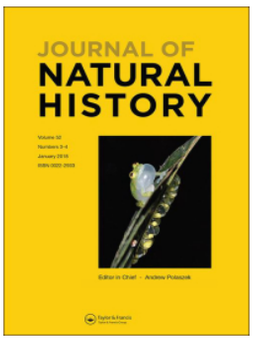

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An annotated checklist of the herbivores and seed predators of *Mimulus guttatus*

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ABSTRACT

Mimulus guttatus (syn: *Erythranthe guttata*) is an important model organism in evolutionary ecology research. However, besides a few scattered reports of a single herbivore species at a time, there has only been one published list of herbivores that attack *M. guttatus*. I combined literature records as well as records from over five years of field surveys to include a range-wide list of species that attack *M. guttatus*. These records included plant populations from the native range in western North America and the non-native ranges in the United Kingdom and Eastern North America. I recorded over 86 species that consumed *M. guttatus* through its native and introduced ranges. In the native range, 77 species were found. In the UK, I reported 22 species of herbivores while in the eastern North America populations I recorded seven species feeding on *M. guttatus*. The native western North America range shared nine species with the UK range (mostly gastropods) and shared five herbivores with the eastern North America populations (mostly generalist mammal herbivores). I expect this list to grow as more studies focusing on plant–herbivore interactions in *M. guttatus* are published. I hope this list starts as a foundation for these future studies.

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Introduction

Mimulus guttatus DC (syn: *Erythranthe guttata*, Phrymaceae) is an important model organism in evolutionary ecology research. Due to its large range, its spread as a non-native species, ease of propagation in the laboratory and greenhouse, varied traits, and the genetic resources available for its study, there have been hundreds of papers published on this herbaceous model plant.

As *M. guttatus* has been developed into a model organism, the characterisations of its herbivore resistance traits have allowed it to be used in investigations of the genetics and evolution of resistance traits (Holeski 2007; Holeski et al. 2013; Lowry et al. 2019), how plant resistance traits interact with herbivores (Rotter et al. 2018) and how these resistance traits are structured across the landscape (Kooyers et al. 2017). These studies have put a spotlight on *M. guttatus* as an increasingly relevant model organism for plant–herbivore interaction studies.

However, besides a few scattered reports of a single herbivore species at a time, there has only been one published list of herbivores that attack *M. guttatus* (Rotter and Holeski

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Figure 1. Field damage and herbivores on *Mimulus guttatus*. (a). Leaf mining damage (*Chromatomyia sp.)* from an Alaskan plant. (b). Aphids attack a plant in California USA. (c). *Philaenus spumarius* feeding along with signs of caterpillar damage on a plant from New Brunswick Canada. (d). Deer feeding damage from plant in Michigan USA. (e). Sawfly larvae feeding on a flower in Scotland United Kingdom. (f). A very photogenic horse feeding on whole plants in England United Kingdom.

2017) and this publication only focused on one group of animals, the Lepidoptera. This is despite the consistent and heavy damage that these plants can receive (Figure 1). A multi-taxa list of herbivores can aid future researchers in understanding the selection pressures from a variety of herbivores in natural populations. Here I present a multi-taxa list of herbivores that were collected from literature records, extensive field collections, and laboratory feeding records.

Methods

Literature records for herbivores feeding on *M. guttatus* included searches of primary literature, field guides, species catalogues, natural history notes, and taxonomic treatments. I also searched local and regional field guides within the native and non-native range of *M. guttatus* to check for local host use by herbivores. In addition to published literature, I looked for records on online databases (e.g. bugguide).

I combined these literature records with over 4 years (2014–2018) of observations and field surveys. Field surveys and observations came from over 80 populations of *M. guttatus* from its native range in western North America, as well as non-native populations in the United Kingdom and eastern North America. These searches were composed of both visual and sweep net surveys. Taxa identified from visual surveys included both invertebrate and vertebrate herbivores. Within the visual surveys, signs of feeding damage were searched for on the plants. Visual surveys were typically timed where I spent around 5 minutes searching in 1 × 1 metre patch of *M. guttatus* and then expanded out systematically to the entire patch. I also used game cameras plus field observations of the

animals feeding. Invertebrates were considered feeding on *M. guttatus* if directly observed feeding or if they were on a plant and were also a species that would likely consume *M. guttatus*. Sweep netting was done only in areas that had high densities of *M. guttatus* so as not to catch insects that may have been feeding on closely growing plants. These sweeps were completed after the visual surveys and timed in a similar manner. All of the searches took place during the growing season. If it was ambiguous that an invertebrate consumed *M. guttatus* I would collect the animal alive when possible and feed it *M. guttatus* material in the lab. For more details on sampling methods see Rotter et al. (2019). I then used literature records to try to assess the relative degree of dietary specialisation that an animal has on *M. guttatus*. All specimens are stored at Northern Arizona University.

Summary

I recorded over 86 species that consumed *M. guttatus* through its native and introduced ranges (Appendix 1). Almost all the records came from field surveys and new observations with three records from literature records alone. In the native range, 77 species were found. In the UK, I found 22 species of herbivores while in the eastern North America populations I found seven species feeding on *M. guttatus*. The native western North America range shared nine species with the UK range (mostly gastropods) and shared five herbivores with the eastern North America populations (mostly generalist mammal herbivores) (Figure 2).

Of the groups of herbivores, Lepidoptera (20 species) and Gastropods (18 species) are by far the most species-rich groups of herbivores feeding on *M. guttatus* (Figure 2). This

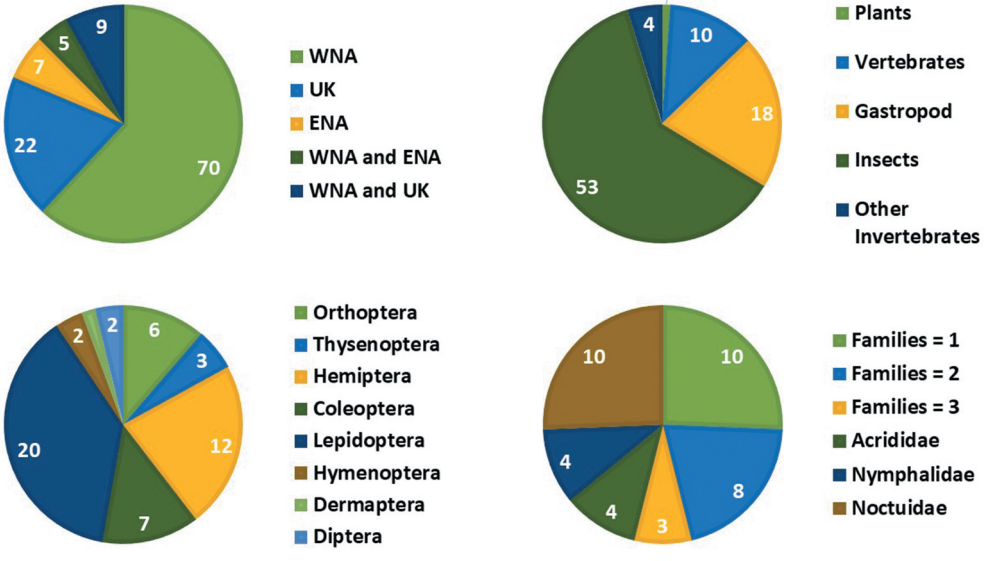

Figure 2. Herbivore richness in surveys and literature records of animals feeding on *Mimulus guttatus*. (a). Species richness for different regions of *M. guttatus* range WNA = western North America, UK = United Kingdom, ENA = eastern North America. (b). Species richness between different major groups. (c). Insect species richness of insect orders. (d). Insect species richness for insect families.

skew in groups could be from two reasons. First, Lepidoptera were the singular focus of their own study and were specifically sought out (Rotter and Holeski 2017). This group is also one of the most studied groups of insects and the access to literature and regional treatments greatly expanded my ability to find feeding records. The high number of gastropod records was driven in large part by this group's generalist feeding habits as well as their ubiquity in the United Kingdom, where many of the species records for this taxa came from. Lastly, some of the groups actually present on *M. guttatus* may be severely under-represented in this study, specifically the true bugs. Many of these taxa are poorly defined and there may be cryptic species that I was unable to detect. For example, the genus *Graphocephala* contains at least 17 species in North America Tripplehorn and Johnson (2005) Although I only report this herbivore at the genus level, it is likely there are several species that may regularly attack *M. guttatus.*

The great majority of the recorded species that consume *M. guttatus* should be considered to be dietary generalists. In all, there are likely only about ten species on this list that should be considered specialists. Of these suspected specialists, most are Lepidoptera (as above, this is most likely because of the knowledge of lepidopteran diet breadth is greater in general). In addition to the Lepidoptera, there was one Coleoptera (specimens in the poorly taxonomically resolved genus *Allosirocalus)* as well as several species of leaf-mining Diptera that are very common in several regions of the native range. I found very little evidence of specialists outside of the native *M. guttatus* range in western North America. In the UK I found no evidence of introduced specialist herbivores from western North America or that a specialist herbivore native to the UK had 'switched' to feed on *M. guttatus*. For example, in the UK I searched for the Curculionidae *Cionus scrophulariae*, which is present in the UK and is a specialist on plants that shares the same class of phytochemicals (phenylpropanoid glycosides) to *M. guttatus* (Brock 2014). I did not find any evidence of this species feeding on plants or in the vicinity of *M. guttatus* in the UK. This was further supported by several ad-hoc field attempts to feed *M. guttatus* to *C. scrophulariae*. However, in a few of the eastern North America populations, the specialist Lepidoptera *Junonia coenia* and *Euphydryas phaeton* were present as adults. Although neither was found exhibiting any behaviour that suggested their use of *M. guttatus* in eastern North America, it would not be surprising if they did use these non-native *M. guttatus* plants. *Junonia coenia* readily consume and oviposit on *M. guttatus* in the native western North America range while *E. paeton* uses species that also produce phenylpropanoid glycosides to *M. guttatus* (Scott 1986; Jimenez and Riguera 1994). I expect this list to grow as more studies focusing on plant–herbivore interactions in *M. guttatus* are published. I hope this list starts as a foundation for these future studies.

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Disclosure statement

No potential conflict of interest was reported by the author.

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Data Availability Statement

All specimens are stored at Northern Arizona University.

Geolocation Information

Data was collected from western North of America north of Mexico including the Black Hills region of Wyoming and South Dakota. Sites in eastern North America were located in Michigan, New York, and New Brunswick Canada. The United Kingdom, excluding Northern Ireland, was also sampled.

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Appendix 1.

Organisms that have been found or have literature reports of feeding on *M. guttatus*. ENA: Denotes a species found consuming *M. guttatus* only in Eastern North America.

UK: Denotes a species found consuming *M. guttatus* only within the United Kingdom.

+ Denotes a species found consuming *M. guttatus* in the non-native range and in the native range.

Bold – Denotes a species with a suspected narrow (specialist) diet breadth that is limited to *M. guttatus* or its relatives (Scrophulariaceae *senso lato*).

Plants

A dodder was discovered attached to a single individual of *M. guttatus* in north central Idaho USA. Although a parasite and not an herbivore (but probably worthy of inclusion here: Pennings and Callaway 2002) it is included here as a natural history note. The dodder in question is a generalist plant parasite of mostly herbaceous plants (Costea and Stefanović 2012) and it is reasonable to assume that this plant could be at least a somewhat regular parasite on *M. guttatus*.

Convolvulaceae

Cuscuta occidentalis

Vertebrates

Although often producing heavy damage when they occur, vertebrates are only a small portion of the herbivore diversity of *M. guttatus*. Most of the damage they cause most likely comes not from a preference for *M. guttatus* but as happenstance during regular grazing by herbivores. For instance, in the United Kingdom, *M. guttatus* has successfully colonised many wet pastures. Within these pastures there is typically a fairly high density of domestic animals, this density may lend itself to animals taking advantage of almost any palatable plant that can be found. Additionally, in the native range, vertebrate herbivores may impose an important fitness cost to *M. guttatus* as many of the observations of Cervidae preferentially consume the taller flower and seed-bearing shoots. Many of these records came from direct observations and game cameras with one literature record. I made one observation of birds (lesser goldfinch) that were consuming the seeds from a population of *M. guttatus*. Damage caused by birds was suspected several times although it was only confirmed during this single observation. Birds feeding on seeds may be rare but could have important impacts on individual plant fitness.

Aves
Fringillidae
Spinus psaltria (Observed feeding on seed heads)
Mammalia
Bovidae
Ovis aries [UK]
Bos taurus +
Cervidae
Odocoileus virginianus[ENA]
Odocoileus hemionus
Cervus Canadensis
Cricetidae
Ondatra zibethicus
Microtus californicus (Popovic and Lowry 2019)
Equidae
Equus caballus[UK]
Leporidae
Leppus spp.+
Gastropoda

Although encountered feeding frequently on *M. guttatus* in only two regions (North America Pacific Coast and the UK) snails and slugs are among the most destructive herbivores of *M. guttatus*. Some of the most extreme damage observed on *M. guttatus* consisted of gastropod damage, and the cryptic feeding nature of gastropods (e.g. feeding at night, totally consuming a seedling) may have concealed capturing the full extent of damage caused and their diversity. Gastropods may also act as significant predators of seedlings, which would have gone unrecognised in our observational field surveys. For example, seedlings in the Northern Arizona University greenhouse were decimated by *Deroceras leave* slugs. These slugs exhibited clear preferences for specific seedling genotypes in the greenhouse. Preferred genotypes were completely lost to this slug only a few days after germinating.

Several gastropod taxa are found both in the native North America range and the introduced European range of *M. guttatus*. For example, *Cornu aspersum* is introduced in both North America and in the UK (Burke and Leonard 2013) where we observed it feeding on *M. guttatus* within both ranges. This geographic pattern is the same for slug species *Deroceras laeve* were it is a particularly common herbivore, taking advantage of its tolerance to changing water levels and flooding which is a common characteristic of the *M. guttatus* habitat. Some of the species, such as *Cepaea nemoralis*, are found in the UK (natively) and in the North America range (non-native) but have only been observed thus far feeding on *M. guttatus* in the UK. We suspected that where both occur in North America, *C. nemoralis* would consume *M. guttatus*. In addition to these widespread generalists, the species *Oxyloma haydeni* was found consuming *M. guttatus* in the native range at several sites. All gastropod observations came from direct observations in the field as well as follow-up observations of feeding trials.

Agriolimacidae
Deroceras invadens [UK]
Deroceras laeve +
Deroceras reticulatum +
Arionidae
Arion intermedius
Arion ater [UK]
Arion rufus [UK]
Arion fuscatus[UK]
Arion subfucus+
Gastrodontidae
Ventridens demissus
Zonitoides arboreus

Helicidae
Helix pomatia+
Cornu aspersum +
Cepaea nemoralis[UK]
Cepaea hortensis[UK]
Limacidae
Limax flavus
Ariolimax californicus
Ariolimax columbianus
Succineidae
Oxyloma haydeni

Crustacea

Although the terrestrial isopods (suborder Oniscidea) are mainly detritovores, they may occasionally consume fresh plants or at least take advantage of plants that may be vulnerable to increased herbivory (most observations have been on senescing plants). These animals are generally common within populations of *M. guttatus* where they benefit from the wet shady habitats as well as the detritus that this physical environment provides. These records come from direct observations as well as a feeding trial for confirmation.

Armadillidiidae
Armadillidium vulgare
Porcellionidae
Porcellio scaber +

Arachnida

Mites are extremely diverse with many undescribed and cryptic species. Although many are predatory (I collected these predatory mites on *M. guttatus* often), there are numerous species that feed on plants. Within western North America, herbivorous mites are fairly common. The family Tetranychidae are economically important and have been found feeding on *M. guttatus* in the field as well as in the lab. The field records are from sweep netting.

Tetranychidae
Tetranychus telarius
Tetranychus urticae

Insects

Insects are the most diverse group of feeders on *M. guttatus*. They span the dietary generalist/specialist spectrum. Most of the published literature on herbivory and *M. guttatus* has focused on insects.

Orthoptera – This group of mainly generalist insects (Capinera et al. 2004) likely consumes *Mimulus guttatus* frequently. Various Orthopterans were collected from time to time and fed *M. guttatus*. None of the Orthopteran species tested rejected the plant as food and many nymphs could go through multiple instars. *Oecanthus fultoni* (Oecanthinae) have been found on numerous populations of *M. guttatus* as well as populations of *M. cardinalis* (*Erythranthe verbanaceus)*. These populations are mostly glandular populations of *M. guttatus* with *M. cardinalis* being a 'sticky' plant itself. Likely these tree crickets are taking advantage of carrion on the sticky residue and may only occasionally consume plant material (Krimmel and Pearse 2013).

Acrididae
Dissosteira carolina
Melanoplus femurrubrum
Melanoplus bivittatus
Xanthippus corallipes
Oecanthinae
Oecanthus fultoni
Oecanthus quadripunctatus

Thysanoptera – Although occasionally found during field observations and visual surveys, western flower thrips have been most frequently found in the greenhouse as pests. In the greenhouse, this pest has been observed feeding on flowers, where it often can discolour or mottle the

petals. Occasionally the populations can be extremely abundant and cause mass damage on populations in the greenhouse.

Thripidae
Thrips magnus
Thrips tabaci
Frankliniella occidentalis

Hemiptera – The true bugs are abundant herbivores and include some interesting herbivores that likely have large fitness impacts. Both in the field and in the greenhouse aphids can build up to relatively large levels on the plants. These are mostly generalist species. A few of these species, such as the Berytidae, feed primarily on plant material but may also take advantage of carrion associated with the glandular trichomes present on some populations of *M. guttatus*. Spittlebugs have also been the subject of several studies (Eubanks et al. 2005; Ivey and Carr 2005; Holeski 2007; Ivey et al. 2009) and are common on some populations. These insects were observed in the field in both visual and sweep netting sampling.

Aphidae
Aphis gossypii
Myzus persicae
Aleyrodidae
Trialeaurodes vaporariorum
Berytidae
Neides sp.
Cercopidae
Philaenus spumarius +
Cicadellidae
Draeculacephala sp.
Graphocephala sp. – several species
Gyponana sp.
Miridae
Lygocoris pabulinus[UK]
Lygus linerolaris
Membracidae
Stictocephala bisonia
Pentatomidae
Murgantia histrionica

Coleoptera – The beetles are a large group with several common herbivores for *M. guttatus*. Many of the species here are generalists; many will feed on flowers and buds. The members of the genus *Allosirocalus* likely represent a specialist herbivore of *M. guttatus*. However, at this time, this group is in flux with species poorly defined. All beetles were observed feeding on *M. guttatus* in the field through visual and sweep netting surveys.

Curculionidae
Allosirocalus spp.
Otiorhynchus sulcatus
Chrysomelidae
Diabrotica undecimpunctata
Exema sp.
Buprestidae
Acmaeodera sp.
Scarabaeidae
Paracotalpa granicollis
Dermestidae
Dermestes spp.

Lepidoptera – The most well-studied group of *M. guttatus* herbivores with many generalists and specialists found. They have been the subject of a review (Rotter and Holeski 2017) as well as several studies that detail these group interactions with the plants (Holeski et al. 2013; Rotter et al. 2018;

Haber et al. 2018). All the species listed in Rotter and Holeski (2017) are listed here as well as a few additional species that were discovered and identified after 2017 from additional field collections.

Noctuidae
Pyrrhia exprimens
Phlogophora meticulosa[UK]
Spodoptera ornithogalli
Spodoptera exigua
Trichoplusia ni
Helicoverpa zea (Lab record, Haber et al. 2018)
Amphipyra tragopoginis
Annaphila lithosina
Annaphila casta
Autographa pasiphaeia
Geometridae
Pseudopanthera macularia[UK]
Nematocampa resistaria
Herreshoffia gracea
Erebidae
Grammia incurropta
Estigmene acrea
Nymphalidae
Junonia evarete
Junonia coenia
Euphydryas chalcedona
Phyciodes mylitta
Pterophoridae
Amblyptilia pica

Hymenoptera

Mimulus guttatus is associated with many species of Hymenoptera beyond herbivory (e.g. ants tending to aphids and bumblebees visiting flowers). This order is relatively underrepresented for herbivores. There is one notable exception in the sawflies. This group of herbivores with 'Lepiform' larvae can be particularly common. Within the UK there were repeated observational records of *Macrophya albicincta*. This species has typically been recorded as feeding on members of the Caprifoliaceae in the past. In this case, it may be an example of a host shift onto a novel non-native host. Some members of the Caprifoliaceae have been found to contain phenylpropanoid glycosides a broad class of phytocompounds also found in *M. guttatus* (Jimenez and Riguera 1994). Additionally, there was a species of sawfly collected a visual observation from a population in the Eastern North America region as well.

Tenthredinidae
Macrophya albicincta[UK]
Dolerus asper[ENA]

Dermaptera

One species of earwig was found on populations of *M. guttatus*. Although this species tends to prey on other invertebrates as well as eating decaying vegetation, it can cause significant damage to living plants including *M. guttatus* flowers. It has been found in both the native and non-native range (UK and eastern North America) during both sweep netting and visual observations.

Forficulidae
Forficula auricularia+

Diptera

Although generally diverse and a likely pollinator of many *Mimulus* species, their impacts as herbivores are limited to one group of species. All the members of Agromyzidae that feed on *M. guttatus* are leaf miners and likely a specialist herbivore. The larvae can cause severe damage to foliage but have only been observed within leaves that are next to the water or submerged. Additionally, these insects seem to be predominated on plants in the more northern and coastal

populations. There are additional species in this family that attack other monkeyflowers such as *Diplacus arranticus*. Larvae were found during visual observation surveys.

Agromyzidae

Chromatomyia mimuli

Chromatomyia horticola