality in lowland Venezuela described by Machado-Allison et al. 1983) and Rancho Grande, estado Aragua, within Parque Nacional Henri Pittier at about 1,000 m.

Records of association. The literature was searched for information on the association of Staphylinidae with *Heliconia* bracts. Published information on *Belonuchus* and related genera associated with *Heliconia* was augmented by unpublished information from collections made by: (1) the late Richard P. Seifert (RPS), The George Washington University, from Costa Rica and Venezuela, (2) Dale H. Habeck (DHH), University of Florida, from Panama, (3) J. H. Frank (JHF), from Antigua, the Dominican Republic, Jamaica, and Venezuela, (4) R. Barrera (RBR) from Venezuela, (5) Jose Clavijo A. (JCA) and JHF from Venezuela. Specimens collected by RPS were initially identified by the late Ian Moore (University of California, Riverside), all corroborated by JHF, and all later-collected specimens were identified by JHF. Specimens are in the collection of JHF except as noted in Acknowledgments.

Distribution among bracts. Machado-Allison et al. (1983) found that *H. bihai* bracts opened at average intervals of approximately seven days, and described a system for numbering them. The youngest and unopened bract at the tip of an inflorescence is numbered 0, the first opened bract is numbered 1, and the bracts below are numbered consecutively. Bract number thus corresponds approximately to age class in weeks.

On 5-7 August 1983 at the Panaquire study site 10 *H. bihai* inflorescences were selected from a large stand of plants. Each inflorescence had at least 11 opened bracts, to give a total of 137 bracts, 127 of them opened. Beginning at the top of each inflorescence, each bract in turn was cut from the stem and placed in a numbered plastic bag. Field facilities included a work station with binocular microscope. Each plastic bag in turn was opened, the bract it contained was pulled apart in a plastic bowl, the insects it contained were examined (under the microscope when necessary) and enumerated. No attempt was made to collect the preimaginal mosquitoes, whose earlier instars are very small, or mites (Acari), but the sample was representative of the other insects and worms (Annelida) visible to the unaided eye. Some specimens were kept either alive or preserved.

Feeding trials. Adult and larval *Belonuchus* were confined individually in Petri dishes with annelids, and with larvae of the various semiaquatic insects recovered from bracts, and with larvae and pupae of *Toxorhynchites haemorrhoidalis superbus* (Dyar and Knab) (Diptera: Culicidae). *Toxorhynchites* Theobald larvae were collected from bromeliad leaf axils in the study area, but are recorded as occurring there in the *Heliconia* bracts (Machado-Allison et al. 1983). Petri dishes housing *Belonuchus* larvae were supplied with wet, crumpled paper towel to provide moisture and refuges. Petri dishes housing *Belonuchus* adults were supplied with pieces of *Heliconia* bract wall. In the case of the fully aquatic preimaginal stages of *Toxorhynchites*, containers made from deflowered *Heliconia* bracts held sufficient water to immerse instar IV larvae and pupae of this mosquito but still fit within Petri dishes; the water content was shallower than it would have been in a fairly young bract in nature. Nevertheless, as bracts age and senesce in nature they dry out, so the water level passes through a stage just as shallow as in the trial. Adult *Belonuchus* were confined with large prey individuals, but *Belonuchus* larvae were confined with prey of intermediate size. The Petri dishes were examined at intervals during the succeeding days, both to observe predatory behavior on the part of the *Belonuchus* and to record and remove dead prey larvae.



Figure 1. Carlos Machado-Allison examines bracts of *Heliconia bihai* at Panaquire, Miranda, Venezuela in the early 1980s. This plant was incorrectly named *H. caribaea* in his and many other publications on the insect fauna of *Heliconia* in Venezuela based on a description and excellent illustration labeled with that name in Aristeguieta (1961), subsequently shown (Berry and Kress 1991) to be erroneous. Note the vantage point provided by the stepladder, without which the contents of few bracts can be seen. Photo by Phil Lounibos.

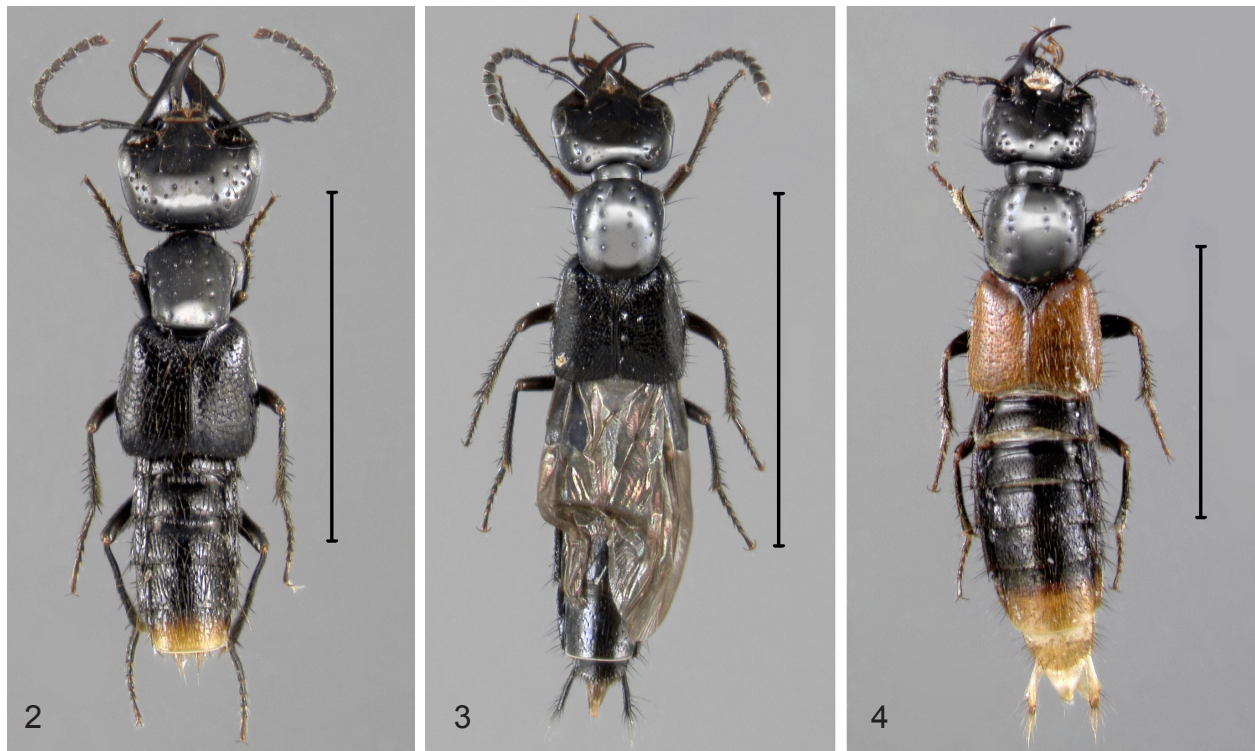


Figure 2-4. *Belonuchus* adult males. 2) *B. cephalotes*. 3) *B. gagates* with wings partially extended 4) *B. satyrus*. Scale line = 5 mm. Adult females have a relatively smaller and less angular head. Photos by Lyle Buss.

Results

Records of association.

***Belonuchus agilis* Erichson 1840.** Originally described from Cuba, this species was later reported from Jamaica (Waterhouse 1878), all without habitat information. Blackwelder (1943) noted that a Cuban specimen in the US National Museum had been collected on a silk cotton tree (*Ceiba* P. Miller), and he indicated he had seen Jamaican examples. It has also been reported from Florida by Frank (2004). New collection records are: Dominican Republic, Prov. Hato Mayor, 24 km N of Hato Mayor, 28-X-1986, under fallen rotting oranges (2 specimens together with 4 specimens of *B. hispaniolus* Blackwelder, whose adults are all-black and smaller). USA, Florida, Dade County, Miami, 9-IV-2004, in decaying *Nolina recurvata* [= *Beaucarnea recurvata* Lem., Ruscaceae], K. Richardson and H. Escobar (4 specimens). [Contrary to statements in Frank (2004) this species has not yet been collected in *Heliconia* bracts – see also note under *B. gagates*].

***Belonuchus antiguae* Blackwelder 1943.** The only published information on this species reports the type series “from inside of scarlet bracts of a large unknown *Heliconia* sp. in dense mesophytic woodlands” near the summit of Boggy Peak (400 m altitude), St. Mary Parish, Antigua (Blackwelder 1943). A series of specimens was collected (JHF) under fallen and rotting grapefruit near Old Road, St. Mary Parish, Antigua, in July 1970, so the species is restricted neither to *Heliconia* bracts nor to higher altitudes.

***Belonuchus cacao* Blackwelder 1943.** This species was known previously only from the type series, collected from rotting cacao husks at Sans Souci, St. David Co., Trinidad (Blackwelder 1943). An additional female specimen was collected (RBR) in November 1982 from a flower bract of *Heliconia bihai* at Panaquire, Estado Miranda, Venezuela. In August 1983, a further female specimen was found (JHF) under fermenting bark of a fallen tree at the same Venezuelan locality.

Table 1. Distribution of 14 invertebrates among *Heliconia* bracts. Each of 10 inflorescences sampled had >10<19 bracts (total bracts = 137). Bract no. (BR) corresponds to age class (in weeks). The number of bracts (NO) sampled in each age class (1-18) gave a distributional median of 6 weeks (*). Invertebrates sampled (nos. in columns A-N, distributional median underlined) were: A (annelids), B-H (Coleoptera), B (*Pelosoma* adults), C (*Pelosoma* larvae), D-F (*Belonuchus* adults), D (*B. satyrus*), E (*B. cacao*), F (*B. rufipennis*), G (*Belonuchus* larvae), H (hispine larvae), I (lepidopterous larvae), J-N (dipterous larvae), J (psychodids), K (*Merosargus*), L (*Copestylum*), M (*Quichuana*), N (*Beebeomyia*).

BR	NO	A	B	C	D	E	F	G	H	I	J	K	L	M	N
0	10	0	0	0	0	0	0	0	0	0	0	0	0	3	0
1	10	0	9	1	1	0	0	0	2	0	1	2	0	21	1
2	10	1	14	1	1	0	0	1	2	0	1	1	0	29	1
3	10	0	11	0	<u>3</u>	0	0	1	<u>4</u>	2	1	3	0	60	1
4	10	0	<u>18</u>	0	3	0	<u>1</u>	<u>1</u>	2	<u>1</u>	0	6	0	55	0
5	10	1	9	<u>1</u>	0	<u>1</u>	0	0	2	1	2	5	0	52	4
6	10*	0	19	1	0	1	0	1	0	2	2	12	1	<u>40</u>	2
7	10	1	6	2	0	0	0	0	1	0	2	2	1	55	3
8	10	2	4	0	1	0	0	1	0	0	<u>1</u>	<u>12</u>	1	40	<u>3</u>
9	10	4	6	0	0	0	0	1	0	0	4	3	<u>2</u>	41	4
10	10	<u>5</u>	0	0	0	0	0	0	0	0	1	9	2	20	2
11	10	4	1	0	1	0	0	0	0	0	4	1	0	25	3
12	7	2	0	0	0	0	0	0	0	0	0	4	0	5	1
13-18	10	4	0	0	0	0	0	0	0	0	0	3	0	0	4
Total	137	24	97	6	10	2	1	6	13	6	19	63	7	446	29

***Belonuchus cephalotes* (Sharp 1885)** (Fig. 2). This species was described originally from Bugaba, Prov. Chiriquí, Panama, between 240 and 460 m altitude but its habitat seems unrecorded. A series of specimens was collected in March 1976 (RPS) in bracts of *Heliconia bihai* at Rancho Grande, Estado Aragua, Venezuela, at 900 m altitude. In July 1981, at the same locality, an additional 15 specimens were taken (JHF) from bracts of *H. bihai*, as well as nine from bracts of *H. bihai* cv. Aurea. Also in July 1981, 10 specimens were found (JHF) in bracts of *H. rodriguensis* Aristeguieta at Parque Nacional Guatopo, Estado Miranda, Venezuela, at > 200 m altitude. In May 1997, four specimens were found (JCA and JHF) in bracts of *H. bihai* at Tiara, Estado Aragua, Venezuela at 1200 m.

One of us (JHF) revisited the Rancho Grande locality in July 1997, 1999, 2001, and 2005 with other objectives. While there, he noticed a curious behavior by *B. cephalotes* adults. In *H. bihai* cv. Aurea, often present on the outer surface of the bracts, these adults could be observed rotating the abdomen, when they were otherwise still, or when they were walking. Considerable time was spent observing this behavior, but no response was seen either by conspecifics or by other organisms. In July 2009, on yet another visit, he obtained a vantage point in mid-afternoon and partial shade from which he could look down into a few bracts. An adult took up a position on the rachis wall of a bract and then walked down into the water, to a depth of about 3 cm, becoming completely immersed, its body (especially the elytra) covered by a silvery sheen of trapped air forming a plastron. At this disturbance to the water, the *Wyeomyia felicia* (Dyar and Nuñez-Tovar) (Diptera: Culicidae) larvae and pupae dived down from their previous position at the surface to take refuge at the floor of the bract. Within few seconds, the beetle had seized a mosquito pupa with its mandibles, and emerged from the water, carrying the mosquito pupa to the rim of the bract where it was devoured (Fig. 5-11). Three other virtually identical instances occurred within the next 15 minutes. The beetles did not seem to swim, but walked, probably obtaining purchase with their tarsal claws.

***Belonuchus gagates* Erichson 1840** (Fig. 3). Its type locality is Puerto Rico and Cuba, and it is reported from all of the Greater Antilles (Blackwelder 1943) but not the US Virgin Islands (Smetana 1991). Its presence in Dade and Monroe counties in Florida was reported by Smetana (1991, 1995). Its habitat was reported as “dead-meat traps, from crowns of *Tillandsia* [Bromeliaceae], from beneath dung and fresh chips, from the rotting “fruit” at the base of an imported palm [perhaps in reality a *Pandanus* cf. collection locality 50B and p. 423], in rotting grapefruit, and from under chips and rubbish on stumps”

(Blackwelder 1943). It and its larvae were found (JHF) abundantly under fallen, rotting citrus fruit in 1969-1972 in Jamaica. In 1985 it was found (JHF) in Jamaica at the following localities in flower bracts of *Heliconia caribaea* cv. Gold: St. Thomas Parish, path from Cornpuass Gap to Millbank, 3-V-1985 (20 specimens), and Portland Parish, Comfort Castle, 5-V-1985 (16 specimens). These adults are entirely black, typical of the species. The latter locality and habitat also yielded one specimen of an unidentified *Belonuchus* species differing in several respects including having a much reduced pronotal series of punctures, hind angle of head without a ridge, and the apical segments of the abdomen yellow. [This corrects statements in Frank (2004)].

***Belonuchus hispaniolus* Blackwelder 1943.** Adults are entirely black. New collection records (all by JHF) are as follows: Dominican Republic, Prov. Hato Mayor, 7 km S of El Valle, 28-X-1986, in bract of *Heliconia caribaea* cv. Gold (1 specimen), 24 km N of Hato Mayor, under fallen rotting oranges (4 specimens together with 2 specimens of *B. agilis*), Haiti, Département de l'Ouest, Grenier, about 3000 ft, 24-XI-1970, under rotten orange (2 specimens), below Kenscoff, 28-XI-1970, in pile of rotten banana stems (2 specimens), Montrouis, 7-VII-1977, in rotting breadfruit (1 specimen).

***Belonuchus mimeticus* Sharp 1885.** The Panamanian type locality of this species also is Bugaba, at 240 to 460 m altitude, and there is no original information on its habitat. In September 1982, a female specimen was taken (DHH) from a bract of *Heliconia mariae* Hook in Gamboa, Prov. Panamá, Panama, and four additional specimens (DHH) from flowers of *Hedychium* J. Koenig (Zingiberales: Zingiberaceae) at El Valle, Prov. Coclé, Panama. *Heliconia mariae* differs from others mentioned in this paper in that its flower bracts are pendent and do not accumulate water. *Belonuchus mimeticus* belongs to a group, currently assigned to *Belonuchus*, whose adults have very large and deep pronotal punctures. Future cladistic studies may call for generic reassignment.

***Belonuchus rufipennis* (Fabricius 1801).** This species ranges from the northeastern USA to Argentina by way of Central America, but is absent from most of the West Indies except Trinidad and Tobago (Blackwelder 1943). Its distribution was later thought to exclude the West Indies apart from Jamaica (no specimens from Jamaica were reported, so this may be an error) and its presence in South America was thought to include only and questionably the northern parts (Smetana 1995). Adults and larvae are predatory, are found in various decaying plant materials, and have been used in attempted biological control of fruit flies (Mank 1923, Blackwelder 1943, Silvestri 1945). Adults were found (JHF) in bracts of *H. bihai* in July 1981 on the campus of Universidad Central de Venezuela, Caracas, as well as at Panaquire, Venezuela.

***Belonuchus satyrus* Erichson 1840** (Fig. 4). This species was described from Colombia without habitat information. Subsequently, it was recorded from Venezuela, and was found in cacao husks in Trinidad (Blackwelder 1943). Specimens were collected (RPS) from bracts of *H. bihai* in March and May 1976 at Rancho Grande, Venezuela. More were taken (JHF) from bracts of *H. bihai* in July 1981 and from cacao husks in February 1982 at Panaquire, Venezuela. Additional specimens were found (DHH) in bracts of *H. mariae* in September 1982 at Gamboa, Panama.

***Odontolinus fasciatus* Sharp 1885.** This species was described originally from 240 to 460 m altitude at Bugaba and on Volcan de Chiriquí, Panama, without habitat information. It was found in bracts of *H. bihai* and infrequently those of *Heliconia imbricata* (Kuntze) as well as on stems of aroids (Araceae) and in plant tissues which exude sap near Rincon de Osa, Prov. Puntarenas, Costa Rica (Seifert 1974). Observations showed that adults entered the water in *Heliconia* flower bracts to capture mosquito larvae, then

Figure 5-11. *Heliconia bihai* cv. Aurea and some of the associated insects at Rancho Grande, Aragua, Venezuela. **5)** A plant with eight bracts. **6)** An adult *Belonuchus cephalotes* revolving its abdomen in typical behavior. **7)** An adult *B. cephalotes* with mandibles open. **8)** Mosquito larvae and pupae mainly of *Wyeomyia felicia* in the water in a bract. **9)** An adult *B. cephalotes* just before it entered the water in a bract. **10)** An adult *B. cephalotes* has captured a mosquito pupa from the water and is preparing to eat it on the rim of a bract. **11)** Another *B. cephalotes* with captured mosquito pupa. Photos by J.H. Frank.

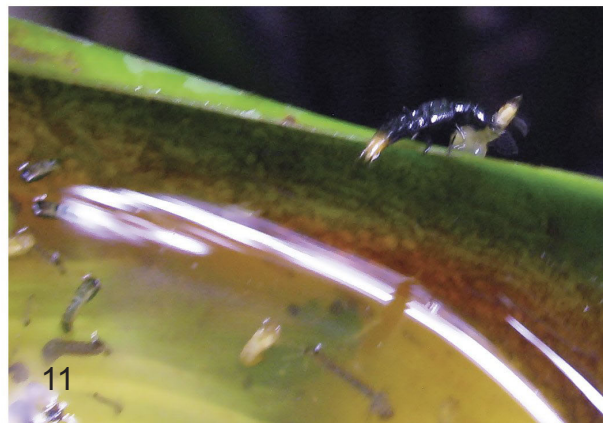
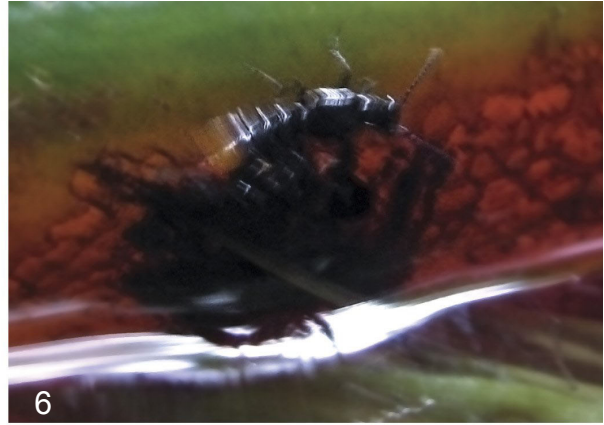


Table 2. Results of feeding trials in which various insect larvae and annelids from *Heliconia bihai* bracts were exposed to predation by *Belonuchus* adults and larvae. Symbols are: - no trial, 0 not eaten, 1 or 2 number eaten.

PREY	PREDATORS		
	<i>B. satyrus</i> larva	<i>B. satyrus</i> adult	<i>B. rufipennis</i> adult
<i>Quichuana</i> larva	1	2	-
<i>Copestylum</i> larva	-	1	-
hispine larva	0	0	-
<i>Toxorhynchites</i> larva	-	2	-
<i>Toxorhynchites</i> pupa	-	1	-
<i>Merosargus</i> larva	2	0	-
<i>Beebeomyia</i> larva	2	1	1
psychodid larva	2	-	-
annelid	0	0	-
pyraustine larva	1	2	-

emerged from the water to devour these prey (Seifert and Seifert 1976a). Population densities of the adults in *H. bihai* inflorescences varied among months and reached a median of 2.5 individuals in August, a higher number than in June or July (Seifert and Seifert 1976a).

***Philonthus* nr. *infirmus* Sharp 1885.** *Philonthus infirmus* was described from altitudes above 1000 m in Guatemala and Panama without habitat information. Seifert (1974) reported this species from bracts of *H. imbricata* near Rincon de Osa, Costa Rica. Adults of a related, but doubtfully conspecific, species were found (DHH) in bracts of *H. mariae* in September 1982 at Gamboa, Panama. At first glance, the six specimens from Gamboa could be mistaken for adults of *B. cephalotes*, because their color pattern is identical and their size almost as large.

Distribution among bracts

The more numerous of the animals collected in the bracts are listed in Table 1. Annelid worms (unidentified) were found principally in older bracts containing decayed floral parts (Table 1). One isopod, one spider, one milliped, four dermapterans, and two ants were found. Among the Coleoptera, adults and larvae of *Pelosoma* Mulsant (Hydrophilidae) were found mainly in younger bracts, as were adults and larvae of *Belonuchus* spp. (Table 1).

The latter included adults of *B. cacao*, *B. rufipennis* and, the most abundant and with largest individuals, *B. satyrus*. Six *Belonuchus* larvae were found of which three were preserved and three were used in feeding trials. Subsequently, one of the larvae pupated, and an adult *B. satyrus* emerged later. Other staphylinids included eight specimens of *Coproporus* Kraatz (representing two species), three of *Piestus* Gravenhorst, and one of *Medon* Stephens, all of whose individuals are much smaller than those of *Belonuchus* and belong to other subfamilies. The larval Hispinae (Chrysomelidae), found in the younger bracts (Table 1), belong probably to *Cephaloleia* Chevrolat and feed by scraping plant tissues (Machado-Allison et al. 1983). The only lepidopterous larvae found were those of an unidentified pyraustine pyralid, which were tunneling into and feeding on the partially submerged flowers. They were concentrated in the younger bracts (Table 1).

The most abundant of the dipterous larvae were those of *Quichuana* Knab (Syrphidae), whose distributional median was at bract number 6, i.e. in bracts of median age (Table 1). All the other dipterous larvae: psychodids, *Copestylum* Macquart (Syrphidae), *Merosargus* Loew (Stratiomyidae), *Beebeomyia* Curran (Richardiidae), and a single specimen of an unidentified tipulid, were concentrated in older bracts like the annelids but in contrast to the Coleoptera and Lepidoptera (Table 1). Distribution of larval mosquitoes (Culicidae) of the genera *Wyeomyia* Theobald, *Culex* L., and *Toxorhynchites* among bracts was not recorded, but has been well studied by Machado-Allison et al. (1983).

Feeding trials at Panaquire

Belonuchus satyrus adults fed by piercing the integument of the prey with the mandibles to feed on the soft body tissues, then abandoning the integument. A struggle between the predator and large larvae of *Quichuana* took place before the prey was eviscerated and subdued. On the other hand, the first prey larva was only partially consumed before the second was attacked. When annelid worms were provided as potential prey, a *B. satyrus* attacked and struggled with one of these (the prey about 4 the length of the predator), before retreating and spending considerable time grooming the mouthparts with the front legs. No further attacks on annelids were observed, nor were annelids killed. Several attacks on *Copestylum* larvae were observed in which the predator evidently was attempting to eviscerate the prey but may have been hindered from doing so by the toughness of the integument. Eventually, however, one of the *Copestylum* larvae was killed and eaten. Little interest was displayed by a *B. satyrus* adult in hispine larvae, which were neither killed nor eaten. A pyraustine larva was killed soon after it was made available to the predator.

Toxorhynchites larvae and a pupa were dragged from the water held in the *Heliconia* bract by *B. satyrus* adults and were then devoured after evisceration. The shallow water did not provide a protective barrier for the preimaginal *Toxorhynchites*.

Belonuchus larvae, all presumed to be those of *B. satyrus*, formed cells from macerated paper towel, and emerged from these cells to attack prey. Prey moving in close proximity to the cells were seized, and the predatory larva retreated backwards into the cell where feeding occurred. The feeding behavior resembled that exhibited by adult *B. satyrus*. Larvae of *Quichuana*, *Merosargus*, *Beebeomyia*, Psychodidae, and Pyraustinae were killed and eaten, but those of Hispinae were not killed and were not observed to be attacked (Table 2).

Only one *B. rufipennis* adult was available. Its feeding behavior when *Beebeomyia* larvae were presented was much like that of *B. satyrus* (Table 2). No feeding trials were attempted with adults of *B. cacao*.

Conclusion and discussion

On experimental results at Panaquire

Machado-Allison et al. (1983) considered the distribution of dipterous and hispine larvae among *Heliconia* bracts at Panaquire, but sampled inflorescences with only eight bracts. Because the present data concern inflorescences with at least 11 bracts, the distributional median for each species is here found to be in bracts of greater age. Nevertheless, the data agree in showing that hispine larvae tend to occur in younger bracts than do those of *Quichuana*, and the latter occur in younger bracts than do those of *Beebeomyia* and *Merosargus*. We believe this to reflect ovipositional preferences by adults of these species, together with food requirements and growth rate of the larvae. Larger larvae of each of these species will tend to occur in older bracts. The distribution of *Belonuchus* among bracts suggests that they occupy predominantly bracts with relatively young and small dipterous larvae. *Belonuchus satyrus* adults were able to kill and eat larvae of all the Diptera with which they were confined. They also ate lepidopterous larvae, but ignored hispine larvae and were repulsed by annelids. The diet of *B. satyrus* larvae was similar to that of the adults. The indications are that these (and probably also *B. rufipennis*) are opportunistic feeders on soft-bodied insects which are represented predominantly in their *Heliconia* bract habitat by dipterous larvae. The adults at least have the ability to drag mosquito larvae out of shallow water for consumption. Larvae of the mosquito *Toxorhynchites* are the largest aquatic predators in the bracts, but are themselves subject to predation by *B. satyrus* adults which thus occupy the apex of the food pyramid.

Nineteen individuals of *Belonuchus* were collected from 10 *Heliconia* inflorescences. This is not much less than the density of 2.5 *Odontolinus fasciatus* per *Heliconia* inflorescence recorded by Seifert and Seifert (1976a) in August in Costa Rica.

These two species (*B. satyrus* and *B. rufipennis*) were not seen to immerse themselves in deep water as did *O. fasciatus* (Seifert and Seifert 1976a) and *B. cephalotes* (this publication).

On *Belonuchus* and other Staphylinidae associated with *Heliconia* bracts

An unresolved question about *B. cephalotes* is why the adults rotate the abdomen. Could this be to disperse a pheromone? Another question is why the color pattern of those adults (black, with the apical abdominal segments yellow) matches the color pattern of *B. agilis* and of *Philonthus* nr. *infimus*. Is it pure coincidence that the yellow color is shared also by the flowers of the *Heliconia* spp. that some of them inhabit?

Seifert and Seifert (1976a) supposed that mosquito larvae formed a major part of the diet of *Odontolinus fasciatus* adults in Costa Rican *Heliconia* bracts. Although newly hatched larvae of 11 *Quichuana* and *Beebeomyia* were eaten, they were thought generally to be unavailable to this predator because of their restriction to partially opened bracts which *O. fasciatus* could not enter. Those investigators made no mention of possible predation by *O. fasciatus* on larger *Quichuana* and *Beebeomyia* larvae, which necessarily occur in older, open bracts, and we do not think that possibility should be dismissed. However, we agree that prey availability in the habitat is the most likely determinant of diet for both *Odontolinus* and *Belonuchus*.

These conclusions are supported by the records of occurrence of these and other *Belonuchus* in other decaying vegetable materials such as cacao husks, bananas, breadfruit, and fallen and rotting citrus fruits. Dipterous larvae usually are abundant in such habitats. It is possible that the natural habitat of at least some of these species is *Heliconia* bracts, but that human cultivation of these crops in the Neotropics expands the habitat available to them, if only at those seasons when rotting husks or fruit harbor concentrations of prey larvae. This association between these *Belonuchus* (and a few close allies) is not pure happenstance because the corollary of the observation is consequential: the family Staphylinidae includes thousands of genera, many of them with individuals of large size, but large individuals of other genera were NOT collected in the *Heliconia* bracts sampled. To the extent that other staphylinids were encountered in the *Heliconia* bracts sampled, they were *Coproporus* (Tachyporinae) and occasionally *Medon* (Paederinae) with much smaller individuals and (undoubtedly) other diets. The hypothesis presented here is that quite a few species of *Belonuchus* (and a few close allies) have evolved an association with *Heliconia* bracts, and this association is most prominent in those species whose adults can immerse totally in water (*B. cephalotes* and *O. fasciatus*) to attack mosquito larvae and pupae. By such attacks they may structure the prey community. Future studies may be used to test this hypothesis.

The stage seems to be set for many more ecological studies to document the fascinating behavior and effects of these and many more *Belonuchus* spp. associated with *Heliconia* spp. Thanks to Berry and Kress (1991) the *Heliconia* spp. can now be identified even by entomologists. Unfortunately, there is no revision of the Neotropical *Belonuchus* species. The senior author (JHF) was able to identify those he encountered only because he believes in the maxim that every insect ecologist should become proficient in identification of at least one taxon of insects, and he selected Staphylinidae (an extremely large family) for attention. The species occurring in the West Indies were documented as 14 by Blackwelder (1943); those of the USA were documented as nine (Smetana 1995) but then *B. agilis* was detected in Florida (Frank 2004) raising the total to 10; many dozens have been reported from the Neotropics. So now we see that the preliminary task is for an insect taxonomist to revise the Neotropical species of *Belonuchus*.

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