

SURVIVORSHIP OF IMMATURE STAGES OF *EURYPEDUS NIGROSIGNATUS*  
BOHEMAN (CHRYSOMELIDAE: CASSIDINAE: PHYSONOTINI)  
IN CENTRAL PANAMA

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**Abstract**

Larvae of the leaf beetle *Eurypedus nigrosignatus* Boheman carry fecula and cast skins on their dorsa forming a protective device, commonly called a fecal shield. Survival from egg to adult eclosion, natural enemies, and relation to its hostplant, *Cordia curassavica* (Jacq.) Roem. and Schult. (Boraginaceae) were assessed. Overall survival was 2%; eggs and fourth instars were less susceptible to enemies than were early larval stages and pupae. Predation accounted for the low survival of larvae, whereas parasitism for a low success rate of pupae. Six different predators including three spiders (Arachnida), a pentatomid, a reduviid (Heteroptera), and an ant (Hymenoptera) were observed. Reared parasitoids included a chalcidid (Hymenoptera) and a tachinid (Diptera). The fecal shield increases in size throughout larval development; however, the shield of prepupal individuals is partially lost. Shield chemical content very closely reassembles that of a particular host plant. Although the lower terpenoid concentration (per weight) in shields decreases with larval development, bigger shields as a unit contain larger amounts. Adults spend the Panamanian dry season buried in the ground directly under host plants. *Eurypedus nigrosignatus* is under intense selective pressures in Central Panama.

**Resumen**

Las larvas del escarabajo *Eurypedus nigrosignatus* Boheman acumulan heces y mudas sobre su dorso formando un artefacto defensivo llamado el manto fecal. La sobrevivencia desde la deposición de huevos hasta la eclosión de adultos, los enemigos naturales, y su relación con su planta hospedera *Cordia curassavica* (Jacq.) Roem. and Schult. (Boraginaceae) fue evaluada. La sobrevivencia total fue de 2%; los huevos y el cuarto estadio fueron menos susceptibles a los enemigos que los estadios larvales más jóvenes y las pupas. La depredación fue el principal factor en la sobrevivencia baja de las larvas, mientras que el parasitismo por el bajo rendimiento de las pupas. Se observaron seis depredadores diferentes incluyendo tres especies de arañas (Arachnida), un pentatomido, un reduviido (Heteroptera) y una especie de hormiga (Hymenoptera). Los parasitoídes criados en el laboratorio incluyen un chalcido (Hymenoptera) y un taquínidio (Diptera). El manto fecal aumenta de tamaño a través del desarrollo larvario; sin embargo, el manto se pierde en los estados prepupales. El contenido químico de los mantos es muy similar al de plantas hospederas particulares. Aunque la concentración (por peso) de terpenoides en los mantos disminuye con el desarrollo larvario, los mantos más grandes como una unidad contienen cantidades más altas. Los adultos pasan la temporada seca panameña enterrados en el suelo alrededor de las raíces su planta hospedera. *Eurypedus nigrosignatus* está bajo presiones selectivas intensas en Panamá central.

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Many Cassidinae are free-living on exposed plant parts (Windsor *et al.* 1992). Due to their preference for apical foliage, their presence tends to be predictable, and their vulnerability to enemies high (Jeffries and Lawton 1984; Cox 1994). A number of studies indicated that cassidine larvae suffer low survivorship rates in their natural habitats (Olmstead and Denno 1993; Becker and Pires Freire 1996; Windsor 1987).

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Natural enemies of cassidine larvae and pupae have been reviewed (Olmstead 1996, and references therein). Ants and hymenopterous parasitoids have a great impact on egg mortality; heteropterans and spiders are major predators of larvae and pupae; ant attacks on larvae are considerable; hymenopterans, especially euplophids and chalcidids, and dipterous parasitoids are recorded as major enemies of cassidine larvae and pupae. Compared to other Chrysomelidae, parasitism is highest in the Cassidinae (Cox 1996).

Larvae of many cassidine beetles accumulate fecula and exuviae on the caudal process of the eighth abdominal segment (*cf.* Stehr 1991:569) to construct a dorsal structure. This remarkable structure, commonly called a fecal shield, varies considerably in shape and size (Muir and Sharp 1904; Fiebrig 1910; Engel 1935; Gressitt 1952; Buzzi 1988; Windsor *et al.* 1992; Chaboo and Nguyen 2003). By reflexing the abdomen, the larva can direct its shield in any direction. The shield is believed to function as mimicry of bird droppings (Balsbaugh 1988), and to serve against desiccation (Engel 1935; Olmstead and Denno 1993; Eisner and Eisner 2000). The shield also functions as a physical barrier against predators (Fiebrig 1910; Engel 1935; Eisner *et al.* 1967; Olmstead and Denno 1993; Eisner and Eisner 2000; Mueller 2002). More recently, evidence supports a function of the fecal shield as a chemical barrier (Gómez *et al.* 1999; Vencl *et al.* 1999). Borowiec (1999) recognized three *Eurypedus* species (tribe Physonotini), all in the New World. The genus' distribution includes Colombia, Guatemala and Nicaragua; and no hostplant was noted. Windsor *et al.* (1992) reported *Eurypedus* sp. for Panama on *C. spinescens* L. Recently, this species was identified as *E. nigrosignatus* Boheman (D. Windsor, pers. comm.). Its distribution within the country is still unknown. I follow the nomenclature proposed by Borowiec (1999), *E. nigrosignatus*. Its host plant *Cordia curassavica* (proposed by this study) is found in all provinces in Panama. Its foliage contains at least three monoterpenoid compositional types and a number of sesquiterpenes, whereas that of *C. spinescens* only contains sesquiterpenes in small amounts (Gómez *et al.* 1999).

Tortoise beetle species feeding on the plant genus *Cordia* construct shields of diverse forms and textures (Windsor *et al.* 1992). Larvae of *E. nigrosignatus* build hairy appendages formed by long, thin filaments glued to the base of the caudal process, where cast skins are also retained (Fig. 1B).

This paper examines aspects of the biology of *E. nigrosignatus*, specifically, construction of the shield, natural enemies and its chemical relation with its host plant.

## Materials and Methods

**Study Site.** Field observations were carried out at the beginning of the rainy season (May–July) during 1996, 1998, and 1999 at the Chepo field site (9°10'N, 79°05'W), 60 km East of the Smithsonian Tropical Research Institute (STRI) in Panama City, and during 2000 at Ft. Kobbe (8°44'N, 79°35'W), 6 km West of STRI. *Eurypedus nigrosignatus* was found on *C. curassavica* at the two sites and also at El Llano-Cartí (9°18'N, 78°57'W), 75 km East. All three locations are in Panama Province, Republic of Panama. This beetle species was not observed during the rainy seasons noted above at Campana (8°43'N, 79°58'W), 70 km West, Panama Province, along an altitude gradient from around 200 to 1,000 m, and around Pedasi (8°38'N, 79°74'W), 350 km Southwest, Los Santos province, where *C. curassavica* is abundant.

**Study Organisms.** *Eurypedus nigrosignatus* exclusively occurs on *C. curassavica* in Central Panama. *Cordia curassavica* is a deciduous shrub, 2–4 m tall, common from sea level to 2,000 m that grows in very disturbed habitats (Miller 1988) all over the country, usually in open fields exposed to intense sunlight and weather conditions. In the field at Chepo, the mid-day temperature, on a sunny day, reaches 40°C and the air humidity can be as low as 40% and as high as 99%. During the dry season,



**Fig. 1.** A) Eggs of *Eurypedus nigrosignatus* deposited in masses (five to 29 eggs) on the abaxial leaf side. B) Second and third instars feeding; C) adults mating; D) pentatomid preying on a third instar. Note that the bug is piercing the larva from the side; thus, avoiding the shield; E) Spider preying on an adult.

*C. curassavica* individuals tend to lose most of their leaves, especially those below the apical ramets. The production of new leaves increases rapidly at the beginning of the rainy season and is accompanied by an increase in the reproductive behavior, oviposition and larval feeding of most Cassidinae in Panama (Windsor *et al.* 1992). During the dry season (January to April), insect activity is almost nil.

Predation was assessed visually; parasitism was evaluated by taking pupae to the laboratory and waiting until parasitoids emerged. Enemies and potential enemies of *E. nigrosignatus* were identified by D. Quintero, Curator of the "Museo de Invertebrados G.B. Fairchild" of the University of Panama, in Panama City, where voucher

specimens were deposited. Beetle species were identified by comparison to specimens identified by Donald Windsor (STRI) deposited in the STRI insect collection. Plant species were identified by type examination at both the Herbarium of the University of Panama and STRI.

**The Fecal Shield.** Larvae or larval broods and with branches of their host plants were transported to the laboratory, in separate plastic bags (Zip-Lock™). Each larva with its shield was weighed, the fecal shield removed with forceps, and larva and shield weighed separately. Weight relations were analyzed by a one-way anova.

**Survival in the Field.** *Eurypedes nigrosignatus* survival on its host plant was evaluated in the field by observing 12 egg masses ( $19.8 \pm 5.3$  eggs; total eggs = 258; range = 11–29) on separate plants. Predation was evaluated by scanning the vegetation for egg masses and larval groups every 2–6 days and noting the remains of fecal shields attached to withered bodies or left on the leaf surface. Parasitism was evaluated by scoring the numbers of parasitoids emerging from pupae in the laboratory. Cumulative survival was calculated by dividing the number of surviving individuals reaching the next stage by the starting number of individuals in the previous stage, times the survival percentage of the previous stage; the first development stage (egg) was taken to be 100% (Cornell and Hawkins 1995). The daily disappearance was calculated for seven of 12 egg masses ( $20.6 \pm 6.4$  eggs; 144 eggs in total).

## Results

**Life History.** Egg masses are laid usually below most apical leaves, on the abaxial leaf side (Fig. 1A); more than one egg mass may occur on the same leaf; the number of eggs per mass ranges from five to 29 ( $n = 24$ ).

Larvae normally hatch from the egg tip after cutting the area just below the tip, and then climb down to the leaf surface. The larval body is completely pale yellow upon eclosion. Within 20 minutes, the head and legs darken, while the rest of the body turns darker yellow. Upon hatching, neonate larvae move generally to the most apical foliage, usually young, tender leaves (Fig. 1B). Larvae feed usually as solitary individuals on the adaxial foliar surface, and upon feeding, start building their fecal shields by successively attaching fine fecal strands to the caudal fork and later by adding exuvia (Fig. 1B). Newer strands are glued onto the base of previous molted and retained exuvia. Emission of fine fecal filaments is accomplished through the extrudable anus, which is rotated by the larva to deliver the filament toward the selected site, resulting in a brush-looking, but symmetrical structure. Larvae stop feeding, extrude and contract the anus upright while the filament is being delivered. When shields are removed in the field, larvae tend to rest on the abaxial leaf side and build a new shield, usually made only of fecal strands, within 15–20 hours. When larvae reach the fourth developmental stage, the shield starts collapsing. Prepupal individuals (fifth instars) are shieldless; pupae use the last molt as a gluing element to attach themselves onto the abaxial leaf surface. Throughout its development, larvae are exposed to harsh weather conditions (heat, light, low and high humidity), and are able to remain on the upper leaf surface even during rain showers.

At Chepo *E. nigrosignatus* adults have both their mating (Fig. 1C) and oviposition peaks from May–July, and oviposition can last until late November. Adults appear to spend the dry season buried in the ground. During excavation of hostplant underground parts in April 1999, two adults emerged from the soil immediately adjacent to hostplant roots.

Other chrysomelids found on *C. curassavica* included two cassidine species and *Ophraea* sp. (Galerucinae). Larvae of the latter were found very often with *E. nigrosignatus* larvae on the same foliage.

Table 1. Weight (mg  $\pm$  SD) of three *Eurypedus nigrosignatus* instars.<sup>1</sup>

Instar	n	Larval body	Shield	Weight ratio <sup>2</sup> (shield/body)
First	44	4.77 $\pm$ 2.28	2.15 $\pm$ 1.10	0.46 $\pm$ 0.12 a
Second	40	13.56 $\pm$ 2.89	5.45 $\pm$ 1.26	0.41 $\pm$ 0.10 ab
Third	18	23.24 $\pm$ 3.62	8.30 $\pm$ 1.37	0.36 $\pm$ 0.07 b

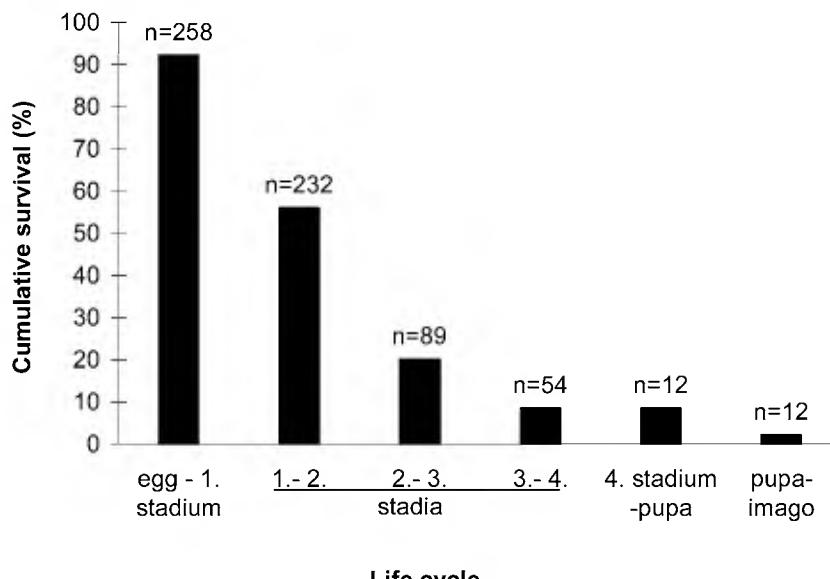
<sup>1</sup> Fourth instars were scarce, and most had a very reduced shield.

<sup>2</sup> ANOVA ( $n = 102$ ;  $F = 5.626$ ;  $P < 0.005$ ). Different letters indicate statistically significant difference between means (Tukey *t*-test,  $P < 0.05$ ).

**The Fecal Shield.** The weight and size of the fecal shield increased with larval growth (Table 1), but not proportionally. Third instars grew faster in relation to their shields, as indicated by the weight ratio of shield to body, which differed significantly from first instars. The shield of fourth instars of *E. nigrosignatus* is often reduced; therefore, data for this stage was not included in calculations.

**Survival.** Egg development time ranged from 8–12 days, larval developmental time (between egg hatch and pupation) was 12–16 days. The pupal stage lasted 8–12 days to eclosion. Total development time from egg deposit to adult eclosion was  $34 \pm 2$  days. Cumulative survival is shown in Figure 2. Overall survival from egg hatching until adult eclosion was 2%. First (57%), second (34%) and third (44%) instars, and pupae (25%) had lower percentage survival than eggs (97%) and fourth instars (100%). All larvae reaching the fourth stadium pupated (100%), whereas 25% became teneral adults. Eight pupae were parasitized, and one failed to eclose.

The daily larval disappearance averaged  $9.5 \pm 10.6$  (range 23.0–0.7) larvae per day for 7 broods. Three broods (19, 23, 29 individuals) of 1st and 2nd instars on adjacent



**Fig. 2.** Cumulative survival (%) for *Eurypedus nigrosignatus* larvae in the field. Numbers on bars indicate the sample size at each stadium.

Table 2. Natural enemies of *Eurypedus nigrosignatus* (larval and adult predation, and pupal parasitism were evaluated).

Larval enemies	Pupal parasitoids
Hymenoptera	Hymenoptera
Chalcididae (1)	Chalcididae (1)
Vespidae (2, *)	
Formicidae (3)	
Diptera	Diptera
Tachinidae (4)	Tachinidae (4)
Sarcophagidae (*)	
Heteroptera	
Reduviidae (5)	
Pentatomidae (6)	
Coleoptera	
Carabidae (**)	
Araneae	
Oxyopidae (7)	
Araneidae (*)	
Thomisidae (8)	
Salticidae (9)	
Amaroubiidae (*)	
Orthoptera	
Mantidae (**)	

(1) *Brachymeria* sp. and *Conura* sp.; (2) *Polybia occidentalis*; (3) *Ectatomma ruidum*; (4) unidentified fly; (5) *Sinea* sp.; (6) unidentified pentatomid; (7) *Oxyopes* sp. and *Peucetia* sp.; (8) two unidentified spiders; (9) unidentified spider. (\*) Potential enemies of larvae and pupae found in the field, but not by actual predation include the vespid *Polistes* sp., dipterid flies, spiders. (\*\*) Potential egg predators include the mantid *Pseudomnioteryx* sp. and a carabid beetle.

plants disappeared completely within a day. The numbers of the other four broods (11, 15, 20, 27 individuals) decreased steadily until the fourth stadium. Fourth instars performed better, although an entire brood of third instars ( $n = 20$ ) survived until pupation. All four groups had parasitized pupae.

**Natural Enemies.** Natural enemies were assessed by direct observation (Table 2). The principal pedestrian enemies were spiders (Oxyopidae, Thomisidae, and Salticidae) and reduviid bugs. Flying enemies included polistine wasps, parasitic flies, and pentatomids. The reduviid *Sinea* sp. attempted to prey upon a first instar, but was deterred by the larva's shield. The reduviid moved backwards and cleaned its proboscis. After four attempts, it moved toward a dead larva a couple of centimeters from the living one and introduced its proboscis into its body. Seven young dead larvae were found on the foliage of this shrub, however, the cause of mortality could not be determined. These dead, dark colored larvae laid on the adaxial surface. The wasp *Polybia occidentalis* Holmgren preyed upon *E. nigrosignatus* larvae by grabbing a larva by its shield and removing the shield during wrestling. After a few minutes the wasp abandoned the shield; by then, the larva had escaped to the lower part of the shrub. *Eurypedus nigrosignatus* larvae start moving their shields in the direction of an approaching object, for instance, the finger or hand of the observer, 20 cm away. On occasion, several larvae would jerkily move their fecal shields simultaneously at the approach of a disturbance. An attack from the rear or side can be more successful. A pentatomid pierced a third instar from the side (Fig. 1D); oxyopids seized larvae from the side and the rear. Spiders trapped larvae by direct attacks or by using the web to impede larval movement. Although no predators were observed attacking neonate larvae, spider webs on the leaf

surface where eggs had been laid, or intermingled along leaf petioles obstructed neonate larvae from walking up to their feeding site (up to 15 cm to eat newly expanded leaves) resulting in death. Spiders were also adult predators (Fig. 1E).

At least six ant species occur on *C. curassavica* shrubs: *Camponotus* sp., *Tapinoma* sp., *Wasmannia* sp., *Crematogaster* sp. and *Paratrechina longicornis* Latreille and *Ectatomma ruidum* L. *Camponotus* sp. often approached the buccal area of larvae, presumably to feed on fluids released from plant tissue wounds made during feeding. *Crematogaster* sp. and *Tapinoma* sp. also fed on wounded plant tissue; they occasionally bit (or touched) the larval body or the shield as did *Camponotus* sp.; the larva moved its shield toward this body area. When the disturbance became more frequent, the larva moved away from the ant and the ants did not search further for them. Ant interactions were more likely to occur when larvae moved suddenly and the ant detected their presence. While *Wasmannia* sp. was present, it did not interact with *E. nigrosignatus* larvae. *Paratrechina longicornis* also was common, but was associated with sap oozing from plant tissue wounds. Except for *E. ruidum*, other ants were not observed preying upon larvae.

*Camponotus* sp. chased spiders and flying insects away, e.g., tachinid flies and chalcidid wasps, especially when these insects landed on leaves with larvae and/or approached *E. nigrosignatus*. *Camponotus* sp. walked on and around larvae, including neonates without shields. On the other hand, *E. ruidum* seized *E. nigrosignatus* larvae, and after removing the shield, carried them to their underground nest, next to shrubs.

Potential enemies were the wasp *Polistes* sp., unidentified sarcophagid flies (Diptera), an unidentified carabid beetle (Carabidae), and the lizard *Anolis auratus* (Daudin). The latter was noticed on a plant hosting one of the three larval broods that disappeared within a day; many fecal shields were found hanging on the abaxial leaf surface and the author suspects the lizard ate them.

Parasitoids included tachinid flies and chalcidid wasps. The chalcidid *Brachymeria* sp. emerged from almost all parasitized pupae. The chalcidid *Conura* sp. was another parasitoid that swarmed frequently in the same micro-habitat.

Although egg predation was not observed at Chepo, disappearance of three egg masses within 2–3 days was noted at Kobbe during 2000. However, it was not quantified.

## Discussion

Egg mortality was low and resulted from failure to hatch rather than from predation or parasitism. Hatching failure has been reported as a cause of egg mortality in *Acromis sparsa* (Boheman) (Windsor 1987). In this species, undeveloped eggs (60%) were more common in habitats where egg parasitism was high. On the other hand, eggs of a number of chrysomelid species are well defended, both physically and chemically (Hilker 1993; 1994 and references therein). Contrary to other cassidine species (Olmstead 1996; Becker and Pires Freire 1996), egg survival contributed greatly to the overall survival of *E. nigrosignatus* at Chepo. However, predation assessment in other sites should be carried out.

The survival of early larval stages of *E. nigrosignatus* dramatically decreased in natural settings; smaller larvae tended to be more susceptible to predation than bigger ones. High natural mortality levels have been reported for other cassidine larvae in the field (Simmonds 1949; Williams 1950; Carroll 1978; Windsor 1987; Olmstead and Denno 1993; Becker and Pires Freire 1996). Small larvae of *Charidotella bicolor* (F.) carrying an exuvial shield and *Deloyala guttata* (Oliver) with a fecal “pad” were killed more often by predators than were bigger larvae even without fecal shields (Olmstead and Denno 1993). Similarly, small larvae of *Physonota alutacea* Boheman, which does

not construct shields, were more frequently removed by predating ants (Williams 1950). Shielded larvae are generally less prone to predation than deshielded ones (Olmstead and Denno 1993; Gómez 1997; Vencl *et al.* 1999; Mueller 2002). In general, lower survival rates, mostly due to natural enemies, have been reported for early instars of a number of native exophytic insects (Cornell and Hawkins 1995).

Ants of *Camponotus* sp., *P. longicornis*, *Tapinoma* sp. and *Wasmannia* sp., were found co-inhabiting with *E. nigrosignatus* larvae. This finding contrasts with reports of *Camponotus zoc* Forel, *C. sexguttatus* (F.), and *P. longicornis* as predators of *P. alutacea* larvae in Trinidad (Simmonds 1949). *Tapinoma* sp. and *Wasmannia* sp. have not been reported as enemies of either cassidines or chrysomelids. The interactions of ants with *E. nigrosignatus* was related to sap oozing from plant tissue wounds produced by beetle larvae. The ant *E. ruidum* preyed on *E. nigrosignatus* larvae upon removal of the shield. In a laboratory arena, the shield elicited an aggressive response from the ant *Myrmica rubra* L. (Gómez 1997; Mueller and Hilker 2000). Predation by vertebrates upon cassidines may be higher than is generally assumed, and may be of great impact (Olmstead 1996). The sudden disappearance of *E. nigrosignatus* larvae in the field may be explained by this.

Parasitism accounted for almost half of the pupal mortality of *E. nigrosignatus*. It is inferred that pupal parasitoids entered their host during its larval stages in the field. Removing pupae from the field may have contributed to lowering their exposure to enemies. Thus, parasitism rates in pupae could be higher than those reported here. It has been suggested that cassidine species carrying a reduced shield or no shield are more prone to parasitism (Windsor 1987). Late instars moved more slowly, carried a reduced shield, and most survived until pupation; however, pupae were highly parasitized. Reduction or loss of the larval fecal shield seems to be common during prepupal stages in the Cassidinae (Olmstead and Denno 1993; D. Windsor, pers. comm.). *Brachymeria* sp., *Conura* sp., and tachinid flies were larval parasitoids of *E. nigrosignatus*. The chalcid *Conura* sp. has been described as a parasitoid of cassidine larvae and pupae, whereas *Brachymeria* sp., is an egg parasite (Heron 1992 as cited by Olmstead 1996). Tachinid flies have been reported as parasitoids of both chrysomelid eggs and immatures, including those of cassidines (Olmstead 1996). Larval and pupal parasitoids produce high mortality in the Cassidinae (Muir and Sharp 1904; Rolston *et al.* 1965; Hawkeswood 1982; Windsor 1987; Olmstead 1996). Larvae of the Cassidinae are more frequently parasitized than are other Chrysomelidae (Cox 1994).

Predation of early instars was the main cause of the dramatic decrease in its overall survival, whereas parasitism largely contributed to pupal mortality. My observations indicate that spiders, wasps and heteropterans were major predators of *E. nigrosignatus* larvae in the field; chalcidid flies were the main parasitoids of larvae and pupae. Survival from egg to adult of *E. nigrosignatus* was quite low in Central Panama indicating that selective pressures on this beetle species are intense. Low survival rates have been reported for other cassidines in natural conditions (Windsor 1987; Olmstead and Denno 1993; Becker and Pires Freire 1996; Olmstead 1996). Major reported predators of the Cassidinae are heteropterans and spiders, whereas euplidids and chalcidiids (Hymenoptera) are important parasitoids (Olmstead 1996).

An important novel observation about the biology of *E. nigrosignatus* is that adults bury themselves around their hostplants during the dry season in Central Panama. The author is not aware of any other report on this matter within the Cassidinae.

*Eurypodus nigrosignatus* was found exclusively feeding on *C. curassavica* at three sites. During fieldwork in different seasons, this beetle species was not found on *C. spinescens* as reported previously (Windsor *et al.* 1992). Although these two plants species may be confused in the field, there are some morphological and ecological traits to differentiate them (Miller 1988). For instance, *C. curassavica* has lanceolate leaves,

and terminal, spicate inflorescences. It also differs from *C. spinescens* in the architecture, leaf color, and their preferred habitat. Whereas the former is found most often in open, dry areas, the latter is commonly found in moist ditches along roadsides. Other distinguishable feature is the peduncle adnate to the petiole in *C. spinescens*. A distinction is the remarkable difference in their volatile terpenoid composition and content (Gómez *et al.* 1999), which can be easily recognized by squeezing a leaf and smelling it. From this study, *E. nigrosignatus* can be considered a specialist on *C. curassavica* to the point that this particular host plant influences the chemical composition of the fecal shield (Gómez *et al.* 1999).

A growing body of evidence indicates that the fecal shield may be a defensive adaptation to predation (Vencl and Morton 1999). Despite the low survival of *E. nigrosignatus*, its shield made it possible for larvae to become invisible to potentially predatory ants, and to distract predatory wasps and escape. Upon contact, the shield functioned to deter predacious bugs. The hairy fecal shield of *E. nigrosignatus* contains lower terpenoids (volatile monoterpenes and sesquiterpenes) derived from the host plant (Gómez *et al.* 1999).

Upon hatching, *E. nigrosignatus* neonates frequently move upward to the most apical foliage, differing from other cassidine neonates (Engel 1935; Hawkeswood 1982; Windsor 1987), and start feeding on the adaxial leaf surface. A similar behavior was observed in neonate larvae of *Galeruca lineola* (Galerucinae), which tend to move upward searching for physical shelter in young rolled leaves of its host plant (Larsson *et al.* 1997). This behavior may also be due to nutritional demands, since young leaves are tender and usually contain more nutrients and water than mature leaves (Coley 1983; Ohmart *et al.* 1985). Young leaves of *C. curassavica* contain higher amounts of lower terpenoids than do mature ones, and glandular trichomes containing terpenes are more accessible on the upper leaf surface (Gómez *et al.* 1999). Specialist herbivores usually feed on young leaves containing higher terpene concentrations (Larsson *et al.* 1986; Björkman and Larsson 1991; Selman 1994). While the fecal shield of *E. nigrosignatus* increases in weight during larval development, the content of lower terpenoid per gram decreases (Gómez *et al.* 1999). However, as a unit, a bigger shield contains higher terpenoid amounts. Shield contents repelled an ecologically relevant predator, the ant *Myrmica rubra* L. (Gómez *et al.* 1999). Moving to the foliage apex may have a negative effect on the larval survival since encounters with potential enemies may be more frequent (Jeffries and Lawton 1984; Cox 1994) due to its exposure to flying enemies. Thus, building a structure with potentially deterrent substances as soon as possible may be beneficial for the larvae.

On the other hand, carrying a defensive structure with waste material containing volatile compounds may be a drawback (Olmstead 1994, 1996) due to the risk of being discovered by enemies that use air-borne cues (kairomones) to find their prey (van Leerdam *et al.* 1995; Alborn *et al.* 1994; Meiners *et al.* 2000). Jerkily swatting the fecal shields simultaneously, as *E. nigrosignatus* larvae do at the approach of a disturbance, may increase the release of volatiles into the air (Olmstead 1994). In this case, carrying a reduced fecal shield as fourth and fifth instars may contribute to decreased parasitism rate by eliminating kairomones released from it. Releasing volatiles into the air from glandular trichome destruction by beetle feeding may also have an adverse effect. Whether or not volatile release affects beetle survival is still unclear.

There is evidence to suggest that the shield of *E. nigrosignatus* retains volatiles. Shields left for two weeks at room temperature retained 85% of volatile terpenes (unpubl. data), suggesting that during larval development (2 weeks), shields offer a stable matrix to hold these compounds. Moreover, most volatile monoterpenes emitted from freshly removed shields during a 6-hr air collection experiment were in an average ratio of 20:1 with respect to total shield concentration (unpublished data),

indicating that emission from the shield can be little, without implying that it is ecologically irrelevant. The shield is hard and stable, what makes it insoluble in apolar and polar solvents (Gómez 1997) and resistant to severe weather conditions ranging from heavy rains to high daily temperatures (see site description above). It contains a very complex mixture of high molecular weight substances that may provide a matrix to solubilize volatile terpenes and slow down their release, contributing to the defensive function of the shield and minimizing encounters with searching enemies. However, these compounds do not account for the remarkably stability of the fecal shield of some Cassidinae.

The heterogeneity of shapes and textures of the cassidine fecal shield is remarkable (Muir and Sharp 1904; Fiebrig 1910; Engel 1935; Gressitt 1952; Buzzi 1988; Windsor *et al.* 1992; Chaboo and Nguyen 2003). A close evaluation of the natural history of each species, enemy types, and physical and chemical traits of fecal shields and host plants may help to explain the role of the shield in the striking radiation of tortoise beetles.

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### Literature Cited

- Alborn, H. T., W. J. Lewis, and J. H. Tumlinson.** 1995. Host-specific recognition kairomone for the parasitoid *Microplitis croceipes* (Cresson). *Journal of Chemical Ecology* 21: 1697–1708.
- Balsbaugh, E. U.** 1988. Mimicry and the Chrysomelidae [pp. 261–285]. In: *Biology of Chrysomelidae* (P. Jolivet, E. Petitpierre, and T. H. Hsiao, editors). Kluwer Academic Publishers, Dordrecht. 615 pp.
- Becker, M., and A. J. Pires Freire.** 1996. Population ecology of *Gratiana spadicea* (Klug), a monophagous cassidine on an early successional Solanaceae in Southern Brazil [pp. 271–287]. In: *Chrysomelidae Biology, Volume 1, Ecological Studies* (P. H. A. Jolivet and M. L. Cox, editors). SPB Academic Publishing, Amsterdam. 443 pp.
- Björkman, C., and S. Larsson.** 1991. Pine sawfly defense and variation in host plant resin acids: a trade-off with growth. *Ecological Entomology* 16:283–289.
- Borowiec, L.** 1999. A world catalogue of the Cassidinae (Coleoptera: Chrysomelidae). *Biologica Silesiae*, Wroclaw. 476 pp.
- Buzzi, Z. J.** 1988. Biology of Neotropical Cassidinae [pp. 559–599]. In: *Biology of Chrysomelidae* (P. Jolivet, E. Petitpierre, and T. H. Hsiao, editors). Kluwer Academic Publishers, Dordrecht. 615 pp.
- Carrol, C. R.** 1978. Beetles, parasitoids and tropical morning glories: a study in host discrimination. *Ecological Entomology* 3:79–85.
- Chaboo, C. S., and T. C. Nguyen.** 2003. Immatures of *Hemisphaerota palmarum* (Bohemian), with discussion of the caudal processes and shield architecture in the tribe Hemisphaerotini (Chrysomelidae: Cassidinae). In: *New contributions to the biology of Chrysomelidae* (P. Jolivet, J. Santiago-Blay, and M. J. Schmitt, editors). Kluwer Academic Press (in press).
- Coley, P. D.** 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–233.
- Cornell, H. V., and B. A. Hawkins.** 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *American Naturalist* 145:563–593.

- Cox, M. L. 1994.** The Hymenoptera and Diptera parasitoids of Chrysomelidae [pp. 419–467]. In: Novel aspects of the biology of Chrysomelidae (P. H. Jolivet, M. L. Cox, and E. Petitpierre, editors). Kluwer Academic Publishers, Dordrecht. 582 pp.
- Cox, M. L. 1996.** Insect predators of Chrysomelidae [pp.23–91]. In: Chrysomelidae biology (P. H. A. Jolivet and M. L. Cox, editors). SPB Academic Publishing, Amsterdam. Vol. 2. 465 pp.
- Eisner, T., E. van Tassell, J. Carrel, L. B. Hendry, and J. Meinwald. 1967.** Defensive use of a “fecal” shield by a beetle larva. *Science* 158:1471–1473.
- Gómez, N. E. 1997.** The fecal shields of larvae of tortoise beetles (Cassidinae: Chrysomelidae): a role in chemical defense using plant-derived secondary metabolites. Dissertation, Naturwissenschaftliche Fakultät, Technische Universität Carolo-Wilhemina zu Braunschweig. 124 pp.
- Gómez, N. E., L. Witte, and T. Hartmann. 1999.** Chemical defense in larval tortoise beetles: essential oil composition of fecal shields of *Eurypedus nigrosignatus* and foliage of its host plant, *Cordia curassavica*. *Journal of Chemical Ecology* 25:1007–1027.
- Gressitt, J. L. 1952.** The tortoise beetles of China (Chrysomelidae:Cassidinae). *Proceedings of the California Academy of Science* 27:433–592.
- Hawkeswood, T. J. 1982.** Notes on the life history of *Aspidomorpha maculatissima* Boheman (Coleoptera:Chrysomelidae;Cassidinae) at Townsville, North Queensland. *Victorian Naturalist* 99:92–101.
- Heron, H. 1992.** Cycloalexy in two South African tortoise beetles (Chrysomelidae:Cassidinae). *Chrysomela* 27:3–4.
- Hilker, M. 1993.** Chemische Ökologie juveniler Entwicklungsstadien der Blattkäfer (Coleoptera, Chrysomelidae). Bayreuther Forum Ökologie. Universität Bayreuth, Bayreuth. Band 5. 186 pp.
- Hilker, M. 1994.** Egg deposition and protection of eggs in Chrysomelidae [pp.263–276]. In: Novel aspects of the biology of Chrysomelidae (P. H. Jolivet, M. L. Cox, and E. Petitpierre, editors). Kluwer Academic Publishers, Dordrecht. 582 pp.
- Jeffries, M. J., and J. H. Lawton. 1984.** Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23:269–286.
- Larsson, S., Haeggstrom, and R. F. Denno. 1997.** Preference for protected feeding sites by larvae of the willow-feeding leaf beetle *Galerucella lineola*. *Ecological Entomology* 22: 445–452.
- Meiners, T., C. Westerhaus, and M. Hilker. 2000.** Specificity of chemical cues used by a specialist egg parasitoid during host location. *Entomologia Experimentalis et Applicata* 95:151–159.
- Miller, J. S. 1988.** A revised treatment of Boraginaceae for Panama. *Annals of the Missouri Botanical Garden* 75:456–521.
- Mueller, C., and M. Hilker. 1999.** Unexpected reactions of a generalist predator towards defensive devices of cassidine larvae (Coleoptera, Chrysomelidae). *Oecologia* 118:166–172.
- Muir, F., and D. Sharp. 1904.** On the egg-cases and early stages of some Cassididae. *Transactions of the Entomological Society of London*, Part 1:1–24.
- Müller, C. 2002.** Variation in the effectiveness of abdominal shields of cassidine larvae against predators. *Entomologia Experimentalis et Applicata* 102:191–198.
- Ohmart, C. P., L. G. Stewart, and J. R. Thomas. 1985.** Effects of nitrogen concentrations of *Eucalyptus blakelyi* foliage on the fecundity of *Paropsis atomaria* (Coleoptera: Chrysomelidae). *Oecologia (Berlin)* 68:41–44.
- Olmstead, K. 1994.** Waste products as chrysomelid defenses [pp. 311–318]. In: Novel aspects of the biology of Chrysomelidae (P. H. Jolivet, M. L. Cox, and E. Petitpierre, editors). Kluwer Academic Publishers, Dordrecht. 582 pp.
- Olmstead, K. L. 1996.** Cassidine defenses and natural enemies [pp. 3–21]. In: Chrysomelidae biology (P. H. A. Jolivet and M. L. Cox, editors). SPB Academic Publishing, Amsterdam. Vol. 2. 465 pp.
- Olmstead, K. L., and R. F. Denno. 1993.** Effectiveness of tortoise beetle larval shields against different predator species. *Ecology* 74:1394–1405.
- Rolston, L. H., R. Mayes, P. Edwards, and M. Wingfield. 1965.** Biology of the eggplant tortoise beetle (Coleoptera: Chrysomelidae). *Journal of the Kansas Entomological Society* 38:362–366.

- Selman, B. J.** 1994. The biology of the paropsine eucalyptus beetles of Australia [pp. 555–565]. In: Novel aspects of the biology of Chrysomelidae (P. H. Jolivet, M. L. Cox, and E. Petitpierre, editors). Kluwer Academic Publishers, Dordrecht. 582 pp.
- Simmonds, F. J.** 1949. Insects attacking *Cordia macrostachya* (Jacq.) Roem. and Shult. in the West Indies. I. *Physonota alutacea* Boh. (Coleoptera:Cassidinae). Canadian Entomology 81:185–199.
- Stehr, F. W.** 1991. Immature Insects, vol. 2. Kendall/Hunt Publishing Co., Dubuque, IA. 975 pp.
- van Leerdam, M. B., J. W. Smith, J. R. Fuchs, and T. W. Fuchs.** 1985. Feces-mediated, host finding behavior of *Cotesia flavipes*, a parasite of *Diatrea saccharalis* (Lepidoptera: Pyralidae). Annals of the Entomological Society of America 78:647–650.
- Vencl, F. V., T. C. Morton, R. O. Mumma, and J. C. Schultz.** 1999. Shield defense of a larval tortoise beetle. Journal of Chemical Ecology 25:549–566.
- Vencl, F. V., and T. C. Morton.** 1999. Macroevolutionary aspects of larval shield defences [217–238]. Advances in Chrysomelidae Biology 1. In: Advances in Chrysomelidae Biology 1 (M. L. Cox, editor). Backhuys Publishers, Leiden. 691 pp.
- Williams, J. R.** 1950. The introduction of *Physonota alutacea* Boheman (Col. Cassid.) into Mauritius. Bulletin of Entomological Research 40:479–480.
- Windsor, D. M.** 1987. Natural history of a subsocial tortoise beetle, *Acromis sparsa* Boheman (Chrysomelidae, Cassidinae) in Panama. Psyche 94(1–2):127–150.
- Windsor, D. M., E. G. Riley, and H. P. Stockwell.** 1992. An introduction to the biology and systematics of Panamanian tortoise beetles (Coleoptera:Chrysomelidae: Cassidinae) [pp. 372–391]. In: Insects of Panama and Mesoamerica: selected studies (D. Quintero Arias and A. Aiello, editors). Oxford University Press, Oxford. 692 pp.

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