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Piotr Naskrecki ^a & Kenji Nishida ^b

^a Conservation International at Museum of Comparative Zoology ,
Harvard University , Cambridge, MA

^b Escuela de Biología , Universidad de Costa Rica , San José, Costa
Rica

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Novel trophobiotic interactions in lantern bugs (Insecta: Auchenorrhyncha: Fulgoridae)

PIOTR NASKRECKI¹ & KENJI NISHIDA²

¹Conservation International at Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA, and ²Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica

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Abstract

Lantern bugs (Fulgoridae) are large (often >35 mm), phloem-feeding insects, most diverse in humid tropical forests. They produce copious amounts of honeydew, which they forcefully eject far from their bodies, and, to date, no organisms have been known to be able to feed on it directly. Here we document a widespread occurrence of direct feeding on lantern bugs' honeydew by other organisms, including snails, to our knowledge the first case of gastropod–insect trophobiosis.

Keywords: *Euglandina*, *Fulgoridae*, insect–mollusc interactions, *Trophobiosis*

Introduction

Lantern bugs (Fulgoridae) are large (often >35 mm), phloem-feeding insects, most diverse in humid tropical forests (O'Brien 2002). Like most “Homoptera” (Auchenorrhyncha+Sternorrhyncha), lantern bugs feed on phloem of plants, and excrete the excess water and carbohydrates in the form of honeydew. Honeydew also contains amino acids (often in concentrations higher than phloem), amides, alcohols, auxins, and salts (Delabie 2001; Woodring et al. 2004). Phloem-feeding insects can produce several times their body mass of honeydew per hour, resulting in the need to mechanically eliminate it from the vicinity of the feeding insects in order to avoid fungal contamination, drowning of the insect (Gullan 1997), or attraction of predators (Bristow 1991). This apparently has led to multiple origins of trophobiotic relationships between honeydew-producing insects and other organisms (Stadler and Dixon 1999). While such direct trophobiotic relationships are best known among ants (Hölldobler and Wilson 1990; Delabie 2001), “homopteran” trophobiosis has also been documented in other Hymenoptera (Camargo and Pedro 2002), Lepidoptera (Nishio 1986; Corke 1999), mammals (Dobson et al. 2005), birds (Endersby 2005), and geckos (Fülling et al. 2001). In most cases of trophobiosis, honeydew-producing insects are small (1–15 mm), sedentary, and gregarious (Delabie 2001). Their honeydew is released slowly, and can be collected

Correspondence: Piotr Naskrecki, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138, USA. Email: p.naskrecki@conservation.org

directly off the insects, providing a stable, renewable resource to honeydew foragers. In contrast, lantern bugs are large, usually solitary, mobile insects that forcefully eject honeydew droplets that often fall meters away. This high-speed ejection of honeydew apparently precludes small-bodied trophobionts, such as ants, from collecting it. With the exception of the giant ant, *Camponotus gigas* (Latreille), possibly feeding on honeydew (Pfeiffer and Linsenmair 2000), and the possible ingestion of cuticular waxes by cockroaches (Roth and Naskrecki 2001), no trophobiotic interactions have yet been recorded in lantern bugs.

Materials and methods

Observations of lantern bugs feeding on phloem and their interactions with other organisms were conducted between March 1994 and December 2005 at two sites in the Atlantic forest of Costa Rica. The first site was located within the borders of La Selva Biological Station (10°26'N, 84°1'W, elevation 150 m), and observations there were made primarily within the station's arboretum and trails leading to it. The second site was located within Braulio Carrillo National Park near El Ceibo ranger station (10°19'40"N, 84°4'43"W, elevation 560 m). Observations at La Selva were done opportunistically throughout the year, during both dry and rainy seasons, while El Ceibo was visited only during the rainy season (November). We made 145 feeding observations of four species of Fulgoridae: *Copidocephala guttata* (White), *Enchophora sanguinea* Distant, *E. stillifera* (Stål), and *Phrictus quinquepartitus* Distant. Because most species of lantern bugs are exclusively nocturnal, observations were made primarily at night between 19:00 and 02:00 h. The only species with both nocturnal and diurnal foraging activity was *E. sanguinea*, and individuals (only males) of this species were observed feeding during both periods. Other observed species showed strictly nocturnal foraging patterns and during the day hid under loose bark, crevices on tree trunks, or, presumably, high in the canopy of the host trees. During the day the mouthparts of nocturnal species were withdrawn from the trunk, and folded between legs on the ventral side of the insect's body. Lantern bugs are oligophagous (Johnson and Foster 1986), and we found them primarily on trees *Terminalia oblonga* (Ruiz & Pav.) Steud. and *Simarouba amara* Aubl., and occasionally on *Castilla elastica* Sessé and *Ocotea cernua* (Nees) Mez.

Lantern bugs eject honeydew through the anal tube and flick individual droplets using a modified 11th abdominal tergite. We measured the speed of ejected honeydew in *E. sanguinea* and *P. quinquepartitus* by photographing it with a stroboscopic flash (Canon 580EX) of a known frequency of light pulses (199 Hz). This allowed us to photograph and calculate the distance traveled by individual droplets between the pulses.

Results

The speed of ejected droplets of honeydew for *E. sanguinea* was 0.796 m s^{-1} (every 30–60 s for a period of 3–5 s, $n=20$), and for *P. quinquepartitus*, 1.695 m s^{-1} (every 5–6 min for a period of 5–6 s, $n=10$). The speed of the honeydew ejection of the remaining species was not measured, but it is presumed to be similarly fast. We recorded five species of cockroaches, six species of moths (Noctuidae and Tortricidae), and one species of pulmonate snail regularly visiting lantern bugs to intercept streams of honeydew (Figure 1). During 145 recorded observations of feeding lantern bugs visiting trophobionts were

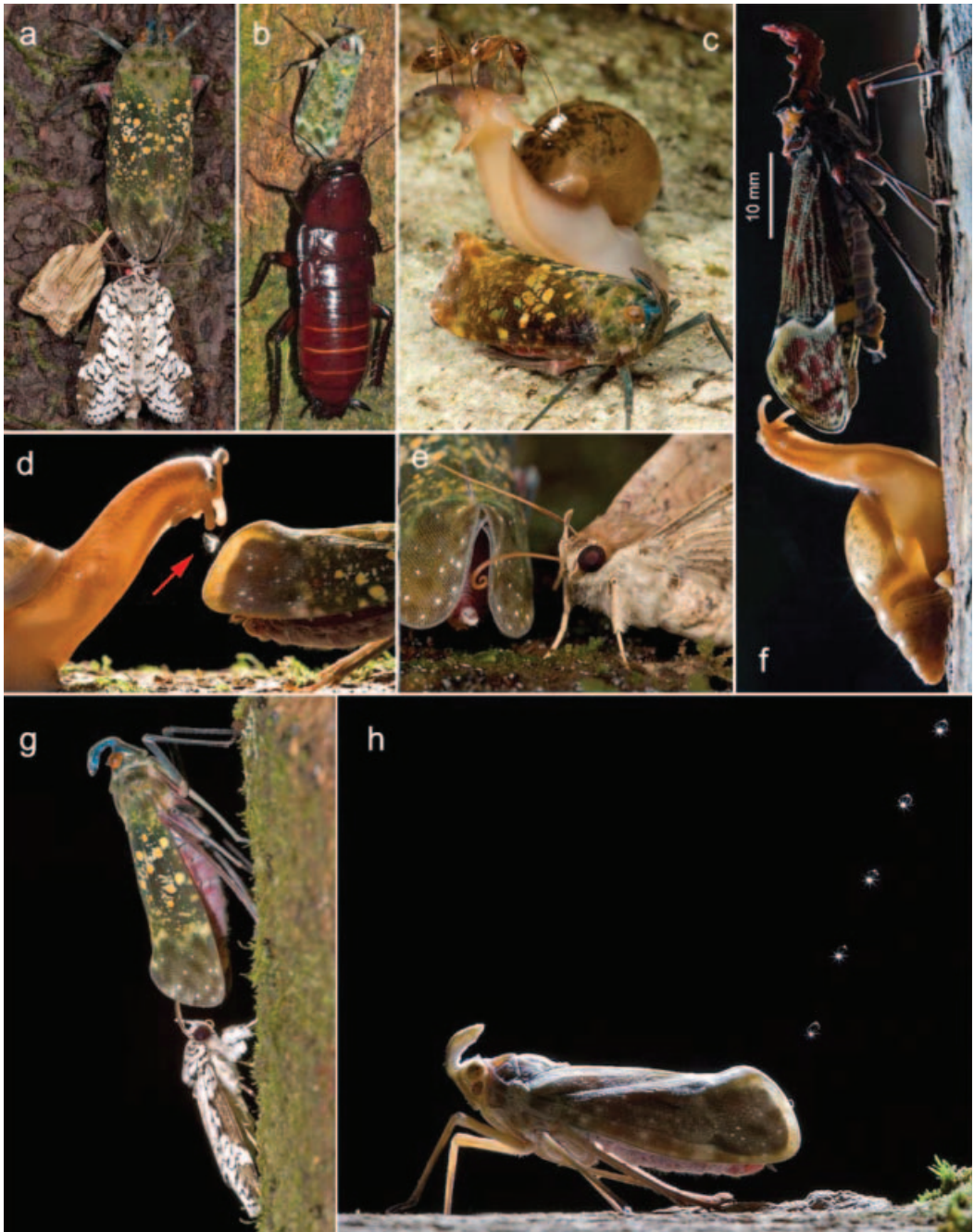


Figure 1. Trophobiotic interactions of lantern bugs (Fulgoridae) with insects and snails. (a) Lantern bug, *Enchophora sanguinea*, with two simultaneous moth guests (small *Platynota* sp. and larger *Elaeognatha argyritis*); (b) *Enchophora sanguinea* tended by cockroach, *Eurycotis* sp. 1; (c) *Enchophora sanguinea* with a trophobiotic snail, *Euglandina aurantiaca*, and kleptotrophobiotic ant, *Camponotus* sp. n.; (d) snail, *E. aurantiaca*, catching a droplet of honeydew (red arrow) ejected by *Enchophora sanguinea*; (e) moth, *Euclystis proba*, waiting for a stream of honeydew; (f) snail, *Euglandina aurantiaca*, with lantern bug *Phrictus quinquepartitus*; (g) moth, *Elaeognatha argyritis* tapping *Enchophora sanguinea* with its antennae, which elicits immediate honeydew production; (h) lantern bug *E. sanguinea* squirting honeydew—this photograph shows a single droplet exposed multiple times with a stroboscopic flash.

Table I. Visitation of lantern bugs by trophobionts.

Visitors	Lantern bugs			
	<i>Copidocephala guttata</i>	<i>Enchophora sanguinea</i>	<i>Enchophora stillifera</i>	<i>Phrictus quinquepartitus</i>
Blattodea				
<i>Eurycotis</i> sp. 1		1		
<i>Eurycotis</i> sp. 2		1		
<i>Macrophyllodromia maximiliani</i> 1				
<i>Macrophyllodromia</i> sp. 1		1		
<i>Macrophyllodromia</i> sp. 2		1		
Lepidoptera				
<i>Elaeognatha argyritis</i>		5		
<i>Euclystis proba</i>		4		
<i>Platynota</i> sp.		3		
Undet. Noctuidae		7		
Undet. Tortricidae		1		
<i>Tigridia acesa</i>		1		
Hymenoptera				
<i>Camponotus</i> sp. n. (JTL-005) ^a		8		3
Gastropoda				
<i>Euglandina aurantiaca</i>		13	1	5

Values are independent observations of trophobiotic interactions. ^aVisitations by ants resulted in feeding on honeydew only in the presence of a snail.

present in 48 (33.1%) cases (Table I). Cockroaches approached the bug from behind or from the side, and positioned their mouthparts above the tip of the bug's abdomen ($n=5$). There often was a physical contact between the cockroach and the bug, either by the cockroach palpating the bug's wings with maxillary palps, or by resting its front legs on the wings. This contact did not appear to elicit any response from the bug. On one occasion we observed two congeneric species of cockroaches (*Eurycotis*) tending the same individual of lantern bugs. Moths usually approached the bugs from the side, positioning their partially expanded proboscis to catch flying droplets ($n=20$). In most cases there was no physical contact between moths and lantern bugs. Sometimes two species of moth were seen attempting to feed at the same time. On four occasions, the moth *Elaeognatha argyritis* Hampson was seen tapping the wings of a bug *Enchophora sanguinea* with its antennae, which resulted in an immediate production of a honeydew stream. The moth resumed tapping as soon as the droplet of honeydew accumulated on its partially extended proboscis was fully imbibed, usually within 30–60 s. On one occasion an individual of *E. sanguinea* feeding during the day (approximately 10:00 h) was repeatedly visited by a nymphalid butterfly *Tigridia acesa* (L.), although the interception of honeydew droplets by the butterfly could not be observed due to the position of the insects on the tree trunk.

A common visitor to lantern bugs was a snail, *Euglandina aurantiaca* Angas ($n=19$). The genus *Euglandina* (Spiraxidae) includes predaceous snails feeding on other gastropods (Thompson 1987). The snails positioned themselves either behind or on the side of the feeding bug, and extended the anterior portion of the foot, forming a wide hood above the bug's abdominal apex. This allowed the snail to catch the stream of honeydew droplets. There was never a physical contact between the snail and the bug. If the insect changed the direction of the honeydew stream, the snail quickly adapted its position to catch it. The snails were able to detect the position of a lantern bug on the tree, and followed whenever

the insect repositioned itself. It is unclear which cues the snails use to find lantern bugs, but the bugs are capable of producing vibrational signals (personal observations), and the snails may use these to locate them. We also observed ants *Camponotus* sp. n. (JTL-005) visit lantern bugs ($n=11$), but they never fed from the stream of honeydew, most likely because the ants were too small to reach the stream. Instead, if the snail was present, the ants climbed the head of the snail and licked honeydew from its body (this behavior may be described as kleptotrophobiosis). The snails did not appear to be perturbed by the ants, and continued feeding for up to 4 h. There were never more than two ants visiting a lantern bug at any given time. Another species of ant, *Ectatomma ruidum* (Roger), was also seen feeding on honeydew accumulated on vegetation below the feeding lantern bug, but never attempted to climb the trunk to approach the bugs.

Discussion

These observations are the first evidence of widespread trophobiosis in Central American Fulgoridae, and the first known case of guest trophobionts capable of intercepting forcefully ejected honeydew in Auchenorrhyncha. This is also the first case of a trophobiotic interaction between a gastropod and an insect. A few snail species are known to be inquilines in ant colonies (Witte et al. 2002; Eguchi et al. 2005) where they feed on remnants of the ants' prey, but no direct trophobiotic relationship between honeydew-producing insects and gastropods has ever been recorded. It is likely that the evolutionary path that led to this behavior might have originated with snails scraping honeydew accumulated on vegetation below the feeding lantern bugs, and eventually following the trail to the source using gustatory, olfactory or tactile cues. Such a mechanism has been proposed to explain the origin of ant-homopteran interactions (Stadler and Dixon 1999).

Endnote

During the preparation of this manuscript a possible trophic interaction between lantern bugs, slugs, and ants (*Leptothorax* sp.) was observed in Papua New Guinea, indicating that the behavior described above may be even more widespread (M. Janda, personal communication).

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