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Abstract. Four species of the genus *Enoclerus* (Coleoptera: Cleridae) are reported to prey on chemically protected Coccinellidae in North America. The possibility that aposematically colored *Enoclerus* also mimic prey ladybird species is discussed, and the further possibility that clerid predators acquire chemical protection through sequestration of ladybird prey's toxic alkaloids is suggested as an important avenue of investigation. The data presented are primarily based on photographs taken by non-specialists, discovered through Internet search. The crowdsourcing of natural history observations can reveal aspects of animal behavior heretofore unreported and even unsuspected.

Key Words. Clerid predation, clerid mimicry, Batesian mimicry, Müllerian mimicry, acquired distastefulness.

Introduction

This paper presents the first substantiated records of species of the genus *Enoclerus* Gahan preying on chemically protected Coccinellidae. As larvae, most Cleridae attack wood-boring beetle larvae and other lignicolous insect larvae. Adult *Enoclerus* are generalized predators and have been observed to feed upon a variety of insect prey belonging to several orders. Species in a number of genera of Cleridae mimic a remarkably broad array of noxious, aposematically colored and patterned insect models (Menier 1985; Mawdsley 1994; Rifkind 2002), and many display the reddish elytra, variously marked with white or black spots, commonly found among ladybird beetles. Although clerid mimicry has been almost exclusively characterized as Batesian, the possibility that aposematically colored *Enoclerus* may sequester poisonous chemicals derived from the haemolymph of their coccinellid prey should be considered and tested. If true, this would implicate some species of *Enoclerus* as Müllerian co-mimics in complexes with coccinellids and possibly other, similarly marked arthropods.

Material and Methods

I observed and photographed *Enoclerus* predation upon Coccinellidae on one occasion (Fig. 4). Three further instances were documented by photographers who posted their images on the Internet (Fig. 1–3). In all, four species of *Enoclerus* were observed feeding upon ladybird beetles. Voucher specimens are deposited in JNRC (Collection of Jacques Rifkind, Valley Village, California, U.S.A.).

Results

On August 17, 2014, Addison Rifkind and I observed and photographed a specimen of *Enoclerus moestus* (Klug) feeding upon a red-colored ladybird beetle (Fig. 4). The pair were on rabbitbrush (*Chrysothamnus* Nutt. sp.) in pinyon woodland (U.S.A., California, Inyo County, Hwy. 168, 7 mi E. Hwy. 395, ca. 1829 m elevation). Unfortunately, we were unable to recover the disarticulated parts of the coccinellid as they fell among the stalks of the plant, so a more precise identification of the prey was not possible. *Enoclerus moestus*, a common montane species in the western U.S., has grey- and black-marked elytra, which render it difficult to see against the pine bark upon which it is most frequently encountered. However, when it flies, or when it is moving vertically on herbaceous vegetation, its bright red ventral abdominal surface is clearly visible. This coloration may confuse or deter potential predators.

On June 3, 2014, Scott Ditzel photographed a specimen of *Enoclerus ichneumoneus* (Fabricius) preying upon the coccinellid *Cycloneda munda* (Say) in his backyard in Dallas, Georgia, U.S.A. (Fig. 1).

The pair was discovered in the early evening on the underside of an oak leaf. *Enoclerus ichneumoneus* is a common species with a broad distribution in the eastern and southern United States.

On October 10, 2002, Bruce Marlin photographed a specimen of *Enoclerus nigripes* (Say) preying upon the coccinellid *Psyllobora vigintimaculata* Say in oak–hickory forest at McKee Marsh Forest Preserve, Warrenville, Illinois, U.S.A. (Fig. 2). *Enoclerus nigripes* is a common species, broadly distributed across the eastern half of North America from Canada to Florida.

On August 8, 2014, Gail Starr photographed a specimen of *Enoclerus spinolae* (LeConte) feeding on a coccinellid beetle (*Coccinella* Linnaeus sp.) (Fig. 3). The pair was discovered on thistle (*Carduus* Linnaeus sp. ?) on S. County Rd. 31, Carter Lake, Larimar County, Colorado, U.S.A. (N 40º 20' 23", W 105º 12' 69"). *Enoclerus spinolae* is distributed across the U.S. Southwest and Midwest, and into northern México. It is associated throughout its range with Agavoideae species, and its larvae have been reported to feed on the larvae of an agave weevil *Peltophorus polymitus* Boheman in *Yucca thompsoniana* Trelease (Foster and Barr 1972). Adult *E. spinolae* are boldly marked with a black head and pronotum, and bright red elytra decorated with black maculae. Of the *Enoclerus* species documented here as predators of ladybird beetles, *E. spinolae* would appear to be the most likely mimic of coccinellid beetles.

Discussion

Coccinellidae are well known for their conspicuous and distinctive coloration. The family includes some drab-colored and cryptically marked species, some of which may be chemically unprotected, but all of the brightly colored red or orange species analyzed so far possess noxious and/or poisonous alkaloids that have been shown to repel many vertebrate and invertebrate predators (Daloze et al. 1995). Indeed, in their review of ladybird chemical defenses, Daloze et al. (1995) concluded that coccinellids "are the most versatile and prolific alkaloid producers of the insect world." Ladybird beetles repel predators in several ways, including the emission of volatile, foul-smelling chemicals and through "reflex bleeding" which can flood the mouthparts of an attacker with alkaloid-laden haemolymph (Holloway et al. 1991). Experiments have shown that coccinellid secretions are unpalatable and potentially harmful or deadly to many species of ants and spiders, some amphibians, lizards, several species of birds, as well as some mammals (Deloze et al. 1995, and references therein). Nevertheless, despite their prodigious chemical defenses, coccinellids are not universally protected: they may be successfully preyed upon by some birds (Majerus 1994), the majority of anuran amphibians (Sloggett 2012), and, among invertebrates, by spiders (Sloggett and Davis 2010), wood ants (Slogget et al. 1999), a pentatomid true bug (Hough-Goldstein et al. 1996), and by some species of coccinellids themselves (Sloggett and Davis 2010). Thus the palatability of Coccinellidae for predaceous *Enoclerus* does not represent an unprecedented case among invertebrates, although it is apparently rare among Coleoptera. It can be assumed that some species of *Enoclerus* have developed a true resistance to the effects of ladybird toxins (rather than tolerance for small amounts), since the quantity of alkaloid presumably ingested after disarticulation and maceration of a relatively large ladybug prey item would presumably be enough to harm or at least repel a clerid without such a physiological adaptation. Sloggett (2012) suggests that resistance to harmful coccinellid alkaloids may have evolved preferentially among generalized predators: those whose modes of predation preclude selection of specific prey items. While this criterion certainly applies to adult *Enoclerus*, which are opportunistic predators known to attack any prey item they can overcome, it applies also to Cleridae in most genera, among whom coccinellid predation has not yet been observed. The evolution of alkaloid resistance in some *Enoclerus* may be related to their diurnal predatory activity and frequenting of flowering plants, behaviors which place them in proximity to aggregations of coccinellids.

Mimicry

Although few *Enoclerus* species can be seen as exact mimics of ladybird beetles, even imperfect mimics have been shown to gain protection when their models (like coccinellids) are relatively common and/or highly toxic (Ruxton et al. 2004). *Enoclerus* often possess bright warning coloration, including among those species observed to feed upon ladybird beetles, and this may confer some protection against the predators (lizards, birds and spiders) that are presumed to exert the greatest selection pressure on diurnally active arthropods. Other Coleoptera are known to both mimic and prey on an aposematically

colored and chemically protected model. For example, the cerambycid beetle *Elytroleptus* Dugès mimics the chemically protected lycid beetle *Lycus* Fabricius, upon which it also feeds (Eisner et al. 1962). And although in this case the predator has not been shown to sequester lycid prey toxins (Eisner et al. 2008), at least one case of coleopteran predator acquisition of protective chemicals from noxious prey has been demonstrated. Eisner et al. (1997) discovered that females belonging to a genus of chemically unprotected firefly (Lampyridae) acquired a defensive steroid by consuming the males belonging to a different, chemically protected genus of firefly. The authors demonstrated that the sequestered toxin was incorporated into the beetles' haemolymph in concentrations high enough to repel predators (jumping spiders) when released through reflex bleeding. And here again, the relationship between predator and prey involves mimicry — a novel, aggressive form in this instance: the female lampyrid lures her male prey by imitating a species-specific flash response to the male's flashing "call" signal.

While most aposematically colored Cleridae are no doubt unprotected Batesian mimics of various noxious models, chemical analysis may eventually reveal that some species belong to Müllerian mimicry rings. Chemically protected Cleridae have been reported in the literature (Mawdsley and Sithole 2010) and I have observed an instance of apparent reflex bleeding in *Chariessa vestita* (Chevrolat), a clerid presumed to mimic a coccinellid or chrysomeline leaf beetle. The possibility that *Enoclerus* may gain chemical protection through the sequestration of coccinellid prey alkaloids would be worthy of investigation. It would provide a second case of chemical protection acquired by a beetle predator from its prey.

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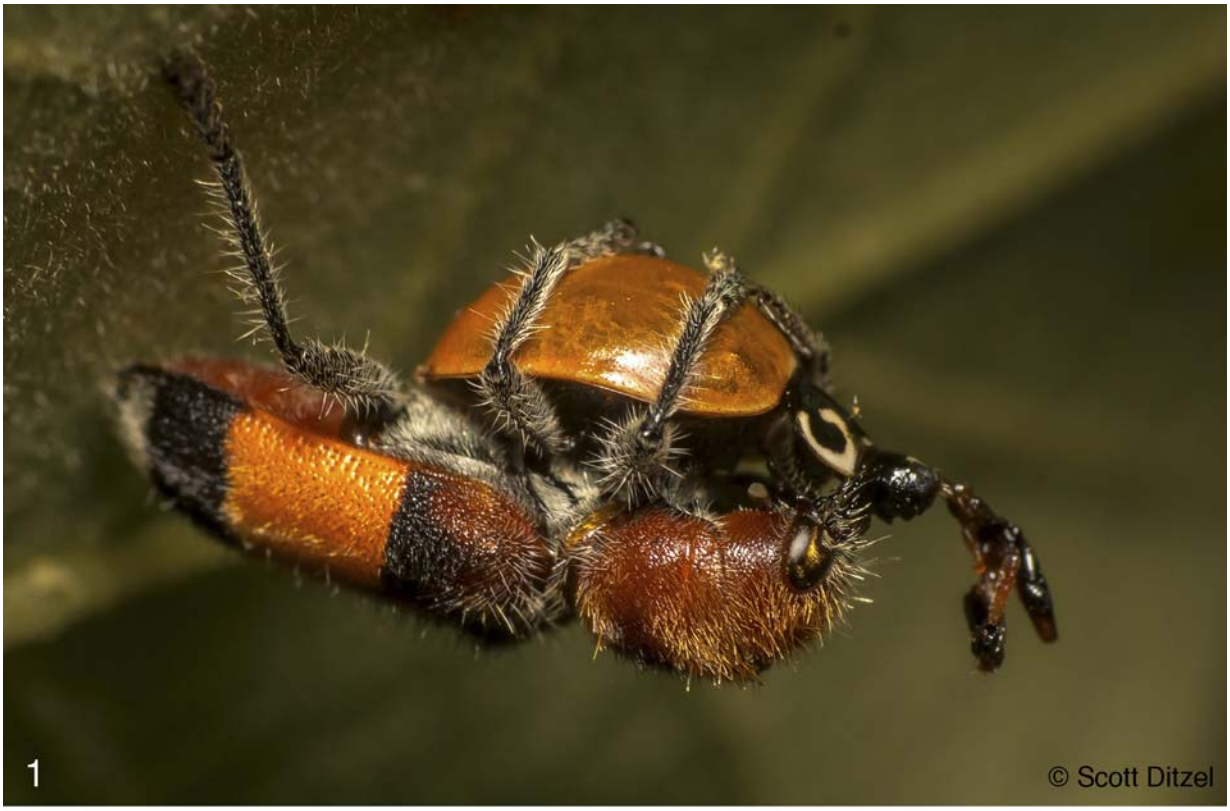

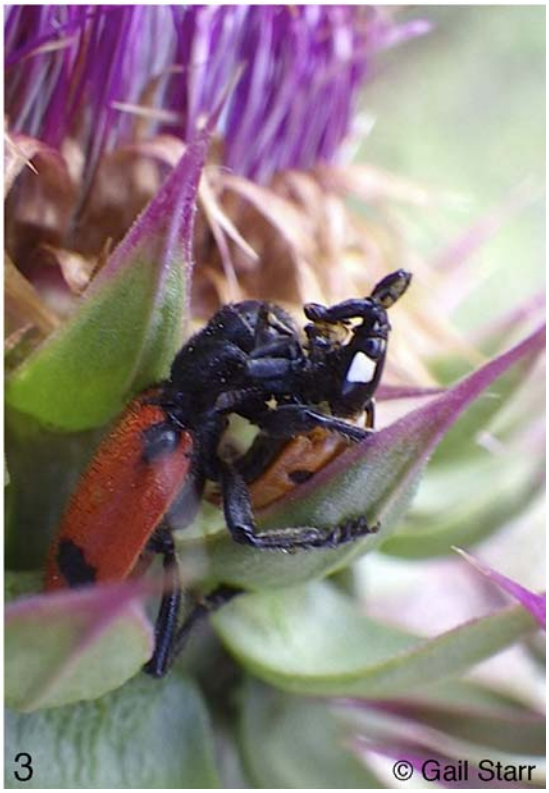

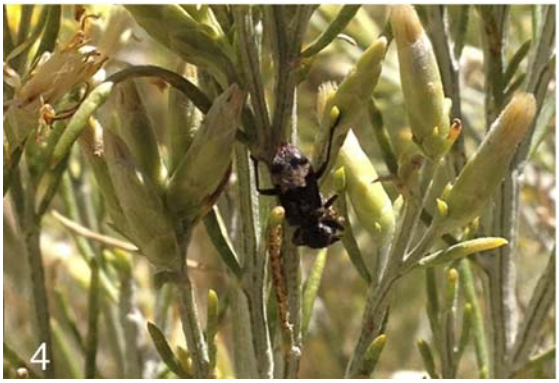

Figures 1–4. *Enoclerus* species feeding on Coccinellidae. **1**) *Enoclerus ichneumoneus* (Fabricius) feeding on *Cycloneda munda* (Say); **2**) *Enoclerus nigripes* (Say) feeding on *Psyllobora vigintimaculata* Say; **3**) *Enoclerus spinolae* (LeConte) feeding on *Coccinella* Linnaeus sp.; **4**) *Enoclerus moestus* (Klug) feeding on unidentified ladybird beetle.