Defensive Behaviors in Leaf Beetles: From the Unusual to the Weird

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1 Introduction

Insects are the most common animals on Earth, accounting for about 1 million of the known 1.6 million named species (Grimaldi and Engel 2005). Because of this remarkable diversity in species and biomass, insects play a fundamental role in ecosystem structure and function. Leaf beetles, known scientifically as the family Chrysomelidae, are a particular group of beetles that specialize in eating and living on plants (Crowson 1981). Over 40,000 species of leaf beetles have been described and these use more than 210 families of plants as hosts (Jolivet and Hawkeswood 1995). Leaf beetles provide many excellent models for illustrating how individuals survive and how species can interact in food chains, communities, and ecosystems.

As their name suggests, leaf beetles are herbivores. Their typical life cycle involves the eggs, larvae, pupae, and adults occurring mostly on their host plant, although some have become highly specialized as soil-dwelling detritivores, or as myrmecophiles (living with ants), or as termitophiles (living with termites). Leaf beetle adults and larvae are the main feeding stages and may use all plant parts – roots, stems, leaves, fruits, and flowers. Aside from general biological interest in how their extraordinary diversity and specialization have evolved, there is much agricultural interest in leaf beetles that have become pests of important food crops and ornamental plants, from rice to corn to orchids (Jolivet and Hawkeswood 1995). A life on plants may be advantageous in many ways because plants are a dominant life form on Earth and have enjoyed a long evolutionary history. The success and diversity of many nonplant species can be attributed to the evolution and dominance of plants. However, plant specialists face many dangers through exposure to abiotic (e.g., temperature, humidity, insulation) and biotic dangers (e.g., predators, prey), and by being restricted to the habitat and food resources offered by their hosts. Chrysomelids appear to face great pressure of attacks from predators (mainly Heteroptera, true bugs) and parasites and parasitoids (Diptera and Hymenoptera)

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(Cox 1994, 1996). Parasites live with but do not kill their hosts; however, parasitoids do ultimately kill their hosts (Eggleton and Belshaw 1992). Adult beetles can escape attacks by flying away or jumping off the plant, but the immature stages are particularly vulnerable since they are soft bodied and move far more slowly by walking on the surface. Here I explore some of the varied, interesting, unusual, and even weird behaviors exhibited in various life stages of leaf beetles.

2 Sociality

One of the most remarkable insect behavioral defenses is that of sociality and maternal care (Wilson 1971). While sociality in ants, bees, and wasps is better studied and known, sociality in other insects is less obvious to many people. Several groups within Chrysomelidae show sociality that arises when females lay clutches of eggs together which then hatch and pave the way for groups of larvae staying together, feeding, and eventually pupating together. This kind of gregarious behavior has several advantages over solitary behavior. For example, by living in a herd, individuals may find more protection from predators and prey. This advantage is more obvious for a herd of cattle, but the principle applies similarly to tiny insects. Group living may also help individuals conquer their host and take advantage of food. A vertebrate analog might be the ease of a pack of wolves over a solitary hunter in taking down a large mammal. In similar fashion, some leaf beetles minimize the effects of highly toxic plants by feeding in groups and each individual shares a small amount of the toxin thus reducing the effect of a single concentrated dose on a single individual.

3 Maternal Care

Some leaf beetles have gone a step further in the evolutionary pathway from solitary to gregarious, as they have become subsocial where the mother stays and cares for her offspring (Costa 2006). True sociality, eusociality, is defined as having overlapping generations so that older offspring helps the parent care for the younger offspring (Wilson 1971). This behavior has evolved multiple independent times within two subgroups of Chrysomelidae, the subfamily Cassidinae (Fig. 1a) and the subfamily Chrysomelinae (Fig. 2a) (Chaboo 2007), a pattern that suggests similar ecological forces may be driving this complex behavior. All the cassidine (tortoise beetle) maternal care species have been discovered in the Neotropics, from Costa Rica to Peru. Chrysomeline species with maternal care have been found in Costa Rica, Brazil, and Japan. Members in these two subfamilies are not directly related, but they exhibit common traits such as having the eggs and larvae living on leaves where they are very exposed (Frieiro-Costa and Vasconcellos-Neto 2003). The leaf beetle mother may coat her egg cluster with offensive chemicals (Hilker 1994) or build

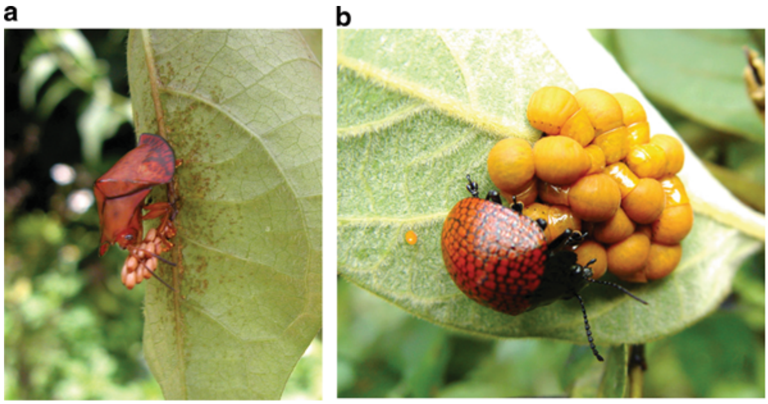

Fig. 1 Maternal care in Chrysomelid beetles. (**a**) Female cassidine, *Acromis spinifex*, guarding her egg clutch in Trinidad (photo, F. Merino). (**b**) Female chrysomeline, *Doryphora* sp., guarding her larvae in Brazil (photo, F. Frieiro-Costa)

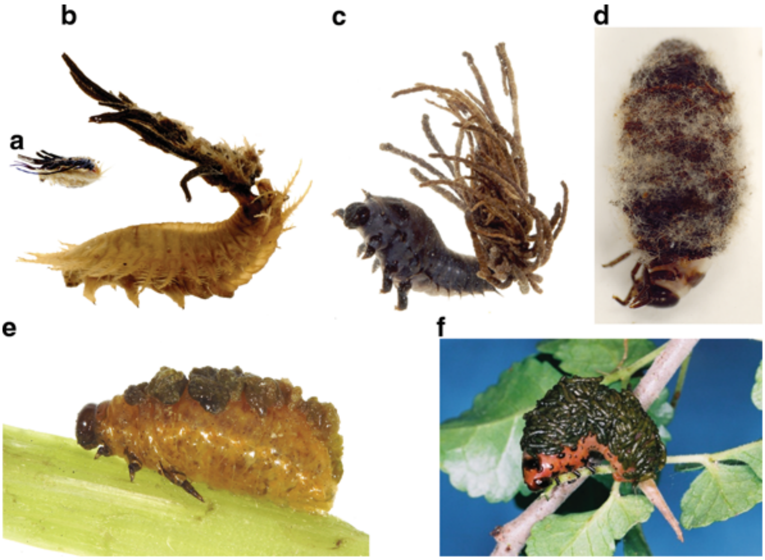

Fig. 2 Defensive shields and cases of Chrysomelid beetle larvae. (**a**) A larva from Panama holding the shield flat and protecting its back, and (**b**) holding the shield vertically, ready to strike, USA. (**c**) A larva with ornate shield, Uganda. (**d**) A larva inside its fecal case coated with trichomes from the host plant, USA. (**e**) A larva with a wet fecal coat directly on its back, USA. (**f**) A larva with a wet fecal coat on its back, South Africa

layers of protective membranes that insulate the eggs and make it harder for a predator or parasitoid to reach the eggs (Hinton 1981). The larvae feed together with the mother always hovering nearby. When a predator or parasitoid approaches, the mother pushes her offspring together to form a tight cluster and then she sits on them, prepared to physically attack the intruder. If the intruder persists, she may lead or push her brood to a new location on the plant (Upton 1996). Apart from physically touching the young, we suspect that other signals (e.g., sound) may aid in the communication between chrysomelid mothers and their offspring, as has been demonstrated in other subsocial insects, e.g., bugs (Crocroft 1996). A cassidine mother will guard her young through their sedentary pupation phase and will only depart when the last young adult has emerged (Chaboo 2001). Chrysomeline females depart earlier as the final larval stages migrate down the plant to pupate solitarily in the soil (Kudo and Ishibashi 1995; Kudo et al. 1995; Kudo and Hasegawa 2004).

4 Defensive Constructions

One of the most bizarre behaviors exhibited by animals exists in Chrysomelidae. Several kinds of the leaf beetles have larvae with an elaborate shield held over the body or a hard portable case worn like a top hat by individuals as they move around the plant. Other animals that construct domiciles, nurseries, or fortresses may produce their own materials (e.g., silk) or use materials from the environment, e.g., the logs of a beaver lodge. Some even use a mix of different materials from multiple sources, e.g., a bird's nest of twigs may be held together by stolen spider silk (von Frisch 1974; Hansell 2005). Animal architecture is a fascinating area of study because it involves so many aspects of an organism's morphology and physiology interacting with its ecology. Chrysomelids can be viewed as miniature builders dealing with similar issues of protection in a harsh environment.

5 Fececology

In a group as large and diverse as leaf beetles, there are many kinds of defense constructions (Fig. 2). In all these various leaf beetle constructions, the material for constructing is most astonishing – the feces of the animal. The subfamily Cassidinae has ~3,000 species whose larvae carry a mobile shield made of dried feces, attached to paired processes at their hind end, and held over the body like an umbrella (Fig. 2a, b) (Chaboo et al. 2007). This shield may be held flat on the dorsum or elevated to hit an attacker. In two other leaf beetle subgroups, the subfamily Criocerinae (~1,400 species) (Vencl and Morton 1999) and in some members of the subfamily Galerucinae [~14,000 species (Chaboo et al. 2007)], the fecal material is simply piled directly onto the back of the animals, with some falling off as the animal moves around but regularly replenished to maintain coverage of the exposed dorsal surface (Fig. 2b, c). In Chrysomelinae leaf beetles (~4,000 species), the mothers take time to build a fecal case entirely around every single egg (Brown and Funk 2005; Chaboo et al. 2008). When the larva hatches, it steps out of the case and flips the case over its body, and thus spends the rest of its life wearing this case like a top hat (Fig. 2d). The case is expanded as the larva grows to accommodate the increasing size. The feces emerge as a semisolid material but harden by exposure to air and thus form an adobe-like hard defense.

Feces are not an obvious building material for many animals but it has the advantage that the animal is always producing it (Olmstead 1994, 1996). Chrysomelids further enhance the effectiveness of their shields and cases using offensive chemicals sequestered from their host plants (Gómez et al. 1999; Vencl and Morton 1998; Vencl et al. 2005; Nogueira-de-Sá and Trigo 2005).

6 Defensive Chemicals

Chrysomelids possess a range of glandular and hemolymph defensive chemicals. It is very interesting in an evolutionary sense that plants produce chemicals to protect themselves from being eaten by herbivores. In the long history of evolution, some herbivores have become specialized to detoxify these chemicals and even to co-opt them for their own development and survival (Blum 1994). Chrysomelids can sequester plant chemicals in all life stages, in the body fluids or in special glands. Some chrysomelids even display warning coloration (aposematism) of bright or contrast colors, e.g., red, yellow, and black, to signal to other animals that they are offensive and not worth eating.

7 Tritrophic Interactions

Up until now, I have discussed species interactions between two tiers, plants and herbivores. But these are only two of the tiers that can connect longer chains of species interactions. Globally, complex trophic relationships have been documented between a few plant families, chrysomelid herbivores, and their carabid beetle parasitoids (Table 1).

Carabidae (ground beetles) is another speciose beetle family with ~40,000 species. Adults and larvae are commonly generalist predators of insects, but some subgroups

Table 1 Tritrophic interactions between plants, chrysomelid beetle herbivores, and carabid beetle parasitoids

Plant	Solanaceae *Solanum*	Burseraceae *Commiphora*	Anacardiaceae *Sclerocarya*	Salicaceae *Salix*	Apocynaceae *Apocynum*
Herbivore	*Leptinotarsa*	*Diamphidia*	*Polyclada*	*Salix*	*Apocynum*
Parasitoid	*Lebia*	*Lebistina*	*Lebistina*	*Lebia*	*Lebia*
		African Poison Arrow Beetles			

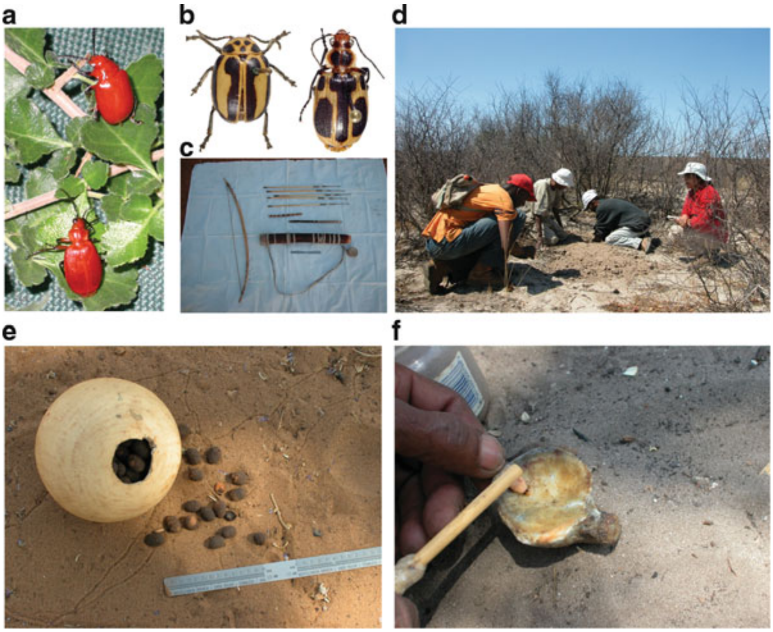

Fig. 3 (**a**) A live Lebistina adult (*bottom*) mimics the color and form of its prey, Diamphidia adult (*top*) on its host plant, Commiphora in South Africa (photo, K. Ober). (**b**) A dead Diamphidia adult (*right*) and its Lebistina parasitoid (*left*). (**c**) A San bushman's hunting equipment, with poisoned arrows. (**d**) Collecting poison beetles in the Tsumkwe Conservancy, Namibia (the *author in red shirt*). (**e**) An ostrich egg full of poisonous beetles. (**f**) Squeezing a poison beetle to apply its juice (hemolymph) to an arrow

have become specialized predators and parasitoids of chrysomelids (Erwin 1979; Weber et al. 2006). Relationships in the plants–chrysomelid herbivores–carabid parasitoids associations have not been studied in detail but display many interesting biological phenomena including plant–insect interactions, beetle life history evolution (free-living to parasitoid), mimicry complexes (carabid parasitoids resemble their colorful aposematic chrysomelid hosts) (Fig. 3a, b), and defensive chemistry (sequestration and de novo synthesis). Some compounds are already known to be so highly toxic that southern African San tribes use crushed chrysomelids to poison the tips of arrows to kill large warm-blooded prey, such as antelopes and giraffes.

8 Arrow Poison Beetles

The San, also known as Ju/'hoansi or !Kung, are among the original inhabitants of southern Africa and have a distinctive clicking language. They are probably most familiar to the public as the central characters in the 1980 comedy film "The Gods must be crazy" and its four sequels (Uys 1980). About 80,000 San are left today, living mainly in Namibia and Botswana (Lee 2003; Lee and DeVore 1998). San hunters collect chrysomelid beetles in the genera *Diamphidia* and *Polyclada* throughout the year to use as poison on their hunting arrows (Breyer-Brandwijk 1937; Mebs et al. 1982). The beetles are not confined to southern Africa, but range from South Africa to the Sahara and into Zanzibar, and are found by locating their host plants, *Sclerocarya* (Anacardiaceae) and *Commiphora* (Burseraceae) (Fig. 3b).

Members of both the Anacardiaceae and Burseraceae have highly interesting chemistry. *Commiphoras* are well known as the sources of frankincense and myrrh, which were once so important medically in ancient times that they were mentioned in the New Testament as the choice of the precious gifts for the baby Jesus. Familiar members of the Anacardiaceae are avocadoes, mangoes, sumac, and poison ivy; these plants produce white or yellow latex that can have irritating properties.

Adult *Diamphidia* and *Polyclada* lay eggs on *Commiphora* and *Sclerocarya* and the hatched larvae go through several developmental stages before migrating underground where they build a protective cocoon. While underground, they develop through the pupal stage and emerge as adults. Larvae of the parasitoid carabid beetles seek out these underground pupae and attach themselves to the latter. The parasitoid feeds on a single host, consumes it completely, then pupates and emerges at the surface as an adult.

The chrysomelid poison arrow beetles are very effective, slowly paralyzing and eventually killing large mammal prey. It is unclear how old this San hunting practice is, but it appears that poison arrows originated in many cultures and in many places (Maingard 1932). For example, the use of poison dart frogs by Chocó Indians in Colombia is a well-known hunting practice (Myers et al. 1978).

Chemical relations between host plants, herbivores, and parasitoids are an interesting theme in this system. Resins of *Commiphora* and *Sclerocarya* have been commercially harvested for use as incense for over 3,000 years. Chrysomelid and carabid beetles are generally known as remarkable chemical factories, with some being lethally poisonous. Chemical analyses of *Diamphidia* pupae isolated a toxic protein, diamphotoxin (De la Harpe and Dowdle 1980; De la Harpe et al. 1983). Coincidentally, a similar molecule, leptinotarsin, has been identified in several species of the North American chrysomelid, *Leptinotarsa*, and its carabid parasitoid, *Lebia* (Hsiao 1978; Crosland et al. 1984). Both diamphotoxin and leptinotarsin act as slow-paralyzing agents and cause death within hours of injection in tested animals. A really interesting question to explore in the future is the reaction of the carabid parasitoid to the chrysomelid toxin – they may not react, or may require the toxin for their own development, or they might even sequester the toxins to use in their own defense. The latter scenario might explain the carabid's own aposematic and mimetic colors that makes it difficult to distinguish their host chrysomelids (Fig. 3a, b).

The San people have tremendous respect for these poisonous beetles – only the chief hunter is allowed to collect the live beetles and store them in ostrich egg shells (Fig. 3c), to be used sparingly or to be exchanged with hunters from other family units scattered throughout the Kalahari region. About ten beetles are crushed into a thick paste that is applied to each arrow (Fig. 3d). Unfortunately, a variety of modern political factors are forcing the San to become sedentary, give up their hunter-gatherer form of life, and stop hunting with poison arrows (Dieckmann 2007). Old indigenous practices such as these are disappearing around the world, but there is still much to understand and learn from such ancient cultures.

The global tritrophic association between host plants, chrysomelid herbivores, and their carabid parasitoids is an undeniably complicated one. The critical first steps in studying the evolution of this association are to systematically document individual relationships and develop evolutionary hypotheses for the taxa involved. Such data will identify the specificity of relationships and possible coevolutionary scenarios, and suggest close relatives that may share similar properties. Thus, evolutionary patterns can guide researchers to expand their database of knowledge and discover larger patterns in nature. While toxic beetles such as *Diamphidia* and *Polyclada* have not yet been discovered in the New World, one can predict that the chrysomelids used for San poison arrows probably represent a tip of the iceberg of diversity. This framework has proven to be a useful guide to discovering New World relatives of the African species that show similar patterns of plant associations in Peru and the Dominican Republic (Chaboo unpublished data). The next step is to examine the underlying chemical patterns that can explain the close association of this group of beetles with particular plant families.

9 Conclusions

After a long evolutionary history and intimate association with plants, dating to the Cretaceous, chrysomelids are extremely diverse in their ecology and behavior today. Elucidating the mode and tempo of their evolution and their relationships at the genetic, chemical, ecological, and evolutionary levels can shed light on how individuals live and survive, form communities and food chains, and interconnect into ecosystems. This chapter discusses just a few remarkable biological patterns in Chrysomelidae.

We remain uncertain about the exact number and distributions of solitary, gregarious, and subsocial chrysomelid species. The present list of known species can frame future field studies with the aim of discovering additional species, unveiling their reproductive biologies, and unraveling the ecological factors that drive social evolution. Similarly, the accumulated data on defensive behaviors for a small fraction of species enable detection of diverse patterns of behavioral, chemical, and physical defenses in all life stages. Now, research must transition to a new, more analytical phase by proposing specific hypotheses to discover additional species and better explain the defense patterns.

The chemistry of chrysomelids remains largely descriptive, identifying the molecules involved. Future research should change focus and explore the metabolic pathways of their creation, which may be due to sequestration directly from the host plant, manipulation of molecular structures, or de novo synthesis. Diamphotoxin and leptinotarsin are still to be compared in detail. It seems unusual, though not improbable over the long course of evolutionary time, for two similar-acting toxic molecules to appear in a clade of 40,000+ species. Phylogenetic connections at the levels of gene, species, and branches of the tree of life must be assessed to determine their relatedness. Their medical significance also awaits exploration – any natural molecule that can act with such toxic precision has potential in drug treatment or drug delivery. Research on the San arrow poison beetles is a race against time; indeed, indigenous tribes in very different geopolitical areas of the world are facing rapid extinction, along with their languages and ancient knowledge of nature.

Chrysomelid leaf beetles are a model system for biological research due to their species diversity, host plant relations, ancient lineage, and diverse biologies. A new generation of interdisciplinary chrysomelid biologists focusing on hyperdiverse tropical areas could greatly contribute to enhancing and expanding fundamental theories and models of life histories, mimicry complexes, chemistry, and species associations.

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