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Host-use patterns of canopy-inhabiting click beetles
(Coleoptera: Elateridae) in a lowland rainforest
in southern Venezuela

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Host-use patterns of canopy-inhabiting click beetles (Coleoptera: Elateridae) in a lowland rainforest in southern Venezuela

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Abstract. The arboreal click beetle fauna (Coleoptera: Elateridae) in a lowland tropical rainforest in southern Venezuela was observed and collected by means of a tower crane for a full year. The evaluation of the elaterid assemblage is part of a general survey of Coleoptera associated with several canopy trees. The Elateridae represented the tenth most species-rich beetle family in the canopy of the crane plot and was therefore selected for a detailed analysis of host-use patterns. In total, 20 species of Elateridae with 402 adult individuals were sampled, including seven singletons. Species were either flower visiting (*Aeolus* Eschscholtz and *Cosmesus* Candèze) or fed mainly on extrafloral nectaries (*Chalcolepidius* Eschscholtz, *Crepidius* Candèze, *Lacon* Castelnau, *Lissomus* Dalman, and *Semiotus* Eschscholtz). The most abundant species was *Aeolus* sp. 1 (N = 306) feeding on flowers of nine different host-tree species. This species was found often in high abundances during the entire flowering period of a single tree species with highest abundances coinciding with the maximum of open flowers. *Aeolus* sp. 1 was recorded almost every month of the year moving usually from one flowering tree species to another comprising possibly the entire local population. This species showed preferences between different tree species and occurred there only at night. Tree species that supported the most species-rich elaterid assemblages were *Ruizterania trichanthera* (Spruce ex Warm.) Marc.-Berti (Vochysiaceae) (N = 8) and *Goupia glabra* Aubl. (Goupiaceae) (N = 6). Only one elaterid species with at least two collected individuals was found restricted to one tree species.

Key words. Amazonia, biodiversity, seasonality, host plants, diet, behavior.

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Introduction

Elateridae Leach, 1815, commonly known as click beetles, contains approximately 10,000 described species worldwide, making it taxonomically the ninth most diverse family of beetles (Ślipiński et al. 2001; Costa et al. 2010), though a working catalog by PJJ includes over 12,000 valid names. Approximately 2,400 species were recorded from South America including 149 click beetles in 41 genera known from Venezuela (Aguirre-Tapiero and Johnson 2014). According to Johnson and Chaboo (2015), Elateridae in the Neotropics are common in forests, savannas, thorn-forests, and scrublands. The species composition between wet and dry vegetation types is different. Most species of click beetle fly well and adult activity is short (Johnson 2002). In temperate regions, most species are diurnal, though more than two-thirds of the Neotropical species are crepuscular and nocturnal. Diurnal species are often found on foliage or at flowers, but little is known of nocturnal habits. Click beetles feed on plant saps comprising plant wounds and weeps, floral and extrafloral nectaries, but also on pollen and flower tissues or decaying fruits. Some species prey on soft-bodied sternorrhynchous insects and their “honey dew” exudates. Larvae are found under bark, in soil, forest duff, or decaying plant materials, especially in fibrous stems and wood (Johnson 2002). Some species have specialized larvae that live in arboreal bromeliads or in epiphyte mats

on trees (Johnson and Chaboo 2015). Wood, duff and epiphyte inhabiting larvae are predaceous on small and immature invertebrates or saprophagous on decay organisms (Johnson 2002). Soil dwelling species are predominantly predaceous or omnivorous, but some are phytophagous on sprouting seeds and roots. Larvae are liquid feeders digesting extra-orally. There are generally 3–5 larval instars normally taking 1–3 years for development.

Insect herbivores and their plant hosts dominate terrestrial biodiversity with beetles representing almost 25% of all known life forms (Hunt et al. 2007). Particularly tropical rainforest canopies are famous for their arthropod species richness, which is often distinct from lower forest strata (Adis et al. 1984; Basset et al. 2001, 2003a; Stork and Grimbacher 2006; Erwin 2013). Beetles often contribute hundreds of species to the fauna of single trees (Kirmse et al. 2003; Ødegaard and Frame 2007; Adis et al. 2010). However, most of our knowledge about canopy-inhabiting beetles in rainforests as revealed to date comes from the fogging method. Fogging and methods such as DNA bar-coding of ingested food are limited not only in the interpretation of temporal associations, but also lack important insights into the behavior of the beetles. One reason for this knowledge gap is the limited direct access to tree canopies. There are only a handful of crane facilities allowing flexible observations *in vivo* in tropical forests (Basset et al. 2003b). The crane project in southern Venezuela, thus far, remained the only one within the world's largest rainforest area, the Amazon basin (Winkler and Listabarth 2003).

To improve the knowledge of canopy-inhabiting elaterid beetles, their occurrence on and their associations with host trees were investigated using the tower crane installed in the study area. For that, the adult click beetles associated with several canopy tree species were observed regularly and sampled at day and night. As resource availability is the most important factor influencing spatial and temporal distribution patterns among arboreal insect assemblages (Wardhaugh 2014), continuous observation and sampling of click beetles will uncover the forces and mechanisms underlying patterns of their distribution and community structure. Only the observation of these beetles in their natural environment will reveal reliable data about true host associations in the temporal and spatial context. Data on the natural history of the canopy communities of Chrysomelidae and Scarabaeidae from the same site were published previously (Kirmse and Chaboo 2018; Kirmse and Ratcliffe 2019). The present study provides observations for the first time on a canopy-inhabiting click beetle assemblage during a complete year. Our study includes data of occurrence, diet, utilized hosts, and behavior of adult elaterids in the canopy of a tropical lowland rainforest in northern Amazonia. Species apparently new to science will be formally described separate from this report.

Materials and Methods

Study site. The crane plot is located in the upper Orinoco region in southern Venezuela (state of Amazonas) close to the black water river Surumoni (3°10'N, 65°40'W; 105 m asl). Anhuf et al. (1999) describe the weather pattern as a gross rainfall of about 3,100 mm. Year to year fluctuations of about 500 mm occur. A strong peak in the annual precipitation is prevalent from May to July and a lower peak in September and October. The average annual temperature in the study area is ca. 26°C. Slight variations between the coolest month (25°C) and the warmest month (26.5°C) are recognized, whereas a daily range of 5–10°C frequently occurs.

The Surumoni area belongs to the Japura/Negro moist forests ecoregion that extends from Brazil to southern Venezuela, Colombia, and Peru, and represents a major habitat type of highest biodiversity conservation priority (Dinerstein et al. 1995). The vegetation is that of a moist lowland tropical rainforest classified as terra firme (Prance 1979). The upper canopy ranges usually from 25 to 27 m in height with only a few emergent trees reaching up to 35 m. The Surumoni crane plot contained average tree species richness for the area. There were more than 800 trees with ≥ 10 cm DBH (diameter at breast height) belonging to 141 tree species within the crane plot of about 1.4 ha. Frequent species in the tree fraction with a DBH of ≥ 10 cm were *Goupia glabra* Aubl. (Goupiaceae), *Oenocarpus bacaba* Mart. (Arecaceae), *Dialium guianense* (Aubl.) Sandwith (Fabaceae), *Ocotea aff. amazonica* (Meisn.) Mez (Lauraceae), and *Ruizterania trichanthera* (Spruce ex Warm.) Marc.-Berti (Vochysiaceae) (Wesenberg 2004). Epiphytes and hemiepiphytes comprising 53 species were relatively rare (Engwald et al. 2000).

Beetle sampling and observations. A canopy crane system, 42 m in height and running on 120 m long rails, was installed at the study site. It covered an area of about 1.4 ha. Using the tower crane, the crowns of tree species in

the upper and middle canopy were searched regularly for species of elaterids during the day as well as during the night. Observed beetles were collected by hand, by net, or through branch and foliage beating. The time spent in observing and collecting beetles on canopy trees was chosen according to available specimens and not structured for quantitative data. Additionally, aerial traps were used to collect flying beetles (Basset et al. 1997). These window traps consisted of two clear acrylic panels fixed in a cross with each a length of 30 cm and a height of 25 cm. Beneath the panels was a plastic tube ending in a container for collecting the insects. The trapped insects were removed every other day. These flight interception traps provided semi-quantitative sampling results. In addition to the hand and trap collections, some elaterids were collected that were attracted to a spotlight used to enable observations at night.

Sampling and observation of adult click beetles were conducted between 1997 and 1999. The fieldwork comprised the following periods: September to November 1997; May to August and December 1998; January to April and October and November 1999, thus enabling cumulative data collection for a full year. The collected beetles were kept in 70% ethanol. The beetles were assigned to morphospecies and identified to the lowest taxon subsequently. The family-group taxonomic classification follows Bouchard et al. (2011). Voucher specimens of beetles are deposited in the Museo del Instituto de Zoología Agrícola 'Francisco Fernández Yépez' (MIZA), Maracay, Venezuela, and in the Botanisches Institut, University Leipzig, Germany.

Beetle characteristics. Our study includes all species of Elateridae collected in the canopy of the crane plot. To avoid singleton random findings, only abundant species are described in detail within the results section. Elaterid species are characterized ecologically corresponding to data and observations gained in the canopy. Species are assigned according to their diel activity either as nocturnal or diurnal species. Host plants include all canopy trees where beetles were sampled and observed. Exclusive species were sampled on only one host-tree species. The main hosts harbored the most individuals and include most feeding observations. The diet and plant tissue/parts consumed were categorized as leaves, extrafloral nectaries, and flowers. The parts utilized by flower-visiting species were not specified since floral feeding by elaterids is generalized among liquids and soft tissues. Question marks indicate that the diet was suggested but not confirmed. The main diet includes food items that were regularly consumed in the canopy. Abundant species were determined by calculating the proportion of all click beetles sampled on one distinct canopy host.

Preferences were indicated by strikingly different abundances of an elaterid species in direct comparison of two known canopy host trees with each crown observed and sampled within the same dates and providing the same kind of resources. If *Aeolus* Eschscholtz sp. 1 was found, for instance, utilizing flowers of two different host species, but occurred in the case of co-flowering only on one of these two host trees then a preference was suggested. To analyze the statistical significance of the differences between each two host-tree species compared we used the Mann-Whitney test for equal medians (Zar 1996).

Feeding trials were used to confirm and verify, respectively, observations in the canopy. Adults of the following five species were tested: *Chalcolepidius limbatus* (Fabricius), *Lacon pollinarius* (Candèze), *Lissomus obconicus* Bonvouloir, *Lygelater indicus* (Herbst), and *Semiotus ligneus* (Linnaeus). Specimens of each species were observed alone or in small groups for a few days or until they died. They were kept in plastic tubes with a height of about 12 cm and a diameter of about 15 cm. The tubes were filled with loam to a height of about 3 cm and supplied with old and young leaves of the recorded host tree. Additionally, the beetles were offered fleshy fruit and flowers of their host trees. The feeding damage was checked every second day and scored visually either as non-feeding, attempting to feed, or regularly feeding. The adult elaterids were kept under the natural temperature regime and natural day/night conditions for the area. However, feeding trials demonstrate potentialities, not necessarily natural associations that might be influenced by multiple ecological interactions (Downey 1962; Ehrlich and Raven 1964). Furthermore, the ability to locate and identify a preferred host may have little in common with the ability to consume a distinct host (Singer 2008). This may lead to the result that beetles in tests feed on more plants or plant parts than they usually utilize under natural conditions. Field observations of insect feeding associations reflect the realized feeding niche (Futuyma and Moreno 1988).

Results

Overview. A total of 20 species with 402 individuals were collected in our canopy plot (Table 1). Seven species (35%) were represented by single specimens, whereas five species (25%) were represented by at least 10 individuals. Most species sampled belong to the subfamily Agrypninae (10 spp.) followed by Elaterinae (7 spp.). Cardiophorinae, Lissominae, and Semiotinae were each represented by only a single species. The morphospecies could be assigned to 14 genera comprising 11 identified species.

Except for three specimens belonging to three species, all elaterids were found exclusively nocturnal in the canopy plot. Fourteen species showed distinct nocturnal behavior. *Chalcolepidius limbatus*, *Crepidius ophthalmicus* Candèze (Fig. 2), and *S. ligneus*, which were observed regularly in the canopy during the night, were found on the ground, on trunk bases, or on herbs in the daytime. Only *Dipropus* Germar sp. 3 (Fig. 3) with three collected individuals was found twice at the ground layer also during the night.

The elaterid species utilized on average 2.2 canopy-tree species (min N = 1; max N = 9). Only one species, *Dipropus* sp. 1, in which at least two individuals were collected, was found restricted to only one tree species. The beetles were collected usually on flowers (N = 6), at extrafloral nectaries (N = 6), or they utilized both resources (N = 4) (Table 2). One species, *Lacais glauca* (Castelnau), was found using all three primary adult food resources on *G. glabra*: flowers, extrafloral nectaries, and fleshy fruit.

Elateridae were mainly recorded from the following seven tree species (Table 3): *Albizia pedicellaris* (DC.) L. Rico, *Senna* cf. *silvestris* (Vell.) H. S. Irwin and Barneby and *Tachigali guianensis* (Benth.) Zarucchi and Herend. (Fabaceae); *G. glabra* (Goupiaceae); *Matayba guianensis* Aubl. (Sapindaceae); *Qualea paraensis* Ducke and *R. trichanthera* (Vochysiaceae). Of these, *A. pedicellaris*, *M. guianensis*, *Q. paraensis*, and *T. guianensis* exhibited mass-flowering. Further recorded host trees are *Hymenopus heteromorphus* (Benth.) Sothers and Prance (Chrysobalanaceae); *O. aff. amazonica* and *Rhodostemonodaphne grandis* (Mez) Rohwer (Lauraceae); *Emmotum acuminatum* (Benth.) Miers (Metteniusaceae); and *Vochysia vismiifolia* Spruce ex Warm. (Vochysiaceae).

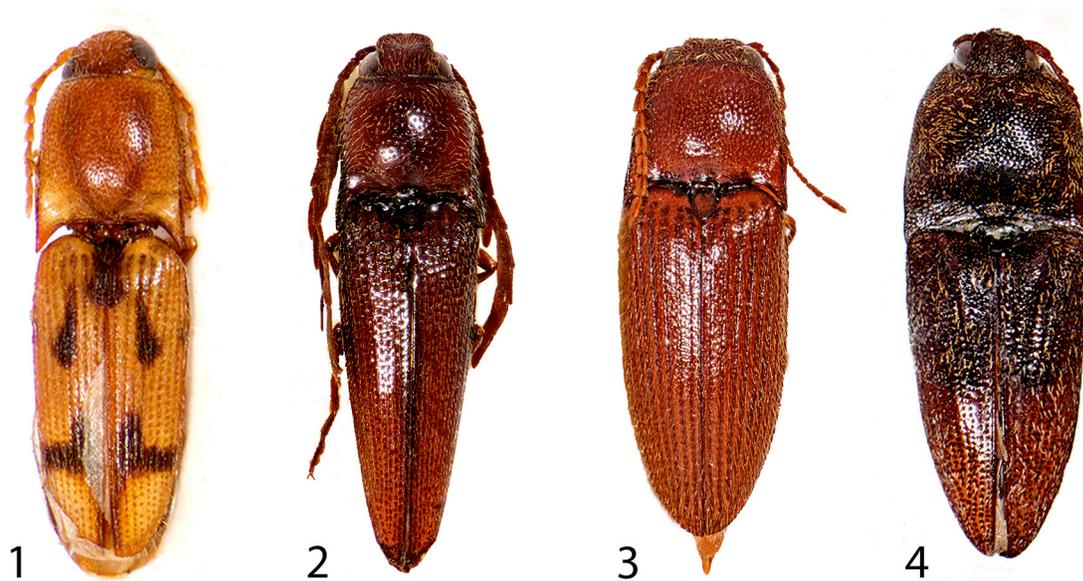
Species characteristics. Three more common and regularly observed species, *L. pollinarius*, *L. obconicus*, and *S. ligneus*, were found among other elaterid species repeatedly on the extrafloral nectaries of *R. trichanthera* in December 1998 and January 1999 (Tables 2 and 4). *Lissomus obconicus* and *S. ligneus* were recorded additionally on the extrafloral nectaries of *S. cf. silvestris* between June and August 1998. Both species mated on this tree species during that period. Although *S. cf. silvestris* had active extrafloral nectaries also in December 1998 and January 1999, *L. obconicus* and *S. ligneus* were not found visiting this tree species in that period. *Chalcolepidius limbatus* was found feeding on nectar secreted on young shoots of *G. glabra* in mid-February and on the extrafloral nectaries of *R. trichanthera* during the end of January 1999 (Table 2).

The most abundant species sampled in the canopy plot was *Aeolus* sp. 1 (Fig. 1; Tables 2–5). It was recorded from nine flowering tree species. This species visited the flowering trees exclusively at night and was collected in almost every month except for February and May. Most individuals were collected on the mass-flowering trees of *M. guianensis*, *A. pedicellaris*, and *T. guianensis* from September to November 1997. The sex ratio of trapped specimens was balanced on these trees. On the other hand, only single individuals were found in January, March, June, July, and December. In September 1997, individuals of *Aeolus* sp. 1 were observed commonly feeding on the flowers of several tree specimens of *G. glabra*. *Aeolus* sp. 1 was not found on *G. glabra* with the start of flowering of *M. guianensis* end of September 1997, although there were still a lot of flowers on this tree species. Instead, from 25 September to 8 October, many individuals of *Aeolus* sp. 1 were observed regularly on a flowering *M. guianensis*. With the start of blossoming of *A. pedicellaris* from 11 October onwards, many individuals of *Aeolus* sp. 1 were found on this tree but not on the flowering *M. guianensis* (except for one individual trapped on 13 October), although *M. guianensis* flowered until 23 October. In early November, a lot of individuals were found on both *Q. paraensis* and *G. glabra*. From 9 November onwards, most individuals were trapped on the flowering *T. guianensis*, even though *Q. paraensis* was still in bloom. Apparently, *Aeolus* sp. 1 preferred the flowers of *M. guianensis* to that of *G. glabra* (Mann-Whitney U = 16.5, $p < 0.01$), the flowers of *A. pedicellaris* to *M. guianensis* (Mann-Whitney U = 0, $p < 0.01$), and the flowers of *T. guianensis* to *Q. paraensis* (Mann-Whitney U = 0, $p < 0.01$).

Host trees. On the regularly monitored tree species *R. trichanthera*, eight species of Elateridae (Table 3) with 24 individuals accounted for the highest record of elaterid species on a single tree species within our canopy plot.

Table 1. Overview of elaterid species recorded in a lowland rainforest canopy, Venezuela, 1997–1999.

Taxon	# species	# individuals
Elateridae Leach, 1815	20	402
Agrypninae Candèze, 1857	10	346
Agrypnini Candèze, 1857	3	15
<i>Lacon</i> Castelnau, 1836	3	15
<i>Lacon bipectinatus</i> Riese, 1989		3
<i>Lacon chabannei</i> (Guérin-Méneville, 1829)		1
<i>Lacon pollinarius</i> (Candèze, 1857)		11
Hemirhipini Candèze, 1857	2	17
<i>Chalcolepidius</i> Eschscholtz, 1829	1	8
<i>Chalcolepidius limbatus</i> (Fabricius, 1777)		8
<i>Lacais</i> Fleutiaux, 1942	1	9
<i>Lacais glauca</i> (Castelnau, 1836)		9
Oophorini Gistel, 1848	3	308
<i>Aeolus</i> Eschscholtz, 1829	2	307
<i>Conoderus</i> Eschscholtz, 1829	1	1
Pyrophorini Candèze, 1863	2	6
<i>Anaïssus</i> Candèze, 1857	1	1
<i>Anaïssus</i> cf. <i>calderi</i> Riese, 2007		1
<i>Lygelter indicus</i> (Herbst, 1784)	1	5
Cardiophorinae Candèze, 1859	1	1
<i>Esthesopus</i> Eschscholtz, 1829	1	1
Elaterinae Leach, 1815	7	30
Ampedini Gistel, 1848	5	18
<i>Crepidius</i> Candèze, 1859	2	14
<i>Crepidius ophthalmicus</i> Candèze, 1859		12
<i>Dipropus</i> Germar, 1839	3	6
<i>Ypsilosthetus</i> Candèze, 1891	1	1
Pomachiliini Candèze, 1859	1	9
<i>Cosmesus</i> Candèze, 1863	1	
<i>Cosmesus discoidalis</i> Kirsch, 1870		9
Lissominae Laporte, 1835	1	10
Lissomini Laporte, 1835	1	10
<i>Lissomus</i> Dalman 1824	1	10
<i>Lissomus obconicus</i> Bonvouloir, 1857		10
Semiotinae Jakobson, 1913	1	15
Campsosterini Fleutiaux, 1927	1	15
<i>Semiotus</i> Eschscholtz, 1829	1	15
<i>Semiotus ligneus</i> (Linnaeus, 1767)		15



Figures 1–4. Click beetle species exemplars from canopy study. 1) *Aeolus* sp. 1, female, length 5.0 mm. 2) *Crepidius ophthalmicus* Candèze, male, length 12.6 mm. 3) *Dipropus* sp. 3, male, length 8.7 mm. 4) *Lacon bipectinatus* Reise, female, length 9.5 mm.

Elateridae represented the fifth most species-rich beetle family on this tree species. Three species, *Anaïssus* cf. *calderi* Riese, *Crepidius* Candèze sp. 2, and *Lacon bipectinatus* Riese (Fig. 4), were found exclusively on this tree species. All elaterids but one were sampled only in periods with young foliage and active extrafloral nectaries on *R. trichanthera* between October and February. The three abundant species, *L. pollinarius*, *L. obconicus*, and *S. ligneus*, were observed repeatedly over several weeks during the leaf flush (Table 4).

Except for the months April and May, different trees of *G. glabra* were monitored on a regular basis. Altogether, six elaterid species (Table 3) with 58 individuals were sampled on trees of *G. glabra* in the canopy plot. Elateridae represented the sixth most species-rich beetle family on this tree species and accounted for the second most abundant beetle family in the window traps ($N = 48$). Two species, *Lacon chabannei* (Guérin-Méneville) and *Esthesopus* Eschscholtz sp., collected only as singletons were found exclusively on this tree species. *Lacais glauca* might feed on fleshy fruit of *G. glabra*, whereas *C. limbatus* fed on the extrafloral nectar secreted on young shoots (Table 2). The abundant *Aeolus* sp. 1 (Tables 2 and 5) was found regularly on flowering trees in August, September, and November 1997 but not in October, although there were flowering trees of *G. glabra* in the canopy plot.

The blossoming of *A. pedicellaris* covered a period of about three weeks from 8 October to 1 November 1997. The abundant species, *Aeolus* sp. 1, showed a maximum abundance within the flowering season from 13–19 October (Table 4), which coincided with the maximum number of open flowers. It was collected regularly throughout the entire flowering season. *Aeolus* sp. 1 was again an abundant flower visitor of *A. pedicellaris* during the blossom period in April 1999. In total, four elaterid species were sampled on *A. pedicellaris* (Table 3); two were represented by only a single specimen. Still, Elateridae were trapped with most beetle individuals on *A. pedicellaris* in both monitored flowering seasons ($N = 41$; $N = 16$).

Elateridae were trapped with the third-most number of individuals on *T. guianensis* ($N = 65$), but three of the four species were singletons (Table 3). During a 4.5 month trapping period in the non-flowering season, only two single elaterid specimens (2 spp.) were recorded on this tree species. The monitored flowering season of *T. guianensis* lasted 18 days from 9–27 November 1997. The abundant *Aeolus* sp. 1 occurred continuously throughout the entire flowering season of *T. guianensis*. The maximum abundance of *Aeolus* sp. 1 (Table 4) coincided with the maximum of open flowers between the 20 and 23 November 1997.

Table 2. Host trees, diet, and months of occurrence of abundant elaterid species in a lowland Venezuelan rainforest canopy, 1997–1999. Abbreviations: EFN = extrafloral nectar; ? = diet suggested.

Species	# host tree species	Main diet	Main host trees	Months of occurrence	Remarks
<i>Aeolus</i> sp. 1	9	flowers	<i>G. glabra</i> <i>M. guianensis</i>	year-round, except for Feb and May	regularly mating on several host trees
<i>Chalcolepidius limbatus</i>	4	EFN	<i>G. glabra</i>	Jan, Feb, Apr 1999; May 1996; Sep, Nov 1997	
<i>Crepidius ophthalmicus</i>	3	EFN	<i>S. cf. silvestris</i> <i>Q. paraensis</i>	Feb 1999; Aug–Oct 1997	
<i>Lacais glauca</i>	5	flowers, EFN, fruit?	<i>G. glabra</i>	Jan–Apr 1999; Sep 1997	
<i>Lacon pollinarius</i>	2	EFN	<i>R. trichanthera</i>	Jan, Mar 1999; Nov 1997; Dec 1998	
<i>Lissomus obconicus</i>	3	EFN	<i>R. trichanthera</i> <i>S. cf. silvestris</i>	Jan 1999; Jun, Aug, Dec 1998	mating in June
<i>Lygelater indicus</i>	2	EFN	<i>S. cf. silvestris</i>	Jul, Aug 1998; Sep 1997	
<i>Cosmesus discoidalis</i>	3	flowers	<i>M. guianensis</i> <i>A. pedicellaris</i>	Sep–Nov 1997	
<i>Semiotus ligneus</i>	3	EFN	<i>R. trichanthera</i> <i>S. cf. silvestris</i>	Jan 1999; Jul 1998; Oct, Nov 1997; Dec 1998	mating and oviposition in July

Table 3. Monitored canopy-tree species and their associated elaterids in a lowland Venezuelan rainforest, 1997–1999. Abbreviations: N ≥ 2: # species excluding singletons; “X” indicates the kind of diet consumed by named elaterid species; EFN = extrafloral nectaries.

Host Tree	Species:				Diet:		
	total	N ≥ 2	exclusive	most abundant	flowers	EFN	fruit
<i>Ruizterania trichanthera</i> (Vochysiaceae)	8	4	3	<i>Lacon pollinarius</i>	1	6	
<i>Goupia glabra</i> (Goupiaceae)	6	3	2	<i>Aeolus</i> sp. 1	2	2	1
<i>Albizia pedicellaris</i> (Fabaceae)	4	2		<i>Aeolus</i> sp. 1	4		
<i>Tachigali guianensis</i> (Fabaceae)	4	1	1	<i>Aeolus</i> sp. 1	3		
<i>Senna</i> cf. <i>silvestris</i> (Fabaceae)	4	3		<i>Lissomus obconicus</i>		4	
<i>Matayba guianensis</i> (Sapindaceae)	3	2	1	<i>Aeolus</i> sp. 1	3		
<i>Qualea paraensis</i> (Vochysiaceae)	3	1		<i>Aeolus</i> sp. 1	3		

Senna cf. *silvestris* was monitored regularly over a period of 10 months. Four elaterid species were recorded on this tree species, including one species represented by only one specimen (Table 3). Several individuals of *L. obconicus*, *L. indicus*, and *S. ligneus* (Tables 2 and 4) fed on the extrafloral nectaries from June to August 1998.

Three flowering seasons of two neighboring trees of *M. guianensis* were monitored. In total, three elaterid species (Table 3), including a singleton of *Ypsilosthetus* Candèze were recorded during all flowering seasons. However, only the main flowering season of tree #446 over 21 days from 18 September to 8 October 1997 has attracted a remarkable number of elaterids. The abundant *Aeolus* sp. 1 occurred regularly throughout this flowering season (Tables 4 and 5). It showed a maximum abundance corresponding to the maximum of open flowers. Due to the occurrence of *Aeolus* sp. 1, elaterids contributed the second most individuals (N = 132) to the total number of trapped beetles on tree #446. During the night, *Aeolus* sp. 1 was the most abundant flower visitor. Although, the flowering season of the neighboring tree #636 followed immediately that of tree #446 in 1997, *Aeolus* sp. 1 was trapped with only one specimen here (compared to 127 individuals on tree #446). During the main flowering season of *M. guianensis* in October–November 1999, also only one individual *Aeolus* sp. 1 was trapped on both trees.

The monitored flowering season of *Q. paraensis* lasted 35 days in 1997. Three elaterid species visited this tree species during the blossom (Table 3). Whereas *Aeolus* sp. 1 was sampled with seven individuals (Table 5), the other two species were recorded only once.

Discussion

Canopy elaterid assemblages. Compared to other beetle families dominating the canopies of tropical forests, elaterids are usually less prominent inhabitants. They comprised only 20 out of 868 beetle species in 44 families recorded on 25 canopy plant species in the canopy plot. Still, the elaterid assemblage represents the 10th most taxonomically diverse beetle family sampled in our canopy plot. Similarly, samplings from other tropical forests commonly report few elaterid species. Stork and Grimbacher (2006) recorded 32 elaterid species from a lowland tropical rainforest in Australia. Chung (2004) sampled only three species in a lowland rainforest in Malaysia,

Table 4. Occurrence of abundant elaterid species either on one or more tree species in a lowland Venezuelan rainforest canopy, 1997–1999. Abbreviations: A.p.: *Albizia pedicellaris*; E.a.: *Emmotum acuminatum*; G.g.: *Goupia glabra*; M.g.: *Matayba guianensis*; R.t.: *Ruizterania trichanthera*; S.s.: *Senna cf. silvestris*; T.g.: *Tachigali guianensis*; V.m.: *Vochysia vismifolia*.

Symbols: * = flowers; ● = extrafloral nectaries; ? = diet unknown; → = successive occurrence; ◆ = simultaneous occurrence; ◆ = simultaneous occurrence.

Species	Host tree, diet and number of individuals collected per date									
<i>Lacron pollinaris</i>	R.t. (1) ●	R.t. (5) ●	R.t. (2) ●	R.t. (2) ●	E.a. (1) *					
	20.XI.1997	19.XII.1998	03.I.1999	10.I.1999	12.III.1999					
<i>Lissomus obconicus</i>	R.t. (1) ?	S.s. (3) ●	S.s. (2) ●	G.g. (1) ●	R.t. (1) ●	R.t. (1) ●	R.t. (1) ●	R.t. (1) ●	R.t. (1) ●	
	01.VI.1998	17.VI.1998	04.VIII.1998	04.VIII.1998	26.XII.1998	08.I.1999	11.I.1999			
<i>Semiotus ligneus</i>	S.s. (1) ●	S.s. (1) ●	S.s. (2) ●	ground (1)	R.t. (1) ●	R.t. (1) ●	V.m. (1) *			
	07.VII.1998	13.VII.1998	17.VII.1998	17.VII.1998	09.X.1997	07.XI.1997	22.XI.1997			
	R.t. (1) ●	R.t. (1) ●	light (1)							
	17.XII.1998	24.XII.1998	Jan 1999							
<i>Aeolus</i> sp. 1	M.g. (1) *	M.g. (33) *	M.g. (39) *	M.g. (14) *	M.g. (23) *	M.g. (5) *	M.g. (12) *	M.g. (1) *		
<i>M. guianensis</i>	25.IX.1997	26.IX.1997	28.IX.1997	30.IX.1997	04.X.1997	06.X.1997	08.X.1997	13.X.1997		
<i>Aeolus</i> sp. 1	A.p. (6) *	A.p. (2) *	A.p. (12) *	A.p. (10) *	A.p. (6) *	A.p. (2) *				
<i>A. pedicellaris</i>	11.X.1997	13.X.1997	15.X.1997	19.X.1997	21.X.1997	23.X.1997				
<i>Aeolus</i> sp. 1	T.g. (5) *	T.g. (12) *	T.g. (13) *	T.g. (3) *	T.g. (2) *	T.g. (20) *	T.g. (6) *			
<i>T. guianensis</i>	12.XI.1997	14.XI.1997	16.XI.1997	18.XI.1997	20.XI.1997	22.XI.1997	24.XI.1997			

Table 5. *Aeolus* Eschscholtz sp. 1 abundance per month (cumulative data presentation) on flowering canopy-tree species in a lowland Venezuelan rainforest, 1997–1999. Symbols: ↑ = successive occurrence; ⇕ = simultaneous occurrence.

Host-tree species	Number of individuals										
<i>Hymenopus heteromorphus</i>											1
<i>Rhodostemonodaphne grandis</i>						2					
<i>Ruizterania trichanthera</i>					1			1			
<i>Tachigali guianensis</i>					61			1			
<i>Qualea paraensis</i>					7						
<i>Albizia pedicellaris</i>					38					14	
<i>Matayba guianensis</i>				87	41						1
<i>Emmotum acuminatum</i>		3	1								
<i>Goupia glabra</i>	1	1	23	9		13					
	Jun 98	Jul 98	Aug 98	Sep 97	Oct 97	Nov 97	Dec 98	Jan 99	Mar 99	Apr 99	Oct 99

whereas Novotny et al. (2004) collected 17 elaterid species from 59 woody plant species in a lowland rainforest in Papua New Guinea. Compared to that, Ulyshen and Hanula (2007) sampled 22 species with flight interception traps on four tree species in the temperate deciduous forest in the USA. Trieff (2002) collected 17 species on numerous trees of *Quercus rubra* L. (Fagaceae) over several years. Sobek (2008) recorded a total of 18 elaterid species with flight interception traps from several tree species in central European deciduous forests. Thus, the species richness of arboreal click beetles seems to be comparable between temperate and tropical moist forests. In contrast, the family ranked fourth of all beetle families in terms of abundances in our canopy plot. Elaterids were also collected in high abundances in the canopy of *Vochysia divergens* Pohl in the Pantanal floodplains in Brazil, where they belonged to the fourth most abundant beetle families (Marques et al. 2002).

Species characteristics. The genus *Lacon* (Agrypninae) is represented by more than 30 species in Latin America (Chassain and Touroult 2018). We found three species of this genus in the canopy, but only *L. pollinarius* was sampled with more than 10 individuals. All but one specimen fed at the extrafloral nectaries of *R. trichanthera*.

Chalcolepidius Eschscholtz is a Neotropical genus with 63 catalogued species recorded and endemic from North, Central, and South America (Casari 2002b), but only *C. limbatus* occurred in our samples. *Chalcolepidius limbatus* is widely distributed from the West Indies through South America south to Paraguay and Uruguay (Casari 2002b). Larvae are subcortical predators in decaying wood, but little is known about the habits of the adults of this genus. They are frequently collected on foliage, flowers, over-ripe fruit, trunks, on the ground, freshly felled trees, and at plant weeps and wounds. Host records of various species of *Chalcolepidius* include *Acacia* L. (Fabaceae), *Baccharis* L. (Asteraceae), *Citrus* L. (Rutaceae), *Ficus* L. (Moraceae), *Mangifera* L. (Anacardiaceae), *Prosopis* L. (Fabaceae), *Quercus* L., *Salix* L. (Salicaceae), and *Sapium* Jacquin (Euphorbiaceae) (Johnson 2001, unpubl. observations; Casari 2002b). We sampled *C. limbatus* on four tree species (*A. pedicellaris*, *G. glabra*,

R. trichanthera, and *V. vismiifolia*) representing three plant families. This is congruent with our observation that *C. limbatus* fed on the extrafloral nectaries of two tree species in the canopy plot.

The genus *Lacais* Fleutiaux includes only three species recorded from Central and South America (Casari 2002a) with *L. glauca* recorded from Suriname, French Guiana, Brazil, and Peru. *Lacais glauca* represents the only elaterid species that could be associated with flowers, extrafloral nectar, and fruits in our study.

Aeolus sp. 1 (Fig. 1) was by far the most abundant elaterid species found in the canopy plot. The genus *Aeolus* is composed by about 200 species, naturally distributed especially in the Americas, but with a few species recorded from Africa (Casari 2006; Girard 2017). Species of this genus live on plants and are commonly associated with flowers. *Aeolus* sp. 1 fed on flowers of nine different tree species. This species moved from one flowering tree species to another flowering one and was found often there in high abundances with maximum abundances coinciding with the maximum of open flowers. It demonstrated flower constancy often throughout the entire flowering period of a flowering canopy tree.

Among the Pyrophorini, we recorded one species, *Lygelater indicus*, of a mainly Amazonian genus with five described species (Costa 1975). The range of *L. indicus* includes French Guiana in eastern Amazonia and Colombia, Ecuador, and Peru in western Amazonia (Aguirre-Tapiero and Johnson 2014). Four specimens of *L. indicus* were observed feeding on the extrafloral nectaries of *S. cf. silvestris*, one visited the flowers of *O. aff. amazonica*.

The genus *Crepidius* (Elaterinae) includes 14 species distributed from Mexico to Argentina and Bolivia (Casari 2008). The two species in our assemblage were often attracted to lights and were also observed feeding on extrafloral nectaries.

The genus *Cosmesus* comprises nearly 80 described species endemic to South America and the southern Lesser Antilles (Johnson et al. 2018). The abundant species *C. discoidalis* Kirsch was sampled on three different flowering trees from September to November 1997.

The Neotropical genus *Semiotus* Eschscholtz (Semiotinae) contains 82 described species (Wells 2007). The genus is most species-rich in Colombia, Ecuador, and Venezuela. *Semiotus ligneus* is known to occur from southern Mexico to northern Argentina and Paraguay. According to Wells (2007), it is the most commonly collected species of the genus and often attracted to lights. We observed specimens predominantly feeding on the extrafloral nectaries of *S. cf. silvestris* and *R. trichanthera* in different months.

Diet and host-use patterns. Extrafloral nectaries obviously play an essential role as diet for arboreal click beetles. Six species were observed exclusively feeding on extrafloral nectaries and five other species utilized extrafloral nectar as part of their diet. Particularly *L. obconicus* seems specialized in this kind of diet. Beetle visitation to extrafloral nectaries has been reported in a few studies (e.g., Keeler 1978; Stephenson 1982; Hespeneide 1985; Agarwal and Rastogi 2010) and was found to play an important role in the nourishment of a large proportion of the entire canopy-beetle assemblage in the lowland rainforest of Venezuela (Kirmse and Chaboo 2019). At the same time, the occurrence of active extrafloral nectaries on leaf-flushing trees largely influences the occurrence of arboreal elaterids. Up to seven species of four different subfamilies visited the same host-tree species (*R. trichanthera*) within the flushing period. A similar distribution shows three repeated observed elaterid species on *S. cf. silvestris*, which were found only during the leaf-flushing period between June and August. The importance of extrafloral nectar for the temporal and spatial distribution of Elateridae could be demonstrated for both abundant species *L. obconicus* and *S. ligneus*, both which utilized mainly extrafloral nectar and visited in similar abundances two different host-trees in different periods.

Although, *L. obconicus* seems to be specialized in the visitation of extrafloral nectaries, it could potentially be leaf-feeding. In the feeding test, specimens of this species fed on young soft leaves of *S. cf. silvestris* but not on that of *R. trichanthera* their second regularly visited host-tree species. *Lissomus obconicus* was the only elaterid species that fed on young leaves in the laboratory test environment.

Flowers represent the other important food resource for the canopy elaterids. Another six species were collected exclusively on flowers and five other species utilized flowers as part of their diet. Within the canopy plot, four different mass-flowering trees attracted up to four click beetle species. Both abundant flower visitors, *Aeolus* sp. 1 and *C. discoidalis*, were attracted to different flowering trees at different times. The most numerous *Aeolus* sp. 1 moved probably comprising the entire local population (including males and females in a balanced ratio) from one flowering tree species to another. Still, the flowering trees were visited often during the entire flowering

season demonstrating temporally restricted flower constancy. Such a constancy of visits is reported, for instance, in a dipterocarp forest with an elaterid species frequenting the flowers on consecutive days (Dayanandan et al. 1990). Though, in case of co-flowering *Aeolus* sp. 1 was often found only on one flowering tree species and was not equally distributed between accepted host trees, respectively. Apparently, *Aeolus* sp. 1 prefers distinct host trees.

Such preferences are well known and were shown particularly for nectars. The sugar content can be distinguished by taste, and some flower visitors show distinct preferences for sucrose or hexose sugars (Rusterholz and Erhardt 1997; Koptur and Truong 1998). Additionally, many studies have shown floral visitor preferences for larger nectar quantities over smaller quantities, for amino acids, and for nectars with higher sugar concentrations (Lanza 1988, 1991; Galetto and Bernadello 1992; Gardener and Gillman 2002; Carter et al. 2006). Also the extrafloral nectar feeders *L. obconicus* and *S. ligneus* probably preferred *R. trichanthera* to *S. cf. silvestris* as they were observed only on *R. trichanthera* when both trees had active extrafloral nectaries in December 1998 and January 1999. Food preferences are well documented in several other beetle taxa, for instance, in rolled-leaf hispines (Cassidinae). Schmitt and Frank (2013) showed that particularly abundant species clearly preferred some plants to others but using sporadically up to six other host-plant species. Depending on local availability of resources and plant phenology preferences may shift as indicated by *Aeolus* sp. 1 (Cowgill et al. 1993; Colley and Luna 2000; Galetto and Bernardello 2003). As not all hosts are of equal value for growth and survival or just available, polyphagous insects tend to have a hierarchy of preference (Firempong and Zalucki 1990; Thompson 1998).

The opportunistic feeding behavior of *Aeolus* sp. 1 might be caused by the unpredictability of food resources. Many tropical plants flower without regularity and synchrony (Sakai 2001). In Costa Rica, for instance, only 29% of the trees showed an annual flowering pattern (Newstrom et al. 1994). Fifty-five percent of the trees flowered more than once a year, often irregularly. The same pattern was found by Wesenberg (2004) in the canopy plot. The flowering phenology of canopy trees showed temporally non-annual reproductive patterns in about 35% of the species. While 27% of all trees had a single flowering event per year, 25% showed several flowering periods per year. Thus, flower visitors need to compensate this unpredictability with flexibility in food choice and good foraging abilities.

Diel and seasonal activity. We found click beetle species in every month of our canopy survey. The five species represented by 10+ individuals were recorded during at least four monthly periods. The abundant *Aeolus* sp. 1 was sampled twice in three and once in four consecutive months. Its occurrence in most months of the cumulative year suggests year-round activity or a possible multivoltine life cycle. The absence of distinct dry seasons in the study area and the polyphagous feeding behavior support probable activity throughout the year. In contrast, more seasonal forests or temperate regions commonly support stronger seasonality in insects (van Asch and Visser 2007; Kishimoto-Yamata and Itioka 2015). For instance, Elateridae in the Brazilian Atlantic rainforest were found active as adults only from November through January (Viviani and Santos 2012). Still, there is in general flexibility in the life cycle of different species even in temperate regions. Jewett (1946) reported that both adults and larvae of *Aeolus mellillus* (Say) in the temperate region of the USA will overwinter. Adults lay eggs for several weeks during spring and summer. Some larvae complete their development in the same season, others complete their metamorphosis in the next spring and summer. Investigations on Curculionidae in Panama showed activity patterns from species that occurred only during short periods or up to an entire year (Wolda 1988). However, most individual adult elaterids show short activity periods (Johnson 2002), but the local population still may have long activity periods. In months without records of single species those could just have fed on host-tree species, which were not included in this study. As the click beetles migrate between different host trees, they possibly visit other host trees not monitored.

This canopy elaterid assemblage is predominantly nocturnal. Distinct diel activity patterns in beetles were recorded from different taxa. In a tropical deciduous forest in Mexico, most of the 648 collected beetle specimens of 26 families were active at night (59.87%), although the 202 morphospecies constituted a similar proportion of nocturnal (41.7%) and diurnal (41.2%) species (Hernández-Camargo et al. 2017). Chrysomelidae were predominately (60.15%) active during the daytime, whereas Scarabaeidae (94.73%) showed mainly nocturnal activity. Bioluminescent species including elaterids in Brazil were mostly active at twilight and night (Viviani and Santos 2012).

Moreover, not only was the diel activity pattern distinct in these canopy species, but the species remained only during their activity phases on their host trees. Three species were found at the ground during daytime, indicating a possible stratum switch for rest. Other species might rest the day hidden elsewhere in the forest. Erwin (2013) described the separation of locations in periods of activity and resting phases in Alleculinae (Tenebrionidae). These beetles feed on tree trunks at night and spend the day in suspended dry leaves. Similar patterns are known for nocturnal click beetles that head for dark areas, dry leaves, epiphyte growth, or ground litter for diurnal periods (PJJ, unpubl. data). On the opposite, also various diurnal pollen-feeding beetles in the forest canopy are known to hide and to rest at night in the understory (Erwin 2013). Reasons that may influence such a strata change and the visitation of host trees only during the phases of activity might be attributed to the fact that tree canopies are exposed habitats. They receive high levels of solar radiation, and thus, fluctuations in relative humidity, air temperature, and wind velocities are noticeably higher in the upper canopy than in the understory (Parker 1995; Szarzynski and Anhuf 2001). Furthermore, the predator and parasite pressure may be lowered with regularly switching the locality. Particularly at lower latitudes and altitudes there is a higher predation risk for insects (Roslin et al. 2017). In addition, possible competition for food resources might be lowered. On the other hand, as elaterids usually utilize non-specific and variable food resources strata switching may be simply a reflection of their opportunism that would be advantageous for omnivores.

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