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THE LEPIDOPTERAN HERBIVORES OF THE MODEL PLANT *MIMULUS GUTTATUS*

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ABSTRACT. *Mimulus guttatus* is a widespread riparian plant native to western North America. Due to its wide distribution and phenotypic variation it has been the subject of many studies incorporating genetic information into ecological and life history evolution studies. *Mimulus guttatus* defends itself from herbivory with physical defenses (e.g. trichomes) as well as a suite of phytochemical defenses; phenylpropanoid glycosides (PPGs). Despite its importance as a model organism little has been done on the herbivores that feed on this plant. We used literature records as well as field observations to construct a list of the Lepidoptera that utilize *M. guttatus* as a food plant. Sixteen species of Lepidoptera within five families were recorded as feeding on *M. guttatus*. Six of these species are classified as generalist herbivores, while the rest have varying degrees of host plant specialization.

Additional keywords: *Mimulus guttatus*, phenylpropanoid glycosides, specialization, host plant, herbivore

Mimulus guttatus D.C. (syn. *Erythranthe guttata* (Fisch. ex DC.) G.L.Nesom, Family Phrymacea) is a plant species complex native to riparian areas of western North America. This species is an important model organism for studies of evolutionary genomics and ecology having been cited in over 1,000 studies. This use is in part due to its tremendous phenotypic variation, including variation in life history (annual vs. perennial; Hall & Willis 2006), leaf morphology (Wu et al. 2010), and anti-herbivore defenses (Holeski 2007a, Holeski et al. 2013). In addition to its large native range, non-native populations of *M. guttatus* occur in eastern North America, Europe, and New Zealand (Stace 2010, Webb et al. 1988).

Mimulus guttatus possesses both physical and chemical anti-herbivore defenses (Fig. 1). Physical defenses include trichomes. Although trichomes can serve as both a defense against herbivores and in physiological and abiotic interactions, evidence suggests that they function largely as an anti-herbivore defense within perennial and/or coastal *M. guttatus* populations (Holeski et al. 2010). Many trichomes produced by the species are glandular with sticky secretions (Holeski 2007a). *Mimulus guttatus* also produces a suite of foliar secondary compounds, phenylpropanoid glycosides (PPGs). Phenylpropanoid glycosides have been shown to deter feeding by generalist herbivores (Cooper et al. 1980, Mølgaard 1986) while specialist lepidopteran

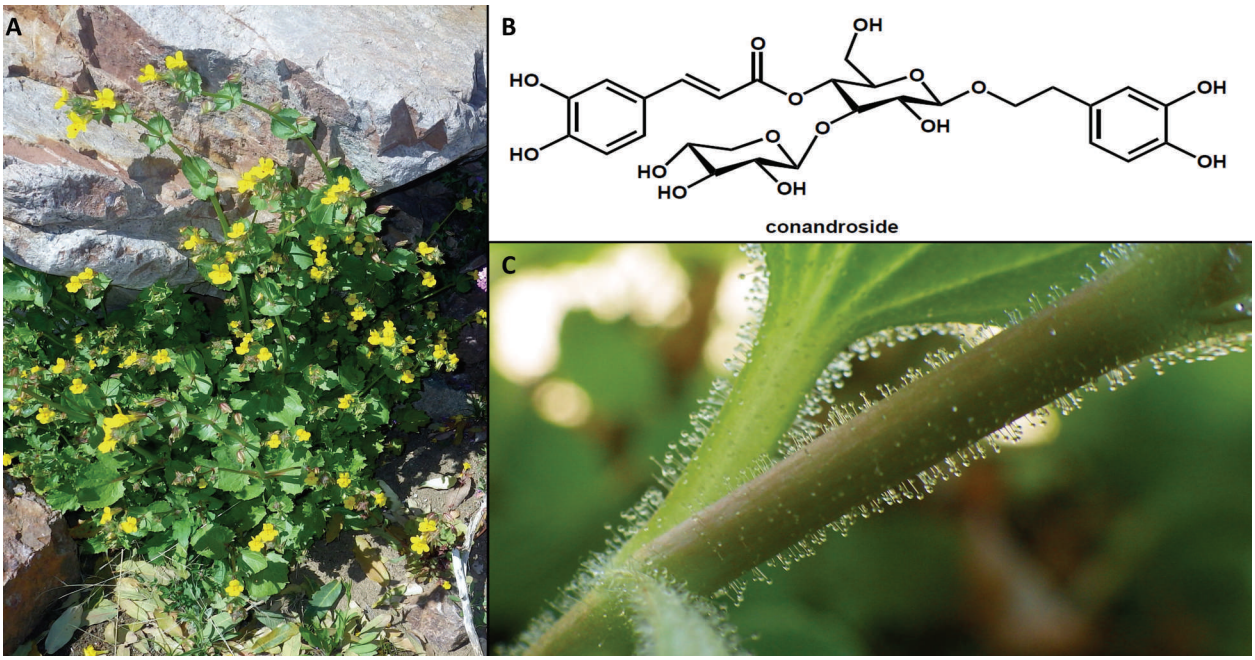

FIG. 1. **A.** *Mimulus guttatus* in a typical habit near flowing water, **B.** Chemical structure of Conandroside, a phenylpropanoid glycoside (PPG) produced by *M. guttatus* that acts as a chemical defense. **C.** glandular *M.guttatus* trichomes, these act as defense from herbivores. Photos by M. Rotter.

FIG. 2. Damage to *Mimulus guttatus* from *Junonia coenia* (Maricopa Co. AZ). Photo by M. Rotter.

herbivores may use at least some PPGs as feeding stimulants (Holeski et al. 2013). Many plant species within the Schrophulariacea sensu lato (where Phrymacea was once included) contain PPGs (Mølgaard & Ravn 1988). This shared phytochemistry leads to many of the same specialist herbivores feeding from plants across the Schrophulariacea sensu lato (Bowers 1988). Despite its defenses, herbivory on *M. guttatus* can still be very damaging to plants (Fig. 2).

Lepidoptera have long been an important order in studies of the co-evolution of plants and their insect herbivores (Ehlrich & Raven 1964). The "arms race" between insect herbivores and plants has driven evolution of novel secondary compounds, as well as the means to sequester or detoxify these compounds within many groups of plants and insects, often leading to evolutionary radiations (Cornell & Hawkins 2003, Marquis et al. 2016). For instance, rapid radiation within the Pieridae butterfly family following an adaptive radiation event in its host plant order Brassicales was most likely due to Pieridae specialization on glucosinolates in Brassicales (Braby & Trueman 2006). A clear picture of the evolution within the Lepidoptera thus necessitates a thorough knowledge of host plant use as well as the host plant range of individual species of Lepidoptera. This review uses literature references as well as our own field observations and rearing records to record the diversity of Lepidoptera that feed on *M. guttatus*. We also discuss the ecological context and chemical ecology of these interactions.

METHODS

To locate *M. guttatus* host records for Lepidoptera we consulted field guides with host records, species catalogues, taxonomic treatments of specific groups, and natural history reports. We checked state and regional field guides from countries where *M. guttatus* is present in order to find species that may use *M. guttatus* only locally. This literature search was combined with over three years (2014-2016) of observational records of Lepidoptera feeding on *Mimulus guttatus*. Over 60 populations of *M. guttatus* throughout its range in western North America were searched for caterpillars. These searches included both visual and sweep net surveys. To be included in our list of species that utilize *M. guttatus* as a host, a caterpillar had to be either observed actively feeding on the plant in the field or was collected from the plant and successfully reared to adulthood on a diet of *M. guttatus* in the lab. To classify the degree of host plant specialization for each Lepidopteran, we recorded a representative list of other species of plants that each Lepidoptera species is known to feed upon

RESULTS AND DISCUSSION

We found 16 species of Lepidoptera within five families that utilize *M. guttatus* as a food plant (Tables 1 & 2). Eight of these species were not previously recorded to feed on *M. guttatus* (Table 2). Of the 16 total species, six are broad generalists while four would be considered specialists on plants in the same clade of families as *M. guttatus* (Scrophulariacea sensu lato). One species has been recorded feeding on other plants within the Lamiaceae (*Stachys* spp.), and for two of the species the only known food plant is *M. guttatus*.

Generalist Lepidoptera found feeding on *Mimulus guttatus*.

The six species of generalist herbivores known to feed on *M. guttatus* are all species with large geographic ranges. For example, *Amphipyra tragopoginis* (Clerck, 1759) (Noctuidae) is a common moth throughout the Holarctic region and can be found throughout the northern portions of the native *M. guttatus* range, although the moth itself may have been introduced to North America (Forbes 1954). *Trichoplusia ni* (Hübner, [1803]) (Noctuidae) is another widespread generalist, with a geographic range covering most of North America, which has been found feeding on *M. guttatus*. We collected this species feeding on multiple *M. guttatus* populations from the northern Cascades to the southern Sierra Nevada Mountains. *Trichoplusia ni* has predilections for members of the Brassicacea but will often feed on any available forb (Powell & Opler 2009;

FIG. 3. **A.** *Herreshoffia gracea* caterpillar from Gila County Arizona. **B.** Freshly emerged adult. Photo by M. Rotter.

FIG. 4. **A.** *Autographa pasiphaeia* caterpillar from Kern county California. **B.** Freshly emerged adult. Photo by M. Rott

Wagner et al. 2011). *Mimulus guttatus* often grows with members of Brassicacea particularly the non-native water cress (*Nasturtium officinale*) (Rotter unpublished data), to which *T. ni* may be initially attracted to and then utilize other plants in the community.

Two generalists that may sequester plant secondary compounds were recorded feeding on *M. guttatus*. The species *Estigmene acrea* (Drury, 1773) (Eribidae) is a widespread generalist throughout North America, and is a pest of many cultivated crops. Late instar caterpillars were collected feeding on *M. guttatus* near Mormon Lake in central Coconino County, Arizona. *Estigmene acrea* was locally abundant at the time of collection (a likely outbreak year in northern Arizona). Although overall a generalist, *E. acrea* does exhibit host plant preferences at different times of its life cycle (Casterjon et al. 2006). As a late-instar caterpillar, *E. acrea* prefer plants that can offer protection from parasitoids via caterpillar sequestration of plant metabolites (Singer et al. 2004). *Grammia incurropta* (Edwards, 1881) (Eribidae) is a common lab species for investigating the evolution of generalist diets (Wagner & Conner 2008), which is also known to sequester and favor plant metabolites in order to "medicate" itself (Smilanich et al. 2011). Records of this species feeding on *M. guttatus* in the field are from Arizona (Michael Singer, personal communication), and the species readily consumes *M. guttatus* in the lab.

There were three records of Lepidoptera feeding on *M. guttatus* outside of its native western North American range, with no records of feeding on *M. guttatus* within its native range. Our records may thus corroborate results of several studies showing that generalist native herbivores may prefer non-native plants (Agrawal & Kotanen 2003, Parker & Hey 2004). The literature record of *Amphipyra tragopoginis* feeding on *M. guttatus* comes from the United Kingdom where *M. guttatus* is a widespread non-native plant (Hancock & Wallace 1986). *Nematocampa resistaria* (Herrich-Schäffer, [1856]) (Geometridae) and *Spodoptera ornithogalli* (Guenée, 1852) (Noctuidae) were recorded feeding on an isolated population of *M. guttatus* (over 1000 km from the next known population of *M. guttatus*) in the Upper Peninsula of Michigan (Ontonagon County). Both of these species are common in eastern North America where they feed on a wide variety of plants (Wagner et al. 2011, Wagner 2005).

Specialist Lepidoptera feeding on *Mimulus guttatus*.

Specialist Lepidoptera that feed on Mimulus guttatus also share other host plant species. For instance the two *Junonia* spp. (Nymphalidae) that feed on *M. guttatus*, as

TABLE 1. Literature references of Lepidoptera feeding on *Mimulus guttatus*.

Family	Species	Geographic Range	Feeding habit	Other Host Plants	Reference
Nymphalidae	*Junonia evarete* (Cramer, 1779)	Southern North America	Leaves	Plantaganacea, Acanthaceae	Stewart et al. (2001)
Nymphalidae	*Junonia coenia* Hübner, [1822]	Southern North America	Leaves	Plantaganacea, Acanthaceae, Verbanacea	Scott (1986), Bowers (1986), Rotter Personal Observation
Nymphalidae	*Euphydryas chalcedona* (Doubleday, 1847)	Western North America	Leaves	Orobanchaceae, Plantaginaceae, Caprifoliaceae, Boraginaceae (some), Rosaceae (some)	Scott (1986), Rotter Personal Observation
Nymphalidae	*Phyciodes mylitta* (Edwards, 1861)	Western North America	Leaves	Asteracea (Cynareae)	Scott (1986), Sewart et al. (2001)
Noctuidae	*Amphipyra tragopoginis* (Clerck, 1759)	Holarctic	Flowers	Generalist	Hancock & Wallace(1986)
Noctuidae	*Annaphila lithosina* Edwards, 1875	California, Oregon	Flowers and leaves	None known	Buckett (1966)
Noctuidae	*Annaphila casta* Edwards, 1890	Northern California, Oregon	Leaves	*Mimulus moschatus*	Powell & Opler (2009), Henne (1967)
Pterophoridae	*Amblyptilia pica* (Walsingham, 1880)	Western North America	Flower buds and seed heads	Scrouphulariaceae, Orobanchaceae, Plantaginaceae, Primulacea, Labiataea, Caprifoliaceae	Matthews & Lott (2005), Rotter Personal Observation
Eribidae	*Grammia incurropta* (Edwards, 1881)	Southwest North America	Leaves	Generalist	M. Singer personal communication

well as *Euphydryas chalcedona* (Doubleday, [1847]) (Nymphalidae), feed on plant species within the Scrophulariacea senso lato as well as other related families (e.g., Plantaginacea, Verbenaceae, and Acanthaceae). We hypothesize that this shared specialization on host plants within and related to the Scrophulariacea senso lato is due to overlap in host plant phytochemical profile. For example, the PPG verbascoside has been reported in many plant species in this group (Jimenez & Riguera 1994; Keefover-Ring et al. 2014). Compounds in another phytochemical group, iridoid glycosides, are present in many of these plants (e.g., Plantaginacea and Verbanaceae) but not *M. guttatus* (M.D. Bowers, personal communication).

The host plants utilized by *E. chalcedona* populations vary by region, as is the case with many Nymphalidae within the tribe Melitanea. For example, coastal California populations of *E. chalcedona* often feed primarily on *Diplacus aurantiacus* (Phrymacea) and populations from the Sonoran Desert feed typically on *Keckiella antirrhinoides* (Plantaginacea) (Kuussaari et al 2004, Rotter personal observation). *Euphydryas chalcedona* use of *M. guttatus* in the wild is likely localized to several populations in California and Nevada, but populations found feeding on other species will oviposit and the larva will feed on *M. guttatus* in the lab. Chemical variation between host plant populations as well as environmental and biotic factors have likely led to local adaptation of *E. chalcedona* populations (Bowers 1986).

The genus *Annaphila* (Noctuidae) contains several species that feed on *M. guttatus*. *Annaphila lithosina* Hy. Edwards, 1875 was documented ovipositing on *M. guttatus*, and its larva feed on flowers of the plant

TABLE 2. Field and laboratory observations of Lepidoptera feeding on *Mimulus guttatus*, not previously recorded.

Family	Species	Location	Date	Feeding Habit	Other recorded host plants	Notes
Erebidae	*Grammia incurropta* (Edwards, 1881)	Captivity		Leaves	Generalist	Laboratory record, M. Singer Personal communication
Erebidae	*Estigmene acrea* (Drury, 1773)	Coconino Co. AZ	9.1.2014	Leaves	Generalist	This was a local outbreak year, reared MR 718
Geometridae	*Nematocampa resistaria* (Herrich-Schäffer, [1856])	Ontonogan Co. MI	6.28.2015	Leaves	Woody plants including, Pinaceae, Sapidanariaceae, Rosaceae, Grossulariaceae	This record is from an introduced population of *M. guttatus*
Geometridae	*Herreshoffia gracea* Sperry, 1949	Gila Co. AZ	4.25.2015	Leaves	None Known	First known larval feeding record, MR 715
Noctuidae	*Spodoptera ornithogalli* (Guenée, 1852)	Ontonogan Co. MI	6.28.2014	Leaves and flowers	Generalist	This record is from an introduced population of *M. guttatus*
Noctuidae	*Spodoptera exigua* (Hübner, [1808])	Captivity		Leaves	Generalist	Laboratory record
Noctuidae	*Trichoplusia ni* (Hübner, [1803])	Fresno Co. CA	5.20.2016	Leaves	Generalist	Common on inland populations in the native range
Noctuidae	*Autographa pasiphaeia* (Grote, 1873)	Kern Co. CA	4.13.2015	Flower buds and leaves	*Stachys ajugoides* and *S.rigida*	MR 716

(Buckett 1966). Prior to 1966 the host plant of *A. lithosina* was unknown, and Buckett speculated that *M. guttatus* may be the only host plant for *A. lithosina*. *Annaphila casta* Hy. Edwards, 1890 (which forms a complex with *A. lithosina* and *A. miona* Smith, 1908) was recorded to readily feed on *M. guttatus* in captivity, and oviposits on *M. moschatus* in the wild (Henne 1967). Further study of the relationship of *Annaphila* spp. and *M. guttatus*, particularly regarding how the moths interact with PPGs could help elucidate the natural history of the beautiful but little-studied *Annaphila*.

Other host records on *Mimulus guttatus*.

During the course of this study two particularly interesting records of Lepidoptera feeding on *M. guttatus* were recorded. The first record is the first documented host plant record for *Herreshoffia gracea* Sperry, 1949 (Geometridae) (Fig. 3). This moth was originally described from Oak Creek Canyon, Coconino County, Arizona (Sperry 1949). We collected several late instar larval geometrid species from *Mimulus guttatus* along Fossil Creek, Gila County, Arizona in April of 2015. Both Oak Creek and Fossil Creek are semi-shaded perennial streams running through canyons on the edge of the Mogollon Rim of northern Arizona. We collected mature caterpillars actively feeding on *M. guttatus*; live caterpillars were also taken back to the lab where they were fed until they pupated. One adult was successfully reared (all other pupae had parasitoid wasps which emerged after 18 days in a chrysalis; Specimen MR 715, Northern Arizona University). *Herreshoffia gracea* has been recorded in Coconino, Cochise, and now Gila Counties in Arizona and Siskyou County in northern California (Moth

Photographers Group, 2016); in every recorded county for this moth *M. guttatus* is a common riparian plant. Although it is not known if *H. gracea* utilizes other plants, many other members of the Geometrid tribe Xanthorhioni are limited in their larval diet breadth (Powell & Opler 2009).

We collected late instar caterpillars of *Autographa pasiphaeia* (Grote, 1873) (Noctuidae) (Fig. 4) from *M. guttatus* along the Kern River, Kern County, California. These were reared in the lab and had adults successfully emerge (Specimen MR 716 Northern Arizona University). This species ranges throughout California and into Oregon (Powell & Opler 2008). Within this range the common host plant is *Stachys* spp. (Lamiacea), which shares a common clade with *M. guttatus* within the order Lamiales (Stevens 2001). Several Stachys species contain verbascoside (Jimenez & Riguera 1994), a PPG that is also present in *Mimulus guttatus*.

Suspected hosts on *Mimulus guttatus*.

There are several records of the Nymphalid *Phyciodes mylitta* (W.H. Edwards, 1861) using *M. guttatus* as a host plant. More often the host plants of *P. mylitta* are listed as members of the Asteracea tribe Cynareae (thistle tribe). *Mimulus guttatus* is thus an odd addition to this group. The first record of *P. mylitta* on *M. guttatus* appears in Scott's work on North American butterflies (1986). It appears that this record may simply have been repeated in later citations. However, *P. mylitta* is common in many areas where *M. guttatus* is present, so further investigation may be warranted.

Spodoptera exigua (Hübner) (Noctuidae) is a widespread generalist that can utilize a wider array of plants as hosts. This species was reared in the lab on *M. guttatus* and could likely utilize it in the wild.

Conclusion

The Lepidoptera fauna that utilizes *M. guttatus* is composed of specialists that also feed on relatively limited numbers of other, related plant species, as well as multiple broad generalists. Although several species have been recorded to have *M. guttatus* as their sole host, this may merely be due to limited records for these Lepidoptera. We are currently conducting no-choice feeding trials using several of the species listed here to characterize the relationship between *M. guttatus* defense traits and herbivore performance. Understanding how these defense traits influence herbivores of *M. guttatus* as well as a thorough knowledge of the diversity feeding on *M. guttatus* will contribute greatly to understanding the evolutionary and ecological history of this model organism.

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