A TALE OF TWO BEETLES: A VAMPIRE AND AN ENIGMA

(INSECTA: COLEOPTERA: MELOIDAE, PYROCHROIDAE)

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The 30 species of blister beetles (Coleoptera: Meloidae) known from the Canadian Prairie provinces[1] are a conspicuous and ecologically important part of the grassland biota. The beetles, which are generally of medium to large size (3 – 25 mm) and often conspicuously colored, are usually found feeding on a variety of flowers.

These beetles are active during the day and do not make much effort to conceal themselves so appear to be vulnerable to predators. However, like many species of conspicuous insects, they have chemical protection. The name blister beetle refers to a toxic chemical, cantharidin (Box 1), in the body of these insects.

The body of a blister beetle, unlike that of most beetles, is not hard and armoured, but rather is leathery and can withstand light attack and mauling by a predator. When attacked or roughly handled, the beetles exhibit reflex bleeding where blood is exuded through the body wall, generally at specific points such as joints on the legs. This blood carries cantharidin and probably other compounds that are deterrents to most attackers. A familiar example of reflex bleeding is shown by lady beetles, which when handled (or tasted[2]), leave a bitter taste from alkaloids in the blood. The blood of blister beetles is avoided by many predators ranging from ants to birds[3] and can blister tender human skin.[4]

Cantharidin, although occurring in the blood, is not evenly distributed throughout the beetle's body. Concentrations tend to be higher in males than in females and are highest in glands in the reproductive system. It has been thought that males produce cantharidin in accessory glands of the reproductive system and transfer most of it to females during mating as females produce little.[5,6] However, recent work suggests that at least some synthesis occurs in the fat body[7], and larvae may also produce the substance. Females lay eggs containing cantharidin that protects them, as well as hatching larvae, from attack by predators and microorganisms.[8] Cantharidin can also function as a pheromone during courtship and as a mating inducer.[3,9]

When someone gets a good idea, it is certain to be copied, and this applies to cantharidin. Beetles in several families related to the Meloidae either have some ability to synthesise the toxin or they pick it up from some other source. Some species of the beetle families Pyrochroidae and Anthicidae are attracted to cantharidin and blister beetles on which they feed. They ingest cantharidin and pass it on to their eggs and larvae, also as a chemical defense against predation. Some mirid bugs (Hemiptera: Miridae[10]) and no-see-um flies (Diptera: Ceratopogonidae, Figure 1) feeding on blister beetles are also attracted to cantharidin.

BOX 1. CANTHARIDIN
(from the Greek "kantharis", a name for blister beetle) - A highly toxic odourless (to humans), colourless compound that is produced by blister beetles (Meloidae) and a few members of a related family. Cantharidin can irritate or blister (vesicate) skin and is highly toxic when ingested. A predator of a blister beetle is likely to have an unpleasant meal, and blister beetle poisoning and even death from ingestion is considered a significant agricultural problem in parts of the US. Horses are especially susceptible to blister beetle poisoning when they ingest either living or dead beetles from grass or hay. However, cantharidin is an imperfect poison for some animals (e.g. frogs, a variety of insects) can tolerate it and some even require it for various life history functions.[3,4,30]

FIGURE 1: Female *Meloe angusticollis* Say feeding on Death Camus (*Zygadenus gramineus* Rydb.). Enlargement - the small no-see-um fly (Diptera: Ceratopogonidae: *Atrichopogon* sp.), a probable cantharidiphile, feeding near the end of the abdomen. Photo credit: D. Larson.

Eisner termed this attraction to cantharidin as cantharidiphilia, and gave examples of insects from the orders Coleoptera, Diptera, Hemiptera and Hymenoptera that are cantharidiphils.[3] The following account is of a local example of a beetle genus of known cantharidiphiles.

The vampire beetle: *Pedilus* (Pyrochroidae)

One group of beetles, members of the genus *Pedilus* Fischer (Pyrochroidae), have been observed feeding on the blood of blister beetles of the genera *Meloe* [4,11,12,13,14,15,16] and *Epicauta*.[15,17] Although the observations involve only a few species of *Pedilus* and two genera of blister beetles, this blood-feeding appears to be widespread, but is probably opportunistic and not necessary for the completion of the life of *Pedilus*.

On 4 July 2021, I observed a feeding aggregation of Nuttall's blister beetle (*Lytta nuttallii* Say) on silvery lupine (*Lupinus argenteus* Pursh), 16 km south of Maple Creek, SK (SW28-9-26 W3) (see The Enigma on the next page). I photographed these beetles and later that day, when examining the photographs, noticed that two blister beetles had objects near the rear end of the body. Enlargement of the photos revealed these were beetles of the genus *Pedilus* that were holding onto the blister beetle's body with their mouthparts (Figure 2). On 5 July, I returned to get better quality photographs and to collect specimens of *Pedilus* to determine the species (Figure 3). Three specimens of *Pedilus* were collected off the elytra of blister beetles along with five additional specimens that were in an excited state and climbing the lupines amongst the blister beetles. These specimens were obviously attracted by the blister beetles, for although specimens of *Pedilus* can be regularly collected by sweeping herbs, grasses, and low bushes in riparian areas and woodlands, I have never previously found an aggregation.

The *Pedilus* specimens on the blister beetles were at the apex of the elytra and on an intersegmental membrane of the abdomen. Several were holding on only by their mouthparts, the legs were appressed against their bodies. When picked up, they disengaged quickly and there was no obvious sign of damage at the point where the mouthparts were attached to the elytra, although I did not closely examine the blister beetles before releasing them. Other observers of this behaviour also noted lack of evident injury to the host, although several reported elytral damage on *Meloe*.[11,13,14] These observations are consistent with the beetles having their mouthparts anchored into the elytra and probably feeding on fluid rather than chewing the host, thus they were probably feeding from blood sinuses in the elytra. Feeding damage has been reported from *Meloe*, which

FIGURE 2: Nuttall's Blister Beetle with two male *Pedilus monticola* feeding at the apex of the elytra and intersegmental membrane of the abdomen. 4 July 2021. Photo credit: D. Larson.

FIGURE 3: Nuttall's Blister Beetle with a male *Pedilus monticola* feeding at the apex of the elytra. 5 July 2021. Photo credit: D. Larson.

differs from most other blister beetles in having reduced, non-functional wings (Figure 1), and the elytra are relatively thin, perhaps making them more susceptible to damage from feeding by *Pedilus*.

The eight collected *Pedilus* specimens are males. In general sweep-net collecting, both males and females have been collected although males of the species predominate (of the 27 specimens in my collection the sex ratio is 21♂: 6♀). It was likely all specimens associated with the blister beetles were males, but the sample size is too small to be certain.

These specimens were pinned and will be deposited in the Royal Saskatchewan Museum. Their identity is uncertain as the taxonomy of North American *Pedilus* is unsettled. They are probably the species Bousquet et al. referred to as *P. longilobus* Fall [1], but they do not match *P. longilobus* in the shape of their genitalia. The genitalia of these specimens most closely resemble published figures of genitalia of

a western species, *P. monticola* Horn[17,18], so I refer them to this species. *Pedilus monticola* has been reported feeding on *Meloe* in BC[10] although it has been suggested that the record actually refers to an undescribed species of *Pedilus*.[20]

The males have the apex of the elytra somewhat tumid with a concave impression. Some species of *Notoxus* (Anthicidae) that have males that feed on cantharidin, have the elytral tips with apical tubercles from which the females feed and obtain cantharidin.[21,22] This is the site on blister beetles where *Pedilus* usually feed, and in turn this modified portion of the male *Pedilus* elytra could be a feeding site for female *Pedilus*. Similar to blister beetles, male *Pedilus* pass cantharidin along to females during mating, and possibly through female feeding on male elytral secretions although this has not been observed. Males of another Prairie species *of Pedilus, P. abnormis* (Horn), have unmodified elytra. Could this mean they do not pass cantharidin on to females or do so only during mating?

Eisner raised the question of where do cantharidiphiles obtain their cantharidin?[3] Blister beetles are the principal source identified to date, so it seems appropriate to examine the biology of the presumed cantharidin doner of this observation.

The enigma: Nuttall's blister beetle (*Lytta nuttallii* Say)

There are three large (length = 7 to 21 mm), vividly metallic blister beetle species of the genus *Lytta* Fabricius that occur in grassland and parkland portions of the Prairie provinces.[23] *Lytta cyanipennis* (LeConte) and *L. viridana* (LeConte) are metallic dark purple, blue, or green all over, whereas *L. nuttallii* is similar except the elytra are metallic dark violet to brassy and the head and pronotum have a coppery reflection (Figures 2, 3, 4). *Lytta cyanipennis* is western and confined to the foothill region of Alberta, *L. viridana* and *L. nuttallii* are widespread in prairie and parkland.

This discussion focuses on *L. nuttallii*, Nuttall's Blister Beetle, as it is the most commonly encountered species and the species on which *Pedilus* was observed to feed. However, *L. cyanipennis* and *L. viridana* are so similar in adult behavior that most observations apply equally well to all members of this group of species, and there is evidence that hybridization among the three may occasionally occur where their ranges overlap.[23,24,25]

Adult Nuttall's Blister Beetles occur most abundantly in June and early July. They are almost always found feeding on flowers of various species of Leguminosae. Marschalek & Young give a long list of plants from which the species has been collected.[20] There are some reports of damage to non-leguminous crops, but it is unlikely that any non-leguminous plant can sustain the insects. Although reported from a variety of plants, *L. cyanipennis* could be maintained in the lab only on *Lupinus*.[23] The plant species I have most frequently found specimens on are various species of milk-vetch (e.g., Two-grooved Milk-vetch (*Astragalus bisulcatus* (Hook), Drummond's Milk-vetch (*A. drummondii* Douglas), Narrow-leaved Milk-vetch (*A. pectinatus* Douglas)) and Silvery Lupine (*Lupinus argenteus* Pursh). Beetles are found on Caragana (*Caragana arborescens* Lam., also a legume) often enough to have the common name Caragana Beetle, but this non-native plant is probably only an incidental host.

The beetles feed on flowers, developing seed pods and sometimes on the leaves.[25] Selander described the feeding of *L. cyanipennis*: "In captivity they feed more or less continuously, day and night. Their fecal material, which is emitted in large quantity, contains great amount of undigested plant tissue; it is presumably this inefficient utilization of food that accounts for the unusually ravenous habits of the beetles."[23]

BOX 2. HYPERMETAMORPHOSIS – is an unusual type of insect development shown by blister beetles, as well as members of a few other insect groups. It is characterized by successive larval stages having quite different forms and behavior. In blister beetles the instar 1 larva (triungulin) is sclerotized and active and seeks out a host, instars 2 – 5 are grub-like feeding stages, instar 6 is a contracted, sclerotized (hardened) non-feeding form (coarctate stage) that passes the winter, instar 7 is grub-like but does not feed, it moults into a pupa which moults to an adult.[23,31]

The beetles seldom occur singly. They are usually observed in aggregations on the food plant where, besides feeding, the beetles are busily engaged in courtship and mating (Figure 4). I refer to these aggregations as circuses (Figure 5). A definition of circus is "an arena for a travelling show of acrobats, trained animals,

FIGURE 4: A mating pair of Nuttall's Blister Beetle on Silvery Lupine. Photo credit: D. Larson.

clowns, etc."[26], and this well describes the frenetic behavior of the beetles. Mating occurs with the sexes joined end to end and the beetles remaining active and feeding so they often end up pulling against or hanging from each other. Copulation lasts a long time, generally within the range of 8 to 10 hours during which time the beetles feed and move about.[27]

It has been suggested that this gregarious habit of adults may function as a mechanism to keep beetles near the site they developed and thus giving newly hatched larvae a better chance of finding suitable food.[23] However, these circuses seem to be congregation on a food source for the purposes of feeding and mating. Groups form when one or a few beetles find a suitable plant and then more individuals are recruited, probably by means of sex or aggregation pheromones.[27] Circuses vary in size from a few beetles to larger groups not exceeding a couple of thousand, but most probably contain fewer than 100 beetles.[25] In a patch of food plants, the beetles are usually on only a localized subset of plants.[25] Typically, circuses break up with the abrupt abandonment of the site as the beetles fly off individually over a few hours so that a large circus one day is gone the next. Dispersal occurs when the edible parts of the food plant, especially flowers and developing seed pods, are consumed, but may also occur even though resources remain.

But this is the enigma, where do the beetles in a circus come from and where do they go? We don't know. The larval stages are known because they have been reared in captivity, but they are unknown in the field. We can speculate on the probable life history based on bits and pieces of information obtained from keeping adults captive, lab rearing larvae, and inferences from other species of *Lytta* whose life history is known.

Blister beetle larvae feed on either the eggs of grasshoppers, or the brood and stores of solitary bees (Box 3). All *Lytta* for which the larval stages are known feed on provisions and immature stages in the nests of wild bees. Thus, our species of *Lytta* are probably bee nest predators. Caged, mated females of the three Prairie species have been observed to lay eggs in burrows in the soil of their cages.[24] Each female digs a burrow 1 to several cm deep, deposits a mass of eggs, and then backfills to cover them. The triungulin hatching from an egg seeks out food by crawling through or over the soil. Thus, Nuttall's Blister Beetles must lay eggs close to the nests of suitable ground-nesting bee hosts as the triungulin larvae have limited mobility. No bee species occurs in high enough density to support the populations of adults seen in most circuses, so females must disperse to egg-laying sites.[25] Church & Gerber found captive females could lay as many as five batches of eggs each with an average of 320 eggs (corresponding to the number of ovarioles[28]), with an average length of 6 to 7 days between batches.[25] Feeding is required to develop each batch of eggs and mating to fertilize them, so over the average life of a beetle, 3 to 5 weeks[25], there must be several movements from feeding and mating sites to oviposition sites then again to a feeding site. Thus, the circuses are likely forming, dispersing and reforming in new locations as food sources become

FIGURE 5: A circus of Nuttall's Blister Beetle on Drummond's Milk Vetch. Photo credit: D. Larson.

BOX 3. THE LARVAL FOOD OF BLISTER BEETLES

Blister beetle larvae feed either on grasshopper eggs or cell provisions and brood in the nests of solitary bees.[32] Adult beetles of species that are bee nest predators either lay eggs in the soil and the first instar larva (triungulin) seeks out host nests, or beetles lay eggs in the soil or on vegetation and triungulin moves to flowers where it waits to latch onto the hairs of a visiting bee which transports it to the nest.

Nuttall's Blister Beetles, based on lab observations and what is known of the immature stages of related species, lay eggs in clusters in the soil and the triungulin probably seeks out nests of ground-dwelling solitary bees. The bee nests consist of a number of cells, each with a bee egg or larvae and provisions of pollen for its development. The blister beetle larva eats the contents of one, or probably more, cells.

available (e.g. host plant species change with the seasonal phenology of the vegetation).

The large size of an adult Nuttall's Blister Beetle necessitates a large host bee, although larval blister beetles are known to devour the contents of more than one cell in a bee nest so smaller bees could be the host with a beetle larva feeding on several cells. The host bees are probably members of the genus *Anthophora* (Apidae, Apinae) as these are the host of some known species of *Lytta*.[23] These are robust bees, the majority of which make non-aggregated nests in flat ground.[29] Interestingly the provisions of their cells are reported to have a distinctive "yeasty" smell,[29] which suggests a cue a blister beetle larva could use in finding a host nest. Leafcutter bees (Megachilidae) are also a possible host for the only report of female Nuttall's Blister Beetles ovipositing in the wild is by Church and Gerber who stated "oviposition sites were all small bare patches located in native grassland vegetation and in light, sandy soil. The remains of a large number of nesting cells of leafcutter bees (*Megachile* sp.) were distributed throughout this area along the riverbank. Though the larvae of *L. vesicatoria* fed on the provisioned materials of *Megachile* species in the laboratory (Selander 1960), it is not known whether this bee is a larval host of *nuttalli*."[25] It is certain that honeybees, bumble bees and domesticated leafcutter bees are not hosts for their nests have been extensively studied without finding Nuttall's Blister Beetles. However, stores and larvae of honeybees and domestic leaf-cutter bees have been used to rear larvae in the lab.[23]

Discussion

There are some good clues as to what the life history of Nuttall's Blister Beetle might be. However, confirming the assumptions and uncovering life history details for this big, brash colourful beetle still offers an interesting challenge and perhaps some surprises for naturalists. Also, these insects seem to reflect the impacts of human activity on the prairies. Most of the records of Nuttall's Blister Beetles feeding on non-leguminous plants and causing crop damage date from the 1930s and since that time the beetles have existed in relatively small populations in areas with natural prairie. The related *Lytta viridana* has largely disappeared from the southern Canadian prairies although I have occasionally found small circuses in southwestern Saskatchewan and adults occasionally in wind-drift of lakes. Church and Gerber attribute these population declines to intensification of agriculture which has reduced habitat for wild bees.[25] The state of these blister beetle populations is probably a good proxy for the state of larger ground nesting prairie bees, although we do not know which ones.

One has to ask what is the significance of the observation of *Pedilus* feeding on *Lytta nuttallii*? Studies on the pyrochroid beetle *Neopyrochroa flabellata* show that males accumulate cantharidin and use it to induce females to mate.[3] Cantharidin is not essential for mating to occur, but it greatly enhances a male's chance of success. Does the female need cantharidin to develop and lay eggs, or do the eggs need the protection of cantharidin? Again, we don't know. Given the erratic movements and local variation in abundance of Nuttall's Blister beetles, they would seem to be a very uncertain source of cantharidin if it is an essential material for *Pedilus*. Likely, male *Pedilus* are facultative feeders on cantharidin from whatever source is available and perhaps those males lucky enough to find a source have enhanced reproductive success. This possibility suggests that there are chemical webs we are hardly aware of hidden within the familiar ecological webs.

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P.S. My first job as a high school student was working as a summer student in 1961 for Dr. Norman Church and his technician Bill Pelham at the Agriculture Research Station, Lethbridge Alberta. Church was interested in the hormonal control of metamorphosis in insects and the hypermetamorphosis of blister beetles was especially interesting. Thus, he wanted large numbers of larvae in various stages of development. It was found that larvae of wheat-stem sawfly were acceptable food for larval *Lytta* but each sawfly larvae had to be dissected out of its wheat-stem home. That was my work. It was rather dull, but compensated for by wonderful days in the field watching, collecting and chasing dispersing blister beetles. Since then, I have not been able to see blister beetles without feeling nostalgia and wonder.