Drosophilids of the Midwest and Northeast

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Introduction
I. Introduction

A. PURPOSE OF THE GUIDE

*Drosophila melanogaster* has been of foundational scientific importance since the early years of the 20th Century in studies of genetics, development, and molecular biology. With growing recognition of homologies between genes in *Drosophila* and those in humans, the scientific importance of this species continues to grow, and it is now being used as a model organism in studies of such topics as addiction and innate immunity.

*D. melanogaster* belongs to the family Drosophilidae, which comprises 73 genera and over 4300 species (Bächli 2016), making it nearly as diverse as the entire class of Mammals. The family is worldwide in distribution and ecologically diverse, with various species inhabiting most terrestrial ecosystems on earth. Such diversity, anchored by perhaps the most important model species in biology, provides almost limitless opportunities to explore the genetic and evolutionary basis for all manner of morphological, physiological, behavioral, ecological, and symbiotic variation.

The present guide is intended to provide a gateway for students, teachers, and researchers at all levels to the study of the Drosophilidae of the Midwest and Northeast regions of the United States, as well as adjoining regions in Canada. For researchers, the guide is intended to facilitate identification of our local species that they might be interested in studying or otherwise be unfamiliar with. For teachers, the diversity of drosophilids in our area provides abundant opportunities to develop new field and laboratory exercises for their classrooms. Finally, we hope that our guide will inspire young people to take a close look at nature and perhaps develop a lifelong interest in natural history and science.

A new feature of Version 2.0 of this guide is the bedtime story, which is meant to reach out to kids of very young age. The story was written and designed by our co-author Tessa Steenwinkel (a second-year undergraduate student) and drawn by our illustrator Natalia Werner (7 years old). We wish that parents and educators read it to their children, hoping to set a precedent of how exciting science books can be.

We focus on the Midwest and Northeast for several reasons. First, we are both based in this area (the Upper Peninsula of Michigan and western New York), and most of our research has focused on species in this region. Second, being at temperate latitudes, this region harbors a moderate, but not overwhelming, level of diversity, providing plenty of material for scientific study. Finally, there are a great many colleges and universities in this part of the country, and one of our goals is to show students and faculty that there are abundant opportunities for research on drosophilids using species that can be found in one’s backyard or nearby woods.

B. HOW TO USE THE GUIDE

The species in this guide are presented along phylogenetic lines, not taxonomically or alphabetically, so that closely related species are presented sequentially. Our phylogenetic arrangement is based on a consensus of several recent studies (Perlman et al. 2003; van der Linde et al. 2010; Morales-Hojas and Vieira 2012; Rabosky and Matute 2013; Russo et al. 2013; Itzumitani et
al. 2016). As more genes (or genomes) and species are sequenced, adjustments to the phylogeny may be necessary. One consistent finding of these studies is that the genus *Drosophila* is paraphyletic. As a result, species of several genera, including *Scaptomyza*, *Zaprionus*, and *Mycodrosophila*, are phylogenetically nested within *Drosophila*, and are thus presented as such in our guide.

For each species, we present photographs of average-looking male and female flies, as they would appear live under the microscope, including dorsal and lateral views. A dorsal view with 1 mm scale to indicate the relative sizes of flies is included at the beginning of the text section for each species.

We also include photos of the male and female wings, whose general coloration and shading patterns provide good identification marks. The photos include notes on key traits to look for in the various species. Finally, for each species, we include a set of photos showing the range of phenotypic variation often seen in the wild. While some species show very little variation, others are so variable that one might be tempted to call them different species.

In addition to photos, we include for each species a “traffic light” box with three salient features of a species, which give an indication that the reader is on the right track in identifying a specimen; text describing additional key features by which to identify flies; a brief description of similar species and how to distinguish them; and suggestions on how to collect and culture that species. Finally, for each species we have written a page or two on various aspects of its biology, including:

**Taxonomy**: Subgenus and species group. In some cases, we provide an overview of its relationship to other species or a few words on the species group.

**Distribution**: Known distribution in our area, based largely on literature sources, but to some extent on our own collections as well. We also mention range shifts of native species and whether a species is invasive.

**Breeding sites**: Our focus is on breeding sites (i.e., where adult flies oviposit and larvae feed) rather than where adult flies feed and can be captured, based largely on literature sources.

**Modes of reproductive isolation**: Between focal species and close relatives.

**Meiotic drive**: Primarily sex-ratio meiotic drive, as this is most readily evident in non-model species and can have important effects on behavior, ecology, and evolution.

**Parasites and pathogens**: Including nematode parasites, parasitoid wasps, and pathogenic fungi, bacteria, protists, and viruses.

**Endosymbionts**: We focus on maternal-transmitted bacterial symbionts, of which two are known in *Drosophila*—*Wolbachia* and *Spiroplasma*.

**Behavior**: Both sexual and non-sexual.

**Life history**: This includes variables such as egg and clutch size, rate of development, and age of reproductive maturity.

**Physiological ecology**: Adaptations to various environmental conditions, including adaptation to climate change.

**Miscellaneous curiosities**: (though not labeled as such): Includes features such as transposable elements and B chromosomes.

In cases where we have been unable to find any
information about a particular topic for a given species, we have omitted that section from a species page. For some species, notably *D. melanogaster*, one could devote a lifetime writing 1000s of pages, while for some others, essentially everything that is known can be summarized in a few sentences. For some species, we have taken the liberty of suggesting potentially interesting lines of future research. For ease of use, the references for each species are listed at the end of the text for that species, rather than compiled in a single comprehensive list at the end of the book.

While the use of technical terms and language can be highly efficient for communication among professionals, such terms can present significant hurdles to understanding by others. Accordingly, we have tried to minimize the use of non-essential technical language in our descriptions of the species in our guide.

The last general guide to the Drosophilidae that included our region was *The North American Species of Drosophila*, published in 1921 by A.H. Sturtevant, who had previously, as a graduate student at Columbia University, developed the concept and practice of genetic mapping. Since the publication of his book, numerous new species of Drosophilidae have been described in our area, and research on various aspects of the biology of *Drosophila* has exploded. In addition, our area has been invaded by several species of drosophilids that were not present in Sturtevant’s day. Thus, we believe that there is a need for an updated guide to these species.

Remarkably, another group has independently produced a guide to the *Drosophila* of our region (Miller et al. 2017). The authors were kind enough to share their guide with us prior to publication. As a consequence, we have tailored our guide to minimize (or at least reduce) redundancies between our guide and theirs. Because both guides are available online without cost, we encourage users to consult both of them. Miller et al. (2017) is particularly strong in providing: 1) detailed illustrations of the various body parts of *Drosophila*, including genitalia, 2) dichotomous, illustrated keys to both genera of Drosophilidae and species of *Drosophila*, 3) maps showing the specific locations where each species has been collected in our region, and 4) data on the habitats from which museum specimens were collected. Because both guides are freely available online, we saw no need to replicate that information in our guide.

Our guide differs from Miller et al. (2017) in several respects. Our photographs are based on live, rather than pinned, specimens and thus more closely resemble live flies as one might view them under the microscope. We also present photos of the range of phenotypic variation commonly seen in the wild. Finally, we provide brief biosketches of each species, highlighting what we consider to be interesting aspects of their biology, as well as suggesting possible future areas of research on these species.

**C. QUICK KEY TO COMMON SPECIES**

For collectors using baits of fruits, vegetables, or mushrooms, there is a set of relatively common species that one is most likely to encounter. (Of course, the most common species will vary among areas covered by our guide.) For these common
species, we present a non-technical one-page key to enable users to quickly identify many of the individuals that they collect. However, we urge readers to consult the actual pages for these species for further information that may or may not support their initial identification.

This first edition of our guide did not include species belonging to four genera of Drosophilidae: *Rhinoleucophenga*, *Cladochaeta*, *Stegana*, and *Microdrosophila*. These genera are ecologically unusual within the family, and they are unlikely to be encountered using collection methods aimed at *Drosophila*. According to Miller et al. (2017), the larvae of *Rhinoleucophenga* and *Cladochaeta* prey on scale insects and spittlebugs, respectively; *Stegana* feed on dead and diseased trees; and the breeding sites of *Microdrosophila* are essentially unknown. We now included these genera in Version 2.0.

**D. COLLECTION METHODS**

Many Drosophilid species can be collected with a net or aspirator from wild mushrooms, baits, and traps. Close attention should be paid to shelf mushrooms because species that feed on them rarely visit traps and baits. To attract and collect flies, we have used baits or traps of bananas, tomatoes, mushrooms, and beer (see Figure above). Cantaloupe baits are also popular with some fly people. Finally, Malaise traps can be useful to collect species that rarely or never come to traditional *Drosophila* baits.

**Banana traps** can be made of plastic bottles containing a mixture of over-ripe banana, Baker’s yeast, and a few sticks as perching sites. These traps are hung on tree branches to keep them out of reach of other animals, such as raccoons and chipmunks. Banana traps attract drosophilid flies that feed on fermenting fruit. From banana traps,
the flies are collected by opening the bottles inside a fly net, so that the flies can crawl/fly upwards into the net.

**Tomato baits** are made of over-ripe tomatoes that are cut in half and placed on the forest floor, preferably in the shade of trees or fallen logs. Tomatoes attract a very wide range of species, such as those that feed on fermenting fruit, tree sap, and mushrooms; generalist species eagerly visit tomato traps. The only exception is shelf mushroom feeders, which rarely visit any baits.

**Mushroom baits** are made from store-bought white button mushrooms that have been soaked in water for at least 30 minutes. The soaked mushrooms are placed next to fallen logs or at the base of trees in groups of about ten. Try to find spots that are protected from the wind. The flies can be quite skittish and fly off before you have a chance to catch them, so be stealthy in approaching the baits. Mushroom baits attract mushroom-feeding drosophilid species (except shelf mushroom feeders). Flies can also be collected from naturally occurring mushrooms. Individual mushrooms at a certain stage of decay can attract great numbers of flies. Drosophilid species that feed on shelf mushrooms can be aspirated from the underside of these fungi.

Flies from tomato and mushroom baits are collected by placing the net over the food source and gently disturbing the flies so that the fly upward into the net. If using a Drosophila net, swing it back and forth several times to drive the flies into the bottom part of the net, insert a vial, invert, and tap the flies into the vial.

**Beer traps** consist of wide-necked bottles (Frappuccino bottles) with some beer in them. They are hung into trees, covered with a piece of nylon. The nylon should be made wet with some beer by shaking the bottle daily. Especially in the morning hours, flies can be aspirated from the nylon of the traps. In general, different species of flies are attracted to these various baits at different stages of decomposition. Therefore, to get the greatest diversity of drosophilid species, we recommend collecting at baits for at least several days.

Collected flies should be immediately transferred into vials with sugar-agar medium, preferably kept in a cool, shaded spot, and identified at the end of each collection day.

**E: FOOD RECIPES**

**Cornmeal-sucrose-yeast medium**

The following recipe can be used to rear many drosophilid species.

***Continue stirring throughout the whole process***

1. Boil 850 mL of water
2. Add 7.9 g of agar (fine ground, U.S.P., gelidium, Moorhead and Company) and stir until completely dissolved
3. Add 27.5 g of brewer’s yeast
4. Add 52 g of cornmeal
5. Add 11 g of sugar
6. Stir continuously until mixture boils
7. Turn off the heat and stir for 15 minutes
8. Dissolve 2.4 g of tegosept in 9.2 mL of ethanol
9. Add the tegosept/95% ethanol mixture
10. Immediately pour while stirring

**Instant + mushroom food**

1. Add 1 teaspoon Instant Drosophila Medium (Carolina Biological Supply) to a vial.
2. Add 8 mL water
3. Push a dental cotton roll into the food (this serves as a pupation site)
4. Add a slice of store-bought *Agaricus bisporus* mushroom (pushed partway down into the food)

**Instant + cucumber food**

*Same as instant + mushroom, but substituting a piece of cucumber for the mushroom*

**F. IMAGING TECHNIQUES**

All images were taken of anesthetized fruit flies obtained from the field or from laboratory cultures. For portraying complete flies with size markers, the flies were cleaned with a very fine pair of forceps and then fixed to a white paper square with double-sided tape. The paper square was also fixed with double-sided tape on a carbon-dioxide pad, on which the flies were anesthetized during the imaging process. For all other images, the flies were anesthetized with ether for 5 minutes and dissected to expose the key characters. We used an Olympus SZX16 dissection microscope with a Leeds ring light source and an Olympus DP72 camera. At a magnification of 7X for large flies or 10 - 20X for smaller flies, an average of 50 - 60 pictures were taken at different focal planes, starting from the highest elevation point of the fly. The images of flies in this guide were compiled from ~50,000 raw images. We used a white paper cone with a narrower diameter than the ring light to avoid bright reflections from the bodies of the flies. The raw images were z-stacked with Helicon Focus software, and the resulting sharp images were cleaned in Adobe Photoshop. Using the “curves” function, we reduced the background noise to achieve natural colors. After this step, the shadows around the flies and between the bristles
CO₂ pad with paper squares and dissected fruit fly prepared for imaging.

Image rendering and cleaning station.
Fine-cleaning of shadows with a 2-pixel-wide eraser in Photoshop.

Fruit fly before the curve function is applied in Photoshop.

Fruit fly after the curve function is applied in Photoshop.

Fine-cleaning of shadows with a 2-pixel-wide eraser in Photoshop.
were eliminated, using a Wacom digital drawing tablet and the “eraser” function in Photoshop. The cleaned images were finally assembled in Adobe Illustrator.

G. SIZES OF FLIES

Individuals of the same species vary in size, which is due to the sex, genetic factors, and environmental factors, such as the amount of food that was available to the larvae and the temperature at which they developed. Here we illustrate how small, medium-sized, and large flies of the family Drosophilidae compare to each other.

H. ACKNOWLEDGEMENTS

The idea for this book was born when John visited Thomas for the first time as part of a faculty-mentoring grant funded by Michigan Tech, for which we are most grateful. John visited Michigan Tech to give a talk on fruit fly parasitism. Before his arrival, John asked Thomas to place some baits in the nearby forest to have a look at the local drosophilids. The key moment for Thomas was when John swung his net over a mushroom bait, looked into the net without optical aids, and exclaimed to have found the fly that was the topic of his research talk. Thomas was amazed. At brunch just before driving John back to the airport, Thomas asked John to teach him everything he knows about wild fruit flies and offered to take images of all species to preserve John’s knowledge for future generations. That morning on September 15th in 2012 was the birth date of the idea to develop this book.

For very helpful comments and suggestions on various species pages, we would like to thank Yasir Ahmed, Chip Aquadro, Bill Ballard, Jean David, Kelly Dyer, Bill Etges, Jim Fry, David Grimaldi, Ary Hoffmann, Erin Kelleher, Amanda Larracuente, John Luhman, Jan Máca, Greg Loeb, Bryant McAllister, Allen Orr, Domenico Otranto, Daven Presgraves, Andrea Swiegert, Rob Unckless, Amir Yassin, and Roman Yukilevich. We thank Ben Jaszcsak and Megan Werner for permission to use the photographs of Thomas and his daughter Natalia in the “About the authors” and “Introduction” sections, respectively. We thank Edgar Steenwinkel for permission to use Tessa’s portrait in the “About the authors” section. We also thank Gary Steck for his image of Leucophaena maculosa as well as David Grimaldi for sharing live specimens of Drosophila bromeliae. We would like to thank several people at the University of Rochester River Campus Libraries, who enabled us to produce version 1.0 of this book: Jim Barbero for his excellent graphic design and layout of this book, Moriana M. Garcia for guidance through copyright and sharing issues, and Nora Dimmock for overseeing production and publication of this e-book. At Michigan Technological University, we would like to thank Annelise Doll for the oversight of the production and publication, David Holden for the help with the layout and design, and Nora Allred for the help with the copyright and sharing of version 2.0.

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Campus Libraries, and the J. Robert Van Pelt and John and Ruanne Opie Library at Michigan Tech. We also thank the Walmart store in Houghton for their generous donations of overripe produce to support our collections in Michigan.

Finally, we would like to thank all of our past and current students for making our journey to the world of *Drosophila* so endlessly fascinating.

We also thank Natalia Werner for her beautiful fruit fly drawings, which we used as placeholders (5 years old) and the bedtime story (7 years old).

**I. REQUEST TO USERS**

We will continue to search for the species that are currently represented by placeholders, but if users of this guide come across any of these missing species, we would greatly appreciate receiving live samples. To send flies to either of us, we recommend putting them in plastic shell vials containing an agar-based medium (see recipe below). The vials can be packed in a Styrofoam box with packing peanuts and sent to:

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**Sugar-agar medium for collecting and sending flies**

1 L distilled water  
83 g sucrose  
20 g agar

Combine all ingredients in a flask or beaker and bring to a boil for several minutes. Dispense 8 - 10 mL into vials and allow to cool. Add a piece of Kimwipe or something similar to absorb moisture and prevent flies from sticking to the side of the vial.

We also invite the research community – including students and teachers – to let us know about interesting aspects of the biology of these species for inclusion in future editions.

**J. REFERENCES**


Quick Key
II. Quick key to common species

Start with a combination of size and thorax color. Within each box, the species above the dashed line have abdominal bands or spots interrupted at the dorsal midline, and those below have bands that are continuous across the dorsal midline, have spots at the midline, or the entire abdomen is dark (C. amoena). “Small” flies are about the size of *D. melanogaster* at first glance, whereas those that are “large” are noticeably larger than *D. melanogaster*.

<table>
<thead>
<tr>
<th>Body size</th>
<th>Thorax color</th>
<th>C. amoena – two large shaded areas on wings</th>
<th>Z. indianus – four white racing stripes on thorax</th>
<th>suzukii - males with one large spot on wing tip, females with serrated ovipositor</th>
<th>simulans – males with black posterior abdominal segments, sex combs and large genital arch</th>
<th>melanogaster – males with black posterior abdominal segments, sex combs and small genital arch</th>
<th>tripunctata – central spot on 3 abdominal segments; clouded crossveins and vein tips</th>
<th>affinis – see entry to right</th>
<th>algonquin – see entry to right</th>
<th>H. duncani – wings clear</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>Yellow – medium brown</td>
<td>busckii – wings clear, central dorsal stripe splits posteriorly</td>
<td>putrida – wings clear; anterior scutellars convergent; black horseshoe around ovipositor, presutural bristles short, stout and little elevated above thorax</td>
<td>neotestacea – wings clear; anterior scutellars convergent; presutural bristles long, thin and elevated above thorax</td>
<td>recens – clouded crossveins; anterior scutellars divergent; no prescutellars; spotted abdomen, with small lateral row of spots</td>
<td>falleni – clouded crossveins; anterior scutellars divergent; no prescutellars; spotted abdomen, lacking small lateral row of spots</td>
<td>C. amoena – see entry to left</td>
<td>neotestacea – see entry to left</td>
<td>suzukii - see entry to left</td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>Dark brown – blackish</td>
<td>immigrans – transverse bands on abdomen</td>
<td>quinaria – spotted abdomen</td>
<td>palustris – abdomen with two broad longitudinal bands, lateral row of small spots</td>
<td>subpalustris – like palustris, but with S-shaped posterior crossvein, dark clouds on wings</td>
<td>L. varia – large spot on wing</td>
<td>quinaria – see entry to left</td>
<td>robusta – clouded posterior crossvein</td>
<td>paramelanica - wings clear</td>
<td>hydei – each bristle arises from one spot</td>
</tr>
</tbody>
</table>


III. Species Accounts
Subfamily Steganinae

Leucophenga varia

**Leucophenga varia males**

The tip of longitudinal vein L2 is strongly clouded (arrow), posterior crossvein and basal space between L1 and L2 only vaguely clouded

Body large, although variable, the abdominal spot pattern is unmistakable

**Leucophenga varia females**

The tip of longitudinal vein L2 is strongly clouded (arrow), posterior crossvein and basal space between L1 and L2 only vaguely clouded

Body large, although variable, the abdominal spot pattern is unmistakable
Leucophenga varia males

Leucophenga varia females
Males and females of this large species look similar. The abdominal spot pattern cannot be confused with that of any other species in the area. The wings have one prominent marking at the distal end of longitudinal vein L2, while the remainder wing is only faintly pigmented. This species can be reared by collecting wild mushrooms, from which the adults will emerge.

**Taxonomy:** Subgenus Leucophenga

Along with several other genera, *Leucophenga* belongs to the subfamily Steganiniae, which is sister to the great majority of species and genera within the Drosophilidae (Yassin 2013).

**Distribution:** *L. varia* is widespread in the eastern United States, extending at least as far north as Massachusetts and New York (Sturtevant 1921).

**Breeding sites:** Like other species within the genus *Leucophenga*, *L. varia* breeds in decaying mushrooms (Wheeler 1952).

**Behavior:** Although *L. varia* is frequently bred from wild mushrooms, we seldom collect adults of this species by sweep netting over mushrooms at times when other mycophagous drosophilids are present. Perhaps they have alternative adult feeding sites, escape from a mushroom before one starts sweeping, or are active at times of day or night when collections are not typically made.

**Community ecology:** Worthern et al. (1996) placed commercial *Agaricus bisporus* mushrooms in forested areas in South Carolina for several days and identified all Diptera that emerged from them. *L. varia* was identified as a core species in this area, emerging from most of the experimental mushrooms. In some mushrooms, it was the only emerging fly species, while in others, it co-occurred with 1, 2, 3, or 4 other species. Some of the co-occurring species were considered to be satellite species, as they were only found in mushrooms that were also utilized by other species.

**REFERENCES:**


Leucophenga maculosa

FRUIT FLIES PARTYING
(A.K.A. PARTY ANIMALS)

PLACEHOLDER - NO IMAGE AVAILABLE
THIS FRUIT FLY HAS NEVER EATEN A BANANA BEFORE (HENCE THE MESS)
**Taxonomy:** Subgenus Leucophenga
Along with several other genera, *Leucophenga* belongs to a group that is sister to the great majority of species and genera within the Drosophilidae (Yassin 2013).

**Distribution:** *L. maculosa* is widespread in the eastern United States, with records as far north as New York (New York City) and Pennsylvania (Sturtevant 1921). It is more common in the southeast than in our region (Wheeler 1952).

**Breeding sites:** Like other species within the genus *Leucophenga*, *L. maculosa* breeds in decaying mushrooms (Wheeler 1952).

**Endosymbionts:** *L. maculosa* collected in the Chiricahua Mountains in Arizona were found to be positive for infection with *Wolbachia*, a maternally transmitted bacterial symbiont (Stahlhut *et al.* 2010).

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**REFERENCES:**

YOU DON’T WANT TO BE A BANANA
(LOOK AT THESE TEETH!)
THIS IS ONE WILD FRUIT (FLY) PARTY!
Because very little is known about the biology of *Stegana*, except as noted, we base the following accounts on information provided in Lastovka and Máca (1982). The eyes are bright red. The third antennal segment is yellow. The thorax is yellow. The legs are pale yellow. When at rest, the dark wings are folded over the abdomen, as they are in all species of *Stegana*, giving the fly a beetle-like appearance. Are these flies beetles mimics, and if so, of what adaptive significance is this?

**Taxonomy:** Subgenus *Stegana*

**Distribution:** This species has been found almost exclusively in the Northeast (New Jersey, New York, Connecticut, and Pennsylvania), although there is one record from Kansas (TaxoDros 2018).

**Breeding sites:** Lastovka and Máca (1982) state that the life history, including breeding sites, of *Stegana* are largely unknown. Adults are associated with diseased or dead trees. Adults of a European species, *S. mehadiae*, occur with some regularity on beech trunks with the shelf fungus *Fomes fomentarius*. Because *F. fomentarius* is a plant pathogen, this indicates that the beech trees, where *Stegana* occur, are diseased.

**REFERENCES:**


Stegana antiqua

THIS FRUIT FLY THINKS THAT SHE IS PRETTY

PLACEHOLDER - NO IMAGE AVAILABLE
THIS FRUIT IS CRYING BECAUSE WE ONLY HAVE PLACEHOLDERS FOR THE GENUS STEGANA
**Stegana antiqua**
Wheeler 1960

Because very little is known about the biology of *Stegana*, except as noted, we base the following accounts on information provided in Lastovka and Máca (1982). The thorax is light brown to brown, yellow anteriorly, with 3 to 5 longitudinal stripes. The thorax has 10 rows of acrostichal bristles. The wings are brown, paler posteriorly, down-curved, with pale brown to brown veins. The abdomen is light brown to dark brown, darker posteriorly. When at rest, the dark wings are folded over the abdomen, as they are in all species of *Stegana*, giving the fly a beetle-like appearance. Are these flies beetles mimics, and if so, of what adaptive significance is this? Without examining male genitalia, it is difficult to distinguish members of the coleoptrata species group, of which *S. antiqua* and *S. coleoptrata* occur in our region (Bächli et al. 2004).

**Taxonomy:** Subgenus Steganina. Species group coleoptrata

**Distribution:** There are few records of this species. It has been recorded from sites in Massachusetts, New York, Maryland, and Virginia (TaxoDros 2018).

**REFERENCES:**


Stegana coleoptrata

THESE FRUIT FLIES ARE DANCING
(NOTE THE USE OF THEIR WINGS!)

PLACEHOLDER - NO IMAGE AVAILABLE
THIS FRUIT FLY WANTED TO BE PAINTED WITH WATER COLORS (INCLUDING HIS BANANA)
**Stegana coleoptrara**  
(Scopoli 1763)

Because very little is known about the biology of *Stegana*, except as noted, we base the following accounts on information provided in Lastovka and Máca (1982). The eyes are dull red. The third antennal segment is black. Thorax is dark brown to brownish black with 10 to 12 rows of acrostichal bristles. The wings are brown anteriorly, light brown posteriorly, curved downwards, with dark veins. The abdomen is brownish black. When at rest, the dark wings are folded over the abdomen, as they are in all species of *Stegana*, giving the fly a beetle-like appearance. Are these flies beetles mimics, and if so, of what adaptive significance is this?

Without examining male genitalia, it is difficult to distinguish members of the coleoptrata species group, of which *S. coleoptrata* and *S. antigua* occur in our region (Bächli et al. 2004).

**Taxonomy:** Subgenus Steganina. Species group coleoptrata

**Distribution:** This widely distributed species has been found at numerous sites within our region, including Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Illinois, Michigan, Wisconsin, Quebec, and Ontario. In North America, its range extends as far south as Florida and as far west as Washington and British Columbia. This species is also present in Europe and Japan (TaxoDros 2018).

**Breeding sites:** In Europe, larvae and pupae of *S. coleoptrata* (or a closely related species) have been found under the bark of poplar, birch, plum, and pine trees, and adults have been found on oak (Lastovka and Máca 1982). Morge (1956) notes that larvae and pupae are often found in association with the frass of bark beetles, under bark that is easily peeled off. Based on the behavior and morphology of larvae, he concludes that the larvae are not predaceous, but rather probably feed on tree sap.

**Parasites:** In Morge’s (1956) study in Germany, he found a high rate of parasitism (~80%) by *Phaenocarpa flavipes* (Braconidae) and *Rhotromeris sp.* (Cynipidae).

**Behavior:** Adults of *S. coleoptrata* occasionally run quickly and jump a few centimeters, while holding their wings in an unusual manner. Morge speculates that this may be an element of courtship behavior (Morge 1956).
REFERENCES:


Rhinoleucophenga obesa

THIS FRUIT FLY MAMA HAS EVERYTHING SHE NEEDS TO BE HAPPY
THIS FRUIT FLY HAS A TOMATO, BANANA, AND MUSHROOM
Rhinoleucophenga obesa
(Loew 1872)

Superficially, this large species looks like a gigantic D. melanogaster, with a body length of 5 mm. However, the wings have clouded crossveins and tips of the longitudinal veins. The thorax has ~12 irregular rows of acrostichal bristles. The thorax is uniformly medium brown, and the tergites are darker brown. The eyes are bright red, and the space between them (the frons) is covered with numerous small bristles. There are no similar species in our area.

Taxonomy:

Distribution: This species was initially recorded from the southeastern United States, from Florida and Alabama north to Tennessee and Virginia (Patterson 1943). It has subsequently been reported from New York state (Poppe et al. 2014), perhaps having expanded its range northwards as a result of climate change since Patterson’s report. The genus Rhinoleucophenga is primarily neotropical in its distribution, with a particularly high diversity of species, including R. obesa, in the pampas (Poppe et al. 2014).

Breeding sites: There is one report that the larvae of R. obesa prey on coccid scale insects in Brazil (discussed in Ashburner (1981). However, Ashburner notes that there is some question about whether the drosophilid was in fact R. obesa, but perhaps may have been another species of Rhinoleucophenga. D. Grimaldi (reported in Poppe et al. 2014) has found that larvae of R. obesa prey on Aclerda scale insects found on grasses in New York.

REFERENCES:


Patterson, J.T. 1943. The Drosophilidae of the Southwest. Univ Texas Publs 4313: 7-216.

**Phortica variegata**

**Phortica variegata males**
- Femur black, tibia yellow with 3 black rings (front leg shown)
- Body large, large brown spots on thorax, abdominal dorsal midline mostly dark
- Wing grayish, posterior crossvein lightly clouded

**Phortica variegata females**
- Femur black, tibia yellow with 3 black rings (front leg shown)
- Body large, large brown spots on thorax, abdomen with high contrast pattern
- Wing grayish, posterior crossvein lightly clouded
*Phortica variegata* males

*Phortica variegata* females
Phortica variegata (Fallen 1823)

Males and females of this very large-sized species look similar. The thorax is grayish and has multiple large dark brown spots. The abdomen is yellowish with bold dark brown pigmentation, notably along the dorsal midline. Legs: the femur is black, the tibia is yellow with 3 black rings. Similar species: Drosophila hydei and D. repleta have smaller spots on the thorax, and their dark abdominal pigmentation is interrupted along the dorsal midline. Phortica variegata visits banana baits and people’s heads.

**Breeding sites:** Little is known about the ecology of P. variegata, but fruits may be an important breeding site, as both males and females of this species are attracted to baits of apples and pears. In contrast, only male flies were attracted to feed on the lachrymal secretions of a human subject in the field (Otranto et al. 2006). We have collected P. variegata at mushroom baits in the wild, but have never bred this species from mushrooms. Gupta and Gupta (1974) report that P. variegata larvae have been found feeding on the sap of a weeping willow tree in Europe.

**Vector for an emerging infectious disease:** Human thelaziasis (HT) is a neglected, but emerging zoonotic disease caused by Thelazia callipaeda (Spirurida, Thelazidae). These nematodes live beneath the eyelid or nictitating membrane, where they feed on lachrymal secretions. Larval nematodes are ingested by Phortica variegata, which are attracted by the host’s eyes (reviewed in Máca and Otranto 2014). P. variegata serves as an intermediate host and vector for these parasites (Otranto et al. 2006). Remarkably, it is only the male flies that are attracted to the lachrymal secretions of humans and other hosts of T. callipaeda, and only male flies serve as vectors for this parasite. Otranto et al. (2006) found that between 1.5% (as determined by dissection) and 4.4% (as determined by PCR) of male flies in Italy were infected with T. callipaeda.

The prevalence of HT has increased significantly in China in recent decades, where it is most frequent among children and in rural areas where there is close contact between humans and other animals, such as dogs, cats, and foxes (Shen et al. 2006). Shen et al. (2006) believe that farm dogs are the main reservoir host for T. callipaeda in China.

In Europe, T. callipaeda has been spreading in recent years, most often infecting dogs (Maia et al.)
The first cases of HT have recently been reported in Europe, including France, Italy, and Spain (Otranto and Dutto 2008; Fuentes et al. 2012). Besides dogs, *T. callipaeda* has been found in red foxes, wolves, beech martins, wild cats, and brown hares in Italy, with infection frequencies ranging from 14% to 50% (Otranto et al. 2009). Given their abundance and high prevalence of infection, foxes appear to be particularly important hosts for this parasite. Molecular genetic data indicate that *T. callipaeda* has recently spread to Europe from Asia, as seven haplotypes for the mitochondrial gene *COI* have been identified in Asia, but only one in Europe (Otranto et al. 2005, 2009).

**Behavior:** In Italy, *P. variegata* exhibits crepuscular activity, perhaps to maximize opportunities to feed on the lachrymal secretions of mammals, which are also active at that time (Otranto et al. 2006).

**REFERENCES:**


Amiota humeralis spots fluorescing in UV light.
**Amiota spp.**

**Taxonomy:** Little is known about North American species of *Amiota*. As their breeding sites are poorly known, they typically do not come to baits used by *Drosophila* collectors, appear to be rare, tend to inhabit the forest canopy, cannot be cultured in the lab, and are likely to include many undescribed, cryptic species. In addition to the three species presented here, there are several other species of *Amiota* in our region that we plan to include in a future edition of this guide. The peak diversity and presumed origin of the genus *Amiota* is eastern Asia (Chen and Toda 2001).


**Breeding sites and ecology:** Little is known about the ecology of these flies. They are typically not collected at fruit baits, but do occasionally come to beer-wine traps in the forest canopy (Bächli et al. 2004). Máca and Otranto (2014) report that protein traps of dead mice can be used to attract *Amiota*. In studies of their vertical distribution within forests, species of *Amiota* are often associated with the canopy (Beppu 1984; Toda 1987; Bächli et al. 2006).

Some species of *Amiota* are attracted to the perspiration, ears, and, particularly, the eyes of humans and other mammals (Malloch and McAtee 1924; Bächli et al. 2004; Máca and Otranto 2014). Malloch (1924) reports collecting adult *A. setigera* at sap from an apple tree.

There are almost no records of the breeding sites of any species of *Amiota*. In their review of the drosophilids of northern Europe, Bächli et al. (2004) report that *A. alboguttata* has been bred from fungi.

**Modes of reproductive isolation:** Species of *Amiota* apparently cannot be bred in the lab and are difficult to find in nature. Therefore, the study of their modes of reproduction will be particularly challenging. Although many species of *Amiota* appear to be morphologically similar, they can differ in male genitalia, suggesting that recent speciation may be going on in these flies (Máca and Otranto 2014).

**Parasites and pathogens:** It is thought that *A. nagatai* may serve as a vector of the eyeworm *Thelazia callipaeda* in Japan (Nagata 1959, 1960).

**Behavior:** Adults of some species of *Amiota* can fly into one’s eyes or ears and can thus be quite annoying (Malloch and McAtee 1924). The significance of this behavior is unknown.
REFERENCES:


Comparison of our three *Amiota* species: left = *A. minor*, middle = *A. humeralis*, right = *A. leucostoma*.
Amiota humeralis

Amiota humeralis males
- White bar above proboscis
- Wing grayish
- Body small - large, 2 white spots on each side of the thorax, abdomen mostly shiny black

Amiota humeralis females
- White bar above proboscis
- Wing grayish
- Body small - large, 2 white spots on each side of the thorax, abdomen mostly shiny black
Amiota humeralis males

Amiota humeralis females
**Amiota humeralis** Loew 1862

Males and females of this medium to large-sized species look similar. Adult size can vary considerably among individuals. The face shows a white bar above the proboscis. The thorax is shiny black and has two white patches on each side, as well as white halteres. The abdomen is mostly black.

**Distribution:** *A. humeralis* has been reported in our region from Maine, New Hampshire, Vermont, Massachusetts, New Jersey, New York, Pennsylvania, Maryland, Indiana, Ontario, and Quebec. Its range extends as far west as Oregon, California, and the sky islands of Arizona (Wheeler 1952; TaxoDros 2018). We found this species in Michigan.

**Fluorescence:** Like most species of *Amiota*, *A. humeralis* flies are decorated with two bright white spots on each side of the thorax and a white band across the face (Wheeler 1952). The three species of *Amiota* covered here also have milky white halteres. Under UV light (365 nm) illumination, the spots on the thorax and band across the face fluoresce brightly, although the haltere does not (see figure). Both males and females have the fluorescent patterns, suggesting that they are not involved in sexual selection. The similarity of the spots among species suggests that they are not involved in species recognition. Thus, the function of these spots remains to be determined. Perhaps they increase visibility of flies from a distance for purposes of finding a mate. Could they startle potential predators, like spiders? Could researchers hunt for these species in the dark using UV lamps, perhaps shedding light on the largely unknown aspects of their ecology?

**REFERENCES:**

Chen, H.W. and Toda, M.J., 2001. A revision of the Asian and European species in the subgenus *Amiota* Loew (Diptera, Drosophilidae) and the establishment of species-groups based on phylogenetic


**Amiota leucostoma**

*Amiota leucostoma* males

- White bar above whitish proboscis
- Legs yellowish (front leg shown)
- Body large, 2 white spots on each side of the brownish thorax, abdomen striped
- Wing grayish, darker anterior than posterior
**Amiota leucostoma Loew 1862**

Males and females of this large-sized species look similar. The face shows a white bar above the whiteish proboscis. The thorax is brownish and has two white patches on each side and white halteres. The abdomen is black and yellowish striped.

**Distribution:** In our region, *A. leucostoma* has been reported from Maine, Vermont, New Hampshire, Massachusetts, New York, Pennsylvania, New Jersey, Ohio, Illinois, Michigan, and Quebec (Wheeler 1952; Chen et al. 2004; TaxoDros 2018).

**REFERENCES:**


**Amiota minor** males

- No white bar above whitish proboscis
- Legs yellowish (front leg shown)
- Wing grayish, darker anterior than posterior
- Body mostly brown, very pale whitish spots (arrows), halteres white (arrow head)
Amiota minor

Amiota minor males
Males and females of this medium-sized species look similar. The thorax is medium to dark brown. Unlike other local species of Amiota, the face lacks a white bar above the proboscis, and the thoracic spots are much less evident, although the halteres are white. The abdomen is mostly black.

**Distribution:** A. minor is widespread in the eastern United States (including Michigan), Ontario and Quebec Canada, extending as far west as Montana and the Huachuca Mountains of Arizona (Wheeler 1952; Chen et al. 2004).

The genus Amiota is believed to have originated in eastern Asia, from which several lineages have colonized North America, as judged by the close similarity of North American and Asian species (Chen et al. 2004). Because Amiota are generally not attracted to the types of baits used by Drosophila collectors, current collection records might substantially underestimate the geographical distribution of these flies.

**REFERENCES:**


Subfamily Drosophilinae

Chymomyza amoena

**Chymomyza amoena males**
- Wing with **two dark bands**
- Body medium-sized and **elongated**

**Chymomyza amoena females**
- Wing with **two dark bands**
- Body medium-sized and **elongated**
*Chymomyza amoena* males

*Chymomyza amoena* females
Chymomyza amoena males

Chymomyza amoena females
This species is very easy to identify. Both sexes have two irregular dark bands across each wing. The tips of the wings are white. The body is narrow and elongated. The thorax is lighter brown than the abdomen. Similar species: Males of *D. suzukii* have a single distal spot on the anterior part of the wing. *Chymomyza aldrichii*, *C. procnemoides*, and *C. procnemis* do not have banded wings. The four *Chymomyza* species of our area differ in the color of their forelegs and wing tips. The forelegs are yellowish in *C. amoena*, dark in *C. aldrichii*, and jet black (except for pale apicals) in *C. procnemoides* (Band 1996) and *C. procnemis*. Additionally, *C. amoena* and *C. procnemis* have white wing tips. Tips for collecting and breeding: This species occasionally visits banana and tomato traps and can be collected over fallen apples. Apples can be used to breed this species.

**Taxonomy:** Group III (Okada 1976); Species group fuscimana

Both molecular and morphological evidence indicate that the genus *Chymomyza* is older than *Drosophila* (DeSalle and Grimaldi 1991; van der Linde *et al.* 2010), having diverged from the lineage leading to *Drosophila* (and several other genera) ~80 million years ago (Beverly and Wilson 1984). Van der Linde *et al.* (2010) place *Chymomyza* and *Scaptodrosophila* as a sister group to *Drosophila*. Thus, comparisons between *Chymomyza* and *Drosophila* could be informative about the ancestral state of the lineage leading to *Drosophila*.

**Distribution:** While the genus *Chymomyza* is distributed worldwide, the native range of *C. amoena* is eastern North America (Okada 1976, Band 1988).

*C. amoena* recently colonized Europe, first being found in the Czech Republic in 1975 (Máca 1985). It has subsequently been spreading across much of northern and western Europe, reaching the Netherlands in 2002 (de Jong and van Zuijlen 2003) and England in 2008 (Clemons 2009).

**Breeding sites:** In its native range in North America, *C. amoena* has been reported to breed in acorns, the husks of black walnut and butternut trees, and crabapples among plants endemic to this area (Band 1988). It is unusual among drosophilids in utilizing nitrogen-rich frassy substrates, such as apples and black walnut hulls, where the frass is produced by a primary pest, such as weevils or moth larvae (Band *et al.* 1999, 2005).

At some point, likely in the 1800s, *C. amoena* underwent a host expansion to domestic apples (*Malus pumila*), a species native to central Asia, but which is now cultivated worldwide (Band 1988). Unlike most species of frugivorous *Drosophila*, which breed in decaying fruits, *C. amoena* can feed on fresh apples, although females cannot oviposit through the skin, which must first be broken by some other agent (Band 1981).
In Europe, *C. amoena* breeds in the same types of resources as in North America. Since these resources were not previously utilized by any drosophilids in Europe, Band *et al.* (2005) conclude that *C. amoena* has moved into a vacant niche in Europe, which is likely to have enabled its spread there.

**Modes of reproductive isolation:** The following account is based on Band’s (1996) studies of three sympatric species of *Chymomyza* - *C. amoena*, *C. aldrichii*, and *C. procnemoides* - at Mountain Lake Biological Station, Virginia. Elements of their aggressive courtship include patterns of wing waving and splaying of the forelegs that differ among the species. In the laboratory, males and females of *C. amoena* and *C. aldrichii* exhibit no interest in the other species. The differences in wing banding and foreleg pigmentation noted above suggest that visual cues are likely to play an important role in isolation between these species. It would be interesting to experimentally manipulate the wing patterns of these species or to examine how the light environment affects levels of behavioral isolation between them.

**Behavior:** Males wave their wings to display territorial ownership for purposes of mating, and they will aggressively chase other males from their territories. Males typically “assault” females in order to mate with them, and they have occasionally been observed to capture females in mid-air, glide to the ground, and copulate (Band 1988). Females do not approach males until they are fertile and ready to oviposit following mating.

**Physiological ecology:** The larvae of *C. amoena* can overwinter in fallen apples, being able to survive prolonged sub-zero °C temperatures, and emerge as adults the following summer (Band and Band 1980). Band and Band (1980) report that larvae do not have elevated levels of glycerol or sugar alcohols, compounds associated with overwintering in some insect species. They therefore speculate that *C. amoena* might utilize proteins for cold hardiness. The larvae achieve cold hardiness by either supercooling (characteristic of larvae collected from walnut husks) or being freeze-tolerant (larvae collected from apples) (Band and Band 1982). Sinclair *et al.* (2009) used synchrotron X-rays to observe the process of ice formation in freeze-tolerant and non-freeze tolerant larvae of *C. amoena*. They found no whole-body or organ level differences between the two types of larvae and suggested that cellular and biochemical mechanisms are likely to underlie the difference between them.

**REFERENCES:**


**Chymomyza aldrichii**

**Chymomyza aldrichii males**

Front legs dark, but not jet black

Body blackish, medium-sized, and elongated

Wing clear, except the costal cell (arrow)
Chymomyza aldrichii males
This medium-sized species has an elongated, slender body typical for flies of the genus *Chymomyza*. Both sexes look similar. The dorsal side of thorax and scutellum are shining dark reddish brown, and the abdomen is a shiny black (Sturtevant 1969; Grimaldi 1986). The legs are all dark. The wings of *C. aldrichii* lack the large dark bands evident in *C. amoena*, although the anterior margin and costal cell of the wings are brown. The wings of *C. aldrichii* further lack the white wing tips present in *C. procnemis* and *C. amoena*. Similar species: In *C. procnemoides*, the thorax is yellow-orange to light brown rather than dark reddish brown, as in *C. aldrichii* (Grimaldi 1986). The black color of the front legs is in stark contrast to the light coloration of the other legs in *C. procnemoides* and *C. procnemis*. Tips for collecting and breeding: We found three males of this species at once in a bucket filled with overripe tomatoes near Escanaba, MI.

**Taxonomy:** Species group aldrichii

**Distribution:** Although most records of *C. aldrichii* in North America are from the western United States, it has also been found in Minnesota and Maine (Wheeler 1952). Toda 1992 reports that this species has invaded Japan.

**Breeding and feeding sites:** *C. aldrichii* occurs around wounded and decaying regions of trees, such as Douglas fir, pine, fir, aspen, poplar, birch, cherry, maple, and oak (Grimaldi 1986; Band 1996). Adults feed and mate at such sites, and the larvae probably feed on sap and associated microbes there. Spieth (1957) discovered larvae of this species developing underneath aspen bark, which was made accessible to ovipositing females as a result of tree wounding.

**Behavior:** Band (1996) reports that males of *C. aldrichii* lock their forelegs in order to engage in wrestling bouts. Given a choice, females in the laboratory prefer the larger of two males.

**Modes of reproductive isolation:** Under laboratory conditions, *C. aldrichii* does not engage in interspecific courtship with either *C. amoena* or *C. procnemoides* (Band 1996).

**REFERENCES:**


Sturtevant, A.H. 1916. Notes on North American Drosophilidae with descriptions of


Chymomyza procnemoides

THIS FRUIT FLY TAKES OFF WITH A TOMATO AND A BANANA
THIS FRUIT JUST ATE A JUICY TOMATO
**Chymomyza procnemoides**  
Wheeler 1952

This medium-sized species has an **elongated, slender body** typical for flies of the genus *Chymomyza*. Both sexes look similar. The **thorax** is yellow-orange to light brown (Grimaldi 1986), and the abdomen is darker. The **wings** are mostly clear. The femur, tibia, and first tarsal segment of the **front legs** are **jet-black**, which is in stark contrast to the other lightly colored legs. The wings of *C. procnemoides* lack the large black spots evident in *C. amoena* and also lack white tips. Similar species: In *C. aldrichii*, the legs are all dark, and the costal cell of the wing is brown. *C. procnemis* has whitish wing tips. Tips for collecting and breeding: Wheeler (1952) notes that *C. procnemoides* is extremely hard to grow in the lab.

**Taxonomy**: Species group aldrichii

**Distribution**: This species is widespread in the United States, with records from Michigan, Indiana, and New York in our region, south to Virginia and west to Texas, New Mexico, and Arizona (Wheeler 1952; TaxoDros 2018). This species may have recently colonized Europe, as a single male was found in Hungary in 1990 (Papp 1992).

**Breeding and feeding sites**: Members of the aldrichii group are associated with tree wounds and decaying wood, with adult flies feeding on sap and bacteria and fungi associated with these sites (Grimaldi 1986). Band (1996) found that, in Virginia, *C. procnemoides* are attracted to newly damaged or cut wild cherry (*Prunus* sp.), striped maple (*Acer pensylvanicum*), red maple (*A. rubrum*), northern red oak (*Quercus rubra*), white oak (*Quercus alba*), chestnut (*Castanea dentata*), and black locust (*Robinia pseudoacacia*). Mating pairs of this species were found on wild cherry, northern red oak, and red maple. Band (1996) has observed that mating pairs of *C. procnemoides* will scurry under loose bark of damaged trees. *Chymomyza* eggs, larvae, and pupal cases were found under such bark, indicating this is an important breeding site. *C. procnemoides* were attracted to bark wounds on almond and apricot trees that had been inoculated with the fungus *Ceratocystis alba* in California (DeVay et al. 1968), and they may serve as vectors for plant-pathogenic *Ceratocystis* on these trees (Moller and DeVay 1968).

**Modes of reproductive isolation**: *C. procnemoides* and *C. aldrichii* are broadly sympatric. Band (1995) has shown that both species can be attracted to the same damaged trees, including a wild cherry in 1986 and a striped maple in 1987, indicating that they likely encounter each other in the wild. Band (1996) placed a single *C. procnemoides* female with a *C. aldrichii* male, and a single *C. aldrichii* female with a *C. procnemoides* male. He saw no courtship or attempted matings in either case. With such a small sample, one cannot say with much certainty that matings between these species do
not occur in the wild. No DNA sequences for these species are listed in GenBank. Thus, it is difficult to predict \textit{a priori} the potential fate of interspecific hybrids, should they ever be produced.

\textbf{Behavior:} Males of \textit{C. procnemoides} engage in headbutting, both in the wild and in the lab, presumably for access to females (Band 1996). Males and females both remate multiple times.

\section*{REFERENCES:}


Chymomyza procnemis

**Chymomyza procnemis males**

- Front legs: femur, tibia, and first tarsal segment black, all other segments very light
- Body medium-sized, elongated, slender, thorax lighter than abdomen, abdomen shiny black
- Wings nearly clear with white tip, costal cell (arrow) grayish

**Chymomyza procnemis females**

- Front legs: femur, tibia, and first tarsal segment black, all other segments very light
- Body medium-sized, elongated, slender, thorax lighter than abdomen, abdomen shiny black
- Wings nearly clear with white tip, costal cell (arrow) grayish
Chymomyza procnemis males

Chymomyza procnemis females
Chymomyza procnemis (Williston 1896)

This medium-sized species has an elongated, slender body typical for flies of the genus Chymomyza. Both sexes look similar. The thorax is a shining reddish-yellow or pale reddish-brown, with black bristles. The abdomen is shining black, contrasting with the much paler thorax. The mid and hind legs are pale, in contrast to the mostly black forelegs. The wings are tinged grayish with a white tip. Similar species: C. procnemoides does not have white wing tips. The legs of C. aldrichii are all dark, including all tarsal segments.

Taxonomy: Group III (Okada 1976); Species group procnemis

Distribution: Chymomyza procnemis was originally known from the Neotropical (including Central America, several Caribbean islands, and Brazil) and Nearctic biogeographical realms (Sturtevant 1921; Gottschalk et al. 2008). Within the United States, this species is primarily southern in its distribution, being found in Florida westward to New Mexico. Within our region, C. procnemis was reported by Sturtevant (1921) to be present in New York, Pennsylvania, New Hampshire, and Illinois. However, Wheeler (1952) concludes that, with the exception of Illinois, these records are of C. procnemoides, a species described several decades after Sturtevant's report. There are more recent records indicating that C. procnemis has colonized Hawaii, Japan, and the Canary Islands (Zimmerman 1938, Okada 1976, Bächli 2017).

Sturtevant (1921) describes several aspects of the biology of C. procnemis, which are mentioned below. However, Sturtevant conducted his studies over 30 years before C. procnemoides was described by Wheeler. Because some specimens originally reported as C. procnemis are more likely to be C. procnemoides, and because Sturtevant did not indicate the source of the flies he studied, it is possible that some of his findings pertain to C. procnemoides.

Breeding sites: Zimmerman (1938) notes that the flies collected in Hawaii were found at flowering pineapple fruits and diced stumps. Wheeler (1952) notes that, in contrast to C. procnemoides, C. procnemis readily comes to baits and can be reared in the lab. This suggests that the two species utilize different types of resources, with C. procnemis more likely to breed in fruits.

Modes of reproductive isolation: We are not aware of any studies of reproductive isolation that focus on this species.

Behavior: Sturtevant (1921) reports that a male will chase a female, push her wings apart when she stops, mount, and attempt to copulate.

Molecular evolution: Kwiatkowski et al. (1997) examined amino acid and nucleotide sequence evolution of the enzyme glycerol-3-phosphate dehydrogenase in several species of Drosophila and Chymomyza. This enzyme plays a critical role in providing energy for flight in these flies. By examining levels of sequence divergence among
species, Kwiatkowski et al. (1997) conclude that the Chymomyza lineage experienced a rapid increase (~9-fold) in the rate of amino acid substitutions soon after its divergence from the Drosophila lineage. This suggests a divergence between these two lineages in their energy requirements for flight.

REFERENCES:


**Hirtodrosophila duncani**

**Hirtodrosophila duncani males**
- Wing nearly unpigmented
- Body medium-sized, one dorsal midline spot on the mostly black abdomen

**Hirtodrosophila duncani females**
- Wing nearly unpigmented
- Body medium-sized, abdomen striped, dorsal midline pigmented
Hirtodrosophila duncani males

Hirtodrosophila duncani females
**Hirtodrosophila duncani** (Sturtevant 1918)

This is a medium-sized species that can be found on shelf mushrooms. Males show an almost entirely black abdomen with a **black dorsal midline spot** on yellow ground. The wings are nearly unpigmented. Females have lighter abdomens with wide black stripes on each segment and an intense black dorsal midline that is made of spots. Similar species: *D. suzukii* females have a large ovipositor, which resembles a chain saw. Females of *D. simulans* and *D. melanogaster* usually have narrower stripes on the abdomen and a less intense dorsal midline. Tips for collecting and breeding: Collect flies from fresh shelf mushrooms. This species also visits tomato traps. We recommend breeding this species on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast and a fresh piece of white bottom mushroom inserted into the food. Later, a small piece of Kimwipe should be inserted into the food, in which the larvae will form pupae.

**Distribution:** *H. duncani* is widespread in the eastern United States, from Texas to Florida in the south northwards to Wisconsin, Michigan, and New York.

**Breeding sites:** *H. duncani* has been bred from multiple species of bracket fungi of family the Polyporaceae (*e.g.*, *Polyporus, Grifola, Laetiporus*, and *Tyromyces*), as well as from bracket-like gilled fungi, such as the oyster mushroom *Pleurotus ostreatus* (Lacy 1984).

**Breeding ecology:** The use of long-lived (*i.e.*, not ephemeral) fungi by *H. duncani* is associated with host specialization in mycophagous drosophilids (Lacy 1984), as the vast majority of rearing records are from the family Polyporaceae. *Mycodrosophila* species show a similar pattern of specialization on polypores.

**Endosymbionts:** *H. duncani* is polymorphic for infection with *Wolbachia* (R. Unckless, pers. comm.).

**REFERENCES:**

Hirtodrosophila chagrinensis

THIS FRUIT FLY ATE A TOMATO
(SHE NEEDS A NAPKIN!)

PLACEHOLDER - NO IMAGE AVAILABLE
THIS FRUIT FLY ASKS YOU FOR FOOD
(HOW CHARMING SHE IS!)

PLACEHOLDER - NO IMAGE AVAILABLE
**Hirtodrosophila chagrinensis**
(Stalker and Spencer 1939)

This is a large-sized species. The thorax is a slightly shiny brown, with a pollinose scutellum (posteriormost section of the thorax). The mesonotum (largest section of the thorax) has two light stripes along the dorsocentral rows, two dark stripes inside these rows, and a light area between the inner stripes. The abdomen is a shiny brownish-yellow with dark brown posterior band on each segment. The wings are clear.

**Distribution:** This species has been collected in Ohio, Wisconsin, Iowa, and New York (Lacy 1984), although it is exceptionally rare. The initial species description by Stalker and Spencer (1939) indicated that only a single specimen had been found by the authors. Out of over 33,000 drosophilids reared from mushrooms collected around Ithaca, New York and the Great Smoky Mountains, Tennessee, Lacy (1984) reared only a single individual of *D. chagrinensis*. In his survey of the drosophilids of New England, Spiess (1949) did not find this species. We have never encountered it.

**Breeding sites:** The only known breeding sites are mushrooms. Lacy (1981) reared a single specimen from a jelly fungus (*Tremella* sp.), and Stalker and Spencer (1939) report that the single individual on which their species description was based was taken from an unidentified species of fleshy fungus.

**REFERENCES:**


**Hirtodrosophila ordinaria**

**Hirtodrosophila ordinaria males**

- Wing grayish with a hint of clouded posterior crossvein pigmentation
- Body large, thorax brown, often darker along the dorsal midline, abdomen yellow with brown stripes that are broadly interrupted along dorsal midline but that reach to the lateral ends of the tergites (arrow)

**Hirtodrosophila ordinaria females**

- 2nd orbital bristle (arrows) much shorter than 1st & 3rd; 1st vibrissa very prominent (arrowhead) (true for both sexes)
- Body large, thorax brown, often darker along the dorsal midline, abdomen yellow with brown stripes that are broadly interrupted along dorsal midline but that reach to the lateral ends of the tergites (arrow)

Genital area dark brown (arrow)

Internal genitalia

Wing grayish with a hint of clouded posterior crossvein pigmentation
**Hirtodrosophila ordinaria**
(Coquillett 1904)

This is a large species. Both sexes look similar, although the males look more spectacular, which is probably why the two sexes were originally described as two different species. The thorax is brown, usually darker along the dorsal midline. The abdomen is light in color with brown stripes that are broadly interrupted along dorsal midline but reach to the lateral ends of the tergites, where they are most intense in color. The wings are slightly grayish with just a hint of a posterior crossvein shade. The second orbital bristle is much shorter than the first and the third, and the first vibrissa is very prominent. In males, the lemon-yellow testes shine through the abdomen, which make a strong contrast to the chocolate-brown bands. The genital area of males is dark brown. The females look more “ordinary” and can be easily confused with females of the melanica species group. Tips for collecting and breeding: This species can be collected from mushroom baits, but it cannot be maintained in the laboratory. Similar species: *Scaptomyza pallida* males closely resemble undernourished males of *H. ordinaria*. Counting the rows of acrostichal bristles (*H. ordinaria* has 8 and *S. pallida* has 2) resolves this problem. Although we have never seen flies of this species, the description of *Drosophila melanura* matches the one of *Hirtodrosophila ordinaria* almost precisely.

**Taxonomy:** Lacy (1982) has determined that *H. ordinaria* Coquillet is synonymous with *D. magnafumosa* Stalker and Spencer and *D. melanderi* Sturtevant.

**Distribution:** Collection records are spotty, with specimens from California, Washington, Minnesota, Quebec, New Hampshire, Massachusetts, New York, and Tennessee (Lacy 1981). Lacy (1981) suggests that the species is widespread across the northern United States and southeastern Canada, extending southwards to the higher elevations in the Smoky Mountains.

**Breeding sites:** *H. ordinaria* breeds in a wide variety of gilled fleshy fungi, as well as several species of polypores (Lacy 1984a, 1984b).

**Population structure:** Lacy (1983) examined the hierarchical genetic structure of *H. ordinaria* populations from Tompkins County, New York and the Great Smoky Mountains National Park, Tennessee. For two allozyme loci, he found little genetic differentiation between regions (NY versus TN), despite there being a broad zone of presumably climatically unsuitable habitat between upstate New York and the high elevations of the Smoky Mountains.
REFERENCES:


Subgenus Sophophora

*Drosophila melanogaster*

*Drosophila melanogaster* males

- Genital arch (arrow) small (5 x smaller than in *D. simulans*)
- Male front leg with sex comb (arrow head)
- Body medium-sized, abdomen vaguely striped, terminal segments are black
- Wings nearly unpigmented

*Drosophila melanogaster* females

- Females are nearly identical to *D. simulans*
- Body medium-sized, abdomen is striped, dorsal midline of abdomen is dark
- Wings nearly unpigmented

*Females are nearly identical to *D. simulans*!*
Drosophila melanogaster
Meigen 1830

This is a fairly small-sized species. Males show a black tip of the abdomen, prominent sex combs on their forelegs, and wings without markings. Females usually have light abdomens with dark stripes on each segment and a dark dorsal midline stripe. Similar species: D. simulans looks extremely similar in external appearance, and the females cannot reliably be distinguished. The posterior lobe of the genital arch of males is much larger in D. simulans than in D. melanogaster. D. suzukii has a similar general appearance to D. melanogaster but is larger. Males of D. suzukii have a large black spot on the anterior distal tip of each wing. D. suzukii females have a large oviscapt with a saw-tooth edge that is readily seen under the microscope. Lightly colored D. algonquin and D. affinis females are somewhat similar to dark D. melanogaster females. Culturing these individuals is the best way to identify the species, as the next generation gives rise to males that are easily identified. Tips for collecting and breeding:

D. melanogaster is a common guest in virtually every kitchen and fruit market in the summer and fall months. They are attracted to banana, cantaloupe, and tomato baits. This species can be reared on cornmeal-sucrose-yeast medium or instant Drosophila food, each with a few grains of Baker’s yeast.

Taxonomy: Subgenus Sophophora. Species group melanogaster

D. melanogaster is sister to the simulans complex, which comprises D. simulans, D. sechellia, and D. mauritiana. The two lineages are estimated to have split in Africa ~3 million years ago (Garrigan et al. 2012).

Distribution: D. melanogaster is native to equatorial regions of Africa, from which it has spread out as a human commensal to become cosmopolitan, having colonized every continent except Antarctica (Lachaise et al. 1988). Genomic analyses reveal that the greatest levels of genetic variation occur in southern central Africa (e.g., Zambia and Zimbabwe), suggesting that this may be the region where the species arose (Pool et al. 2012). Based on extensive collection records, it is likely that D. melanogaster colonized New York State some time between 1865 and 1875, and soon thereafter it started appearing in other parts of the Northeast and Midwest (Sturtevant 1921; Keller 2007).

Breeding sites and ecology: D. melanogaster breeds in a wide variety of decaying fruits that are either grown by or associated with humans. It is commonly found in houses, grocery stores, fruit markets, orchards, vineyards, cider mills, and wineries, but is much less abundant out in the woods (Sturtevant 1921). Although this species has played a central role in studies of genetics and evolution for over 100 years, little is known of its ecology, including its original breeding sites in its...
native range in Africa (Lachaise et al. 1988; Keller 2007). Candidates include the decaying fruits and occasionally flowers of plants belonging to the Annonaceae, Apocynaceae, Caesalpiniaceae, Moraceae, Palmaceae, Pandanaceae, Rubiaceae, Sapotaceae, Solanaceae, and Zingiberaceae (Lachaise et al. 1988).

In an apple orchard population of D. melanogaster, there is significant genetic differentiation among flies emerging from individual decaying apples (Hoffmann and Nielsen 1985). These authors developed a model suggesting that the emerging flies are the offspring of only 2-3 females, despite the large numbers of adult flies that can often be found there. It could be that the first reproductively mature females to arrive at a breeding site produce most of the offspring that survive to adulthood, with the offspring of later arriving females succumbing to larval competition.

**Modes of reproductive isolation:** D. melanogaster is to some extent ecologically isolated from D. simulans, the other cosmopolitan member of the melanogaster group, in that D. melanogaster is more attracted to ethanol-containing breeding sites (McKenzie and Parsons 1972). Since these flies often mate at their breeding sites (Markow 1988), this ecological difference will reduce encounter rates between the two species in the wild. Even when D. melanogaster and D. simulans do encounter each other, phenomonal differences between them contribute to behavioral isolation (Coyne and Oyama 1995).

The first experimentally produced hybrids between Drosophila species were obtained by reciprocal crosses between D. melanogaster and D. simulans (Sturtevant 1921). Crosses between D. melanogaster females and D. simulans males yield only female offspring, as the males suffer hybrid inviability. The females, though viable, are sterile. The reciprocal cross, remarkably, yields primarily male hybrid progeny, which are sterile, with occasional females. This latter result is one of the few exceptions to Haldane’s Rule in Drosophila. The production of inviable or sterile hybrid offspring precludes traditional genetic analysis of the genetic basis of these traits. Nevertheless, through the use of sophisticated genetic tricks, some of the genes underlying these cases of hybrid inviability and hybrid sterility have been identified, and in several cases, the interacting genes appear to be involved in various sorts of genetic conflict (Presgraves 2007, 2010).

Although D. melanogaster has no very close relatives, it may be in the very early stages of speciation. There exists strong behavioral isolation between the population of D. melanogaster in Zimbabwe and populations from other regions of the world. The isolation is particularly strong in interactions between females from Zimbabwe and males from other populations (Wu et al. 1995). It is interesting to note that Zimbabwe falls within the region where D. melanogaster arose (see above). Experimental manipulations have shown that female mating preferences are governed little, if at all, by visual or acoustic signals produced by males, but that male-produced pheromones (cuticular hydrocarbons) are important (Grillet et al. 2012). Such asymmetric behavioral isolation among populations of D. melanogaster, based on olfactory cues, is very similar to the situation in D. subquinaria.

Further geographic differentiation in mating preferences has recently been discovered in D. melanogaster (Yukilevich and True 2008). The species now comprises at least three mating preference groups that exhibit significant sexual isolation from one another: Zimbabwe, southeastern United States, and Bahamas /
West Africa. It remains to be seen whether there is additional geographic differentiation in mating preferences among *D. melanogaster* populations in other parts of the world. It would be worthwhile testing whether other cosmopolitan species of *Drosophila* are undergoing a similar type of differentiation.

**Meiotic drive:** Sex chromosome meiotic drive is unknown in *D. melanogaster*, but the species is polymorphic for *Segregation Distorter (SD)*, which causes meiotic drive on the second chromosome. This drive - responder system has been subject to extensive genetic studies since the 1950s (reviewed in Larracuente and Presgraves 2012). In populations worldwide, *SD* occurs at similar frequencies (≤5%), suggesting the existence of a stable polymorphism. However, recent studies reveal that there has been recent and ongoing turnover of *SD* chromosomes in natural populations (Presgraves *et al.* 2009; Brand *et al.* 2015).

**P-elements:** There is an immense literature on the genetics, evolution, and molecular biology of *P*-elements, one of the first selfish genetic elements discovered in eukaryotes (recently reviewed in Kelleher 2016). We will just touch a few salient aspects of these transposable elements, which have the potential to spread throughout the genome by a cut-and-paste mechanism. Molecular and biogeographic evidence strongly suggests that *P*-elements jumped from *D. willistoni* to *D. melanogaster* - mediated perhaps by mites - in the mid 20th Century somewhere in the Americas. From there, they rapidly spread out to populations of *D. melanogaster* across the rest of the world. Crosses between male flies that carry *P*-elements and females that do not result hybrid dysgenesis in their offspring, which is characterized by male recombination, high mutation rates, and sterility. This indicates that there is a substantial fitness cost in populations polymorphic for carrying *P*-elements. Remarkably, suppression of *P*-element transposition, which can be mediated by the Piwi-interacting RNA pathway, evolved in concert with the spread of *P*-elements (Kelleher 2016). The rapidity of *P*-element spread and suppression of transposition provides a glimpse of the extraordinarily dynamic nature of *Drosophila* genomes.

**Parasites and pathogens:** *D. melanogaster* has become a model system for the study of innate immunity and thus it is important to know what sorts of infectious pathogens and parasites it confronts in nature. However, far more is known about the parasites and pathogens of *D. melanogaster* in areas where this cosmopolitan species is associated with humans than in its original range. If the parasites and pathogens confronted in the newly colonized areas present novel selective challenges, this could be evident at the genomic level, thus facilitating discovery of genes that may underlie resistance or tolerance to these infections. The notable parasites and pathogens that have been discovered include the following:

**Bacteria:** Metagenomic studies indicate that *D. melanogaster* is infected with numerous bacteria in the wild (Corby-Harris *et al.* 2007; Chander *et al.* 2011). These include several species of *Providencia* that vary in their virulence to flies (Galac and Lazzaro 2011).

**Parasitoids:** *D. melanogaster* can serve as host to the following parasitoid wasps: *Asobara tabida*, *Phaenocarpa persimilis*, *Trichopria* sp., *Pachycrepoides dubius*, *P. vindemiae*, *Spalangia erythromera*, *Spalangia drosophilae*, *S. erythromera*, *Trichomalopsis micropterus*, *Ganaspis xanthopoda*, *Leptopilina boulardi*, and *Leptopilina heterotoma*, *Tanycarpa punctata* (Carton *et al.* 1986; Davis *et al.* 1996).
*melanogaster* exhibits genetic variation in resistance to *Asobara tabida*, and, significantly, there is a negative genetic correlation between such resistance and larval competitive ability (Kraaijeveld and Godfray 1997).

**Viruses:** The first virus discovered in *D. melanogaster* was the sigma virus, a vertically-transmitted, negative-sense, single-stranded RNA rhabdovirus, which causes CO$_2$ sensitivity in infected flies (L’Heritier 1957). Molecular phylogenetics studies of sigma virus isolates suggest that sigma was either recently acquired by *D. melanogaster* or that there has been a recent selective sweep of a new sigma virus variant (Carpenter *et al.* 2007; Wilfert and Jiggins 2014). Recent metagenomic screens have revealed that *D. melanogaster* from natural populations harbor at least 24 different species of viruses, including DNA, double strand RNA, positive-strand RNA, and negative-strand RNA viruses (Webster *et al.* 2016). Some of these, such as Galbut virus, occur at high prevalence in most populations of *D. melanogaster*, whereas most others occur much more sporadically (Webster *et al.* 2015). Perhaps the sporadic cases are indicative of episodic outbreaks and crashes, although this has not been studied.

**Trypanosomatids:** *D. melanogaster* is subject to infection by an unidentified trypanosomatid parasite, with a mean infection prevalence in Ohio of 9% (Ebbert *et al.* 2001). Laboratory assays indicate that *D. melanogaster* is susceptible to infection with the trypanosomatid *Jaenimonas drosophilae*, which causes substantial increase in adult mortality of the flies (Hamilton *et al.* 2015).

**Fungal pathogens:** Although several other species of *Drosophila* in Ohio were found to be infected with the fungal pathogen *Coccidiascus legeri*, none of the *D. melanogaster* from this area were infected (Ebbert *et al.* 2003).

**Nematodes:** Nematode-parasitized individuals of *D. melanogaster* were not found among 73 individuals collected in the Netherlands (Gillis and Hardy 1997). However, Welch (1959) found that the nematode *Parasitylenchus diplogenus*, which appears limited to flies of the genus Sophophora, could parasitize *D. melanogaster* in the laboratory. It would be worthwhile to survey *D. melanogaster* from other areas, notably Africa, to assess the incidence of nematode parasitism.

**Endosymbionts:** *D. melanogaster* is polymorphic for infection with both *Wolbachia* and *Spiroplasma*. The *Wolbachia* strain, wMel, is widespread in natural populations of *D. melanogaster*, occurs at intermediate frequencies in most populations, and causes weak cytoplasmic incompatibility (Solignac *et al.* 1994; Hoffmann *et al.* 1998; Kriesner *et al.* 2016). Long-term monitoring of several sites in eastern Australia reveals that the infection prevalence appears to be stable in some areas, but not others, with infection prevalence higher in warm, low-latitude sites than in cooler areas at higher latitudes (Hoffmann *et al.* 1998; Kriesner *et al.* 2016).

Remarkably, this strain of *Wolbachia* confers a high level of resistance to RNA viruses, as virus-infected flies carrying wMel survive substantially longer than *Wolbachia*-free flies (Hedges *et al.* 2008; Teixeira *et al.* 2008). Even more remarkably, upon transfection to the mosquito *Aedes aegypti*, wMel confers resistance to dengue (an RNA virus for which *A. aegypti* is an important vector) and can spread via cytoplasmic incompatibility within populations of these mosquitoes (Walker *et al.* 2011; Hoffmann *et al.* 2014). Thus, wMel has the potential to be an important tool in controlling the transmission of dengue in human populations, as well as other arboviruses, such as Zika and

A maternally-transmitted male-killing strain of *Spiroplasma* has been found to infect *D. melanogaster* in natural populations in Brazil and Uganda. The infection prevalence appears to be low in these populations, on the order of 2% - 3% in both areas (Montenegro et al. 2005; Pool et al. 2006). The *Spiroplasma* strains from the two continents are very similar genetically, but not identical (Pool et al. 2006). *Spiroplasma* kills male embryos of *D. melanogaster* by interfering with the dosage compensation complex during early development (Veneti et al. 2005; Cheng et al. 2016). Transinfection of *Spiroplasma* from *D. melanogaster* to *D. neotestacea* results in a high level of male-killing (Haselkorn and Jaenike 2015). This is a seemingly surprising result, as the lineages leading to these two species are estimated to have split 50-60 million years ago (Russo et al. 2013). Perhaps *Spiroplasma* targets a conserved element associated with the dosage compensation complex, such as the CLAMP zinc finger protein (Kuzu et al. 2016).

**Physiological ecology:**

**Ethanol:** Both larvae and adults of *D. melanogaster* are substantially more tolerant of ethanol than those of *D. simulans* (McKenzie and Parsons 1972), enabling *D. melanogaster* to utilize fermenting substrates that are unsuitable for most other species of *Drosophila*. Additionally, *D. melanogaster* from temperate regions are substantially more resistant to ethanol than are tropical flies, which may be due largely to a difference between these flies in their resistance to acetic acid, a breakdown product of ethanol metabolism (Fry 2014). The genetics and biochemistry of ethanol resistance have been subject to a great deal of research. More recently, *D. melanogaster* has become a model system for the study of alcohol abuse and addiction (Devineni and Heberlein 2013).

*D. melanogaster* exhibits substantial geographic variation in ethanol resistance that is consistent among regions around the world (reviewed in Fry et al. 2007). Such variation indicates a substantial capacity for local adaptation in this species. Associated with such clines in ethanol tolerance are clines in the frequency of two alleles of the *Adh* (alcohol dehydrogenase) locus (Oakeshott et al. 1982). In populations along the east coast of Australia, there was a significant ~4° latitudinal shift in the *Adh* cline in the ~20-year period between 1979-1982 and 2002-2003 (Umina et al. 2005). There was an even larger clinal shift in the frequency of a common inversion that is not associated with *Adh*. The shifts in the genetic clines are associated with climate changes over this period, including an increase in the mean daily maximum temperature and a decrease in relative humidity (Umina et al. 2005). Thus, the genetic changes in natural populations of *D. melanogaster* strongly suggest that ongoing climate change is having a significant impact on the genetic constitution of this species.

**Mushroom toxins:** Like other non-mycophagous species of *Drosophila*, *D. melanogaster* is highly susceptible to the mushroom toxin α-amanitin, which inhibits RNA polymerase II (Jaenike et al. 1983). It is also highly sensitive to another mushroom toxin, ibotenic acid, with dramatically lower egg to adult survival and longer development times on media containing this compound (Tuno et al. 2007). Given the great diversity of potentially toxic compounds in various species of mushrooms (Ammirati et al. 1985), it would be interesting to see how many of them have more severe effects on *D. melanogaster* than on mycophagous species. This
could give an idea of the magnitude of evolutionary change required to shift to mycophagy.

**Physical stresses:** David *et al.* (2004) review studies of the comparative physiological ecology of *D. melanogaster* and *D. simulans*, finding that, in general, *D. melanogaster* is more resistant to a variety of stresses, including high temperature (knockdown time at 37°C), cold tolerance (survival time at -1°C and wake up time following 16 hours at 0°C), and desiccation (survival time in the absence of food). *D. melanogaster* is also more tolerant of darker conditions, which may contribute to their being more prone to enter buildings (e.g., houses, grocery stores, and wine cellars). These differences are likely to affect multiple aspects of the flies’ ecology, such as microhabitat distribution, activity as a function of weather conditions, and resource use.

*D. melanogaster* exhibits substantial geographic variation in ecophysiological traits, including resistance to high and low temperatures (Hoffmann *et al.* 2002), indicative of local adaptation.

**Life history:** Among seven species of human-associated *Drosophila* in England, *D. melanogaster* was found to have the second highest relative reproductive effort, as quantified by the fraction of total body biomass allocated to reproductive tissue in females (Atkinson 1979). Along with *D. simulans*, *D. melanogaster* occupies one end of the clutch size - egg volume tradeoff spectrum within that community of flies, having relatively large eggs and small clutch size.

*D. melanogaster* exhibits substantial variation in a number of life history components. For example, egg volume increases with latitude among populations both in South America and Australia (Azevedo *et al.* 1996). There is considerable variation among populations in the eastern United States in diapause frequency under standard conditions, ranging from ~35% in populations from Florida to 80% - 90% in populations from New England, suggesting local adaptation to overwintering conditions (Schmidt *et al.* 2005). The flies also differed in age-specific survivorship, being greater in southern flies early in life, but greater in New England flies later in life. Does such geographical variation in life history traits enable these flies to fit into the spatial and temporal structure of their local environments (Southwood 1977)?

Considerable genetic variation exists in natural populations of *D. melanogaster* for lifespan. A genomic analysis of differences between experimental populations selected for postponed senescence revealed that potentially hundreds of genes affect longevity and senescence in this species (Carnes *et al.* 2015). Given the importance of *D. melanogaster* as a model organism, this finding presents abundant opportunities to understand the molecular basis of senescence.

**Behavior:** Numerous aspects of the behavior of *D. melanogaster* have been studied, such as learning, circadian rhythms, and courtship songs, but here we will mention just male territoriality and mating behavior in the wild. Individuals of *D. melanogaster* often mate at their feeding and oviposition sites. Interactions between males result in the exclusion of smaller males from sites where feeding and mating occur, and as a result, such males are excluded from the mating pool (Markow 1988). Territorial males - those that defend specific patches of food against intruding males - experience greater mating success in the laboratory (Dow and von Schilcher 1975, Hoffmann 1987). A whole-genome expression analysis of lines of *D. melanogaster* selected for high or low levels of male aggression revealed the existence of at least 15 genes that affect levels of aggression (Edwards *et al.* 2006). Many of these
genes have evolutionary conserved orthologs in humans, and thus could be considered candidate genes for aggression in our species.

REFERENCES:


Devineni, A.V. and Heberlein, U. 2013. The evolution of Drosophila melanogaster as


doi:10.1371/journal.pntd.0003115.


Welch, H.E. 1959. Taxonomy, life cycle, development, and habits of two new species


**Drosophila simulans**

**Drosophila simulans males**
- Genital arch (arrow) large and tan
- Body medium-sized, abdomen vaguely striped, terminal segments are black
- Wings nearly unpigmented

**Drosophila simulans females**
- Females are nearly identical to *D. melanogaster*!
- Body medium-sized, abdomen is striped, dorsal midline of abdomen is dark
- Wings nearly unpigmented
This is a fairly small-sized species. Males have a black tip of the abdomen, prominent sex combs on their forelegs, and nearly unpigmented wings. Females usually have light abdomens with dark stripes on each segment and a dark dorsal midline stripe. Similar species: *D. melanogaster* looks extremely similar in external appearance, and the females cannot reliably be distinguished. The posterior lobe of the genital arch of males is much larger and of different shape in *D. simulans* than in *D. melanogaster*. *D. suzukii* has a similar general appearance to *D. simulans* but is larger. Males of *D. suzukii* have a large black spot on the anterior distal tip of each wing. *D. suzukii* females have a large oviscapt with a saw-tooth edge that is readily seen under the microscope.

**Taxonomy:** Subgenus Sophophora. Species group melanogaster

**Distribution:** *D. simulans* is cosmopolitan in distribution, being found on all continents except Antarctica. Multiple lines of molecular phylogenetic evidence indicate that *D. simulans* spread out to the rest of the world from East Africa or Madagascar (LaChaise *et al.* 1988; Dean and Ballard 2004; Kopp *et al.* 2005). Although *D. simulans* has been spreading around the world, the rate of spread has been considerably slower than that of *D. melanogaster*, although the reason for this is unclear (J. David, pers. comm.).

**Breeding sites:** Although *D. simulans* and the closely related *D. melanogaster* have for decades been important model systems for the study of genetics and evolution, surprisingly little is known about the ecology of natural populations of these species, including their breeding sites (Capy *et al.* 2004). *D. simulans* is known to breed in several species of native figs in Africa (Lachaise *et al.* 1988). What is known has focused largely on populations in human-associated habitats. In such environments, *D. simulans* breeds in a wide variety of decaying fruits, as well as vegetables and other non-fruit resources (Atkinson and Shorrocks 1977; David and Van Herrewege 1983; W. O. Ballard, pers. comm.). Among seven species of domestic *Drosophila* studied in a fruit and vegetable market in England over the course of 6 months, *D. simulans* was most similar in its breeding site use to *D. melanogaster* (Atkinson and Shorrocks 1977). There is indirect evidence for asymmetric interspecific larval competition between these two species, as the wing length (a measure of overall body size) of *D. simulans* adults emerging from a breeding site was negatively correlated with the number of *D. melanogaster* emerging per unit weight of that breeding site (Atkinson 1979a). In contrast, the wing length of emerging *D. melanogaster* adults was not correlated with *D. simulans* density.

At a vineyard in Australia, adults of both *D. simulans*
and *D. melanogaster* were found at all stages of grape decomposition. However, the larvae of only *D. melanogaster* were found in the earlier, active fermentation stage, whereas the larvae of both species occurred in the post-fermentation stage (McKenzie and McKechnie 1979). The concentration of ethanol was much greater in the earlier decomposition stage, consistent with laboratory findings that *D. simulans* larvae are less tolerant of ethanol than are those of *D. melanogaster* (McKenzie and Parsons 1972). Similarly in France, both *D. simulans* and *D. melanogaster* breed in decaying grapes, in which the ethanol concentration is generally low, but essentially only *D. melanogaster* breeds in piles of grape must, which has much higher concentrations of ethanol (Capy *et al.* 1987).

**Modes of reproductive isolation:** *D. simulans* has been subject to more intensive study of the genetics of reproductive isolation than any other species, plant or animal. In fact, *D. simulans* was discovered as a new species by Sturtevant (1920) when crosses with *D. melanogaster* led inevitably to sterile or lethal hybrid progeny (reviewed in Barbash 2010). The first discovery of a speciation gene (*Odysseus*, which causes hybrid male sterility) was made in molecular genetic comparisons between *D. simulans*, *D. mauritiana*, and *D. melanogaster* (Ting *et al.* 1998). Because *D. simulans* is such an important model species for studies of speciation, it is covered extensively in Coyne and Orr’s *Speciation* (2004).

Recent studies estimate that *D. simulans* split from *D. melanogaster* about 3 million years ago and from *D. sechellia* and *D. mauritiana* about 240,000 years ago (Garrigan *et al.* 2012). The isolating mechanisms among these species include attraction to different breeding sites (where mating occurs) in the field (R’Kha *et al.* 1991), behavioral isolation, conspecific sperm precedence, hybrid sterility, hybrid lethality, and hybrid breakdown. Important recent results include the finding that mutations causing hybrid male sterility (between *D. sechellia* and *D. mauritiana*) accumulate disproportionately on the X chromosome (Masly and Presgraves 2007), that gene flow and introgression between *D. simulans*, *D. sechellia*, and *D. sechellia* continued long after their split nearly a quarter million years ago, and that these introgressed regions are found disproportionately on the autosomes, *i.e.*, the chromosomes with a lower density of genes causing hybrid male sterility (Garrigan *et al.* 2012).

*D. simulans* is sympatric with and currently hybridizing with *D. sechellia* is the Seychelles (Matute and Ayroles 2014). As a consequence, *P*-elements may soon invade *D. sechellia* from *D. simulans*, if they have not done so already (see below).

**Sex-ratio meiotic drive:**¹ *D. simulans* carries three independently derived X chromosome meiotic drive systems (Tao *et al.* 2007). One, termed Paris sex-ratio, has evolved and spread recently, which then triggered the rapid evolution of both autosomal and Y-linked suppressors. Bastide *et al.* (2011) document the rapidity with which such intragenomic conflicts can bring about changes in the frequencies of drive chromosomes. The Paris *X∗SR* chromosome in *D. simulans* is estimated to have invaded Madagascar only within the last 100 years, but it is already declining in frequency due to the spread of suppressors. The frequency of the Paris *X∗SR* is also declining in Kenya, where drive suppression has also spread (Bastide *et al.* 2011). In contrast, the Paris *X∗SR* has spread rapidly in Egypt in recent years, going from 6% to 62% between 2007 and 2012 (Bastide *et al.* 2013).

¹ For terminology, see footnote for *D. affinis*.  

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However, the fate of this driving X in Egypt is probably the same as in Madagascar and Kenya, as its spread in Egypt has been accompanied by an equally rapid increase in the strength of drive suppression.

The other two sex-ratio drive systems – termed Durham sex-ratio and Winters sex-ratio – were discovered by introgressing regions of the D. simulans genome into either D. sechellia or D. mauritiana. These two systems are cryptic within D. simulans, where they are now completely suppressed (Helleu et al. 2016).

**P-elements:** P-elements jumped from D. willistoni to D. melanogaster some time prior to 1950, after which they rapidly spread globally within populations of this species (reviewed in Kelleher 2016). P-elements have now colonized D. simulans in the last few years. P-elements were absent in D. simulans collected from California, Madagascar (where D. simulans may have originated), and the South Pacific prior to 1998, as well as from collections from sub-Saharan Africa made from 2001 to 2009. Yet, P-elements have now been found in D. simulans collected in South Africa in 2012 and in Florida in 2010. The Florida flies have very few P-elements per genome, suggesting a very recent arrival there (Kofler et al. 2015). The P-element in D. simulans differs by a single substitution from that in D. melanogaster, suggesting that the element jumped from D. melanogaster to D. simulans (Kofler et al. 2015). The spread of P-elements in multiple populations of D. simulans was especially rapid between 2006 and 2014 (Hill et al. 2016). As in D. melanogaster, crosses between males that carry P-elements and females that do not leads to hybrid dysgenesis, as manifested in the production of sterile F1 females that have abnormally small ovaries (Hill et al. 2016).

**Parasites and pathogens:** D. simulans from natural populations have been found to harbor at least 10 different species of viruses, including DNA, double strand RNA, and positive-strand RNA viruses (Webster et al. 2015). Resistance to some of these viruses is conferred by maternally-transmitted Wolbachia (see below).

The parasitic wasps Phaenocarpa persimilis, Leptopilina boulardi, and Leptopilina heterotoma have been reported from D. simulans (Carton et al. 1986).

**Endosymbionts:** D. simulans has been colonized by Wolbachia on at least four independent occasions (Ballard 2004). The strains currently circulating in the species have been named wRi, wHa, and wAu of Wolbachia supergroup A, and wMa of supergroup B, with wMa comprising three subtypes (wMa, wNo, and wKi). Because Wolbachia experience strictly maternal inheritance within D. simulans, the evolutionary history of the infections has been inferred by examination of the strain distributions among mitochondrial haplotypes and lineages. This analysis indicates that wMa is the oldest infection, probably predating the divergence of D. simulans from D. sechellia and D. mauritiana, with wHa, wAu and wRi invading later in the history of the species (Ballard 2004). The strains differ in their cytoplasmic incompatibility (CI) interactions (James and Ballard 2000). Strains wHa and wRi exhibit bidirectional incompatibility, and both express CI in crosses between infected males and uninfected females. Strain wAu does not express CI in matings with other strains or with uninfected females. Finally, strain wMa is susceptible to CI in matings with wRi or wHa-infected males, but males of wMa are compatible with females of these other strains, meaning the CI is unidirectional. Finally, matings between wMa males and uninfected females exhibit intermediate levels of CI.
These strains also differ in the degree to which they provide protection against viral infections. Wolbachia strains wHa and wNo provided no detectable protection against the RNA viruses Drosophila C virus and Flock House virus, whereas strains wAu and wRi substantially increased the survival of virus-infected adult flies (Osborne et al. 2009). Strains wAu and wRi are closely related to strain wMel in D. melanogaster that also provides protection against these viruses. Detailed temporal and spatial studies of the prevalence of Wolbachia infection of D. simulans reveal how extraordinarily dynamic these interactions are in natural populations. In the 1980s, one strain of Wolbachia (wRi) swept rapidly through populations of D. simulans in California (Turelli and Hoffmann 1991). In some populations, the prevalence of infection rose from under 10% to near fixation within three years. The rapid spread was initially attributed to cytoplasmic incompatibility, in which the prevalence of infection must exceed a particular threshold before it can spread to effective fixation. More recently, this spread has been re-interpreted as a Fisherian wave, specifically long-distance dispersal in association with human transport coupled with local selection of a favorable variant, as wRi has been found to increase the fecundity of infected females (Weeks et al. 2007; Kriesner et al. 2013). A more recent, and equally striking example of Wolbachia spread in D. simulans has been documented in Australia (Kriesner et al. 2013). In the 1990s, Wolbachia strain wAu occurred at relatively low frequencies along the east coast of Australia. By the mid 2000s, the prevalence of wAu infection had increased substantially in many populations. Around this time, strain wRi first appeared in this region, and in under 10 years, it spread to very high frequency throughout eastern Australia. In so doing, wRi has almost completely displaced wAu in recent years. As in California, the rapid spread of wRi in Australia has been interpreted as a Fisherian wave (Kriesner et al. 2013).

**Behavior:** D. simulans is somewhat less associated with humans than is D. melanogaster, for instance in being less prone to enter human habitations (Watanabe and Kawanishi 1976).

**Life history variation:** Among six species of domestic Drosophila that occur in England, D. simulans has the greatest reproductive effort, defined as the ratio of reproductive to total biomass (Atkinson 1979b). It was at one end of the tradeoff spectrum between clutch size and egg volume, in having the largest relative egg volume among these species and the second smallest relative clutch size. This might indicate that the breeding sites of D. simulans are frequently encountered by flies and thus are heavily competed for. David et al. (2004) note that, in comparison to D. melanogaster, D. simulans has lower fecundity, but slightly faster development (except at temperatures above 28°C), a result consistent with its having larger eggs than D. melanogaster.

**Physiological ecology:** David et al. (2004) review the ecophysiological differences between D. simulans and D. melanogaster. In general, D. simulans is less resistant to environmental stresses, including heat, cold, desiccation, ethanol, and high concentrations of carbon dioxide. D. simulans exhibits less genetically based geographic variation in both morphological and physiological traits than does D. melanogaster (Capy et al. 1993; Gibert et al. 2004). For instance, D. simulans exhibits very little latitudinal variation in ethanol tolerance, whereas D. melanogaster populations in temperate latitudes are much more tolerant than those from tropical regions (David
and Boquet 1975). *D. simulans* also exhibits less geographic differentiation at the genomic level (Sedghifar et al. 2016).

*D. simulans* and *D. melanogaster* also differ substantially in their tolerance of ethanol. Both adults and larvae of *D. simulans* experience greater mortality than *D. melanogaster* in the presence of ethanol, particularly at concentrations ≥ 6% (McKenzie and McKechnie 1972; David and Van Herrewege 1983). Furthermore, whereas females of *D. melanogaster* exhibit a slight oviposition preference for ethanol-containing food, females of *D. simulans* strongly avoid such oviposition sites. The greater ethanol tolerance of *D. melanogaster* is due in large measure to the genes Alcohol dehydrogenase and Aldehyde dehydrogenase (Fry and Saweikis 2006).

**REFERENCES:**


David, J.R. and Van Herrewege, J. 1983. Adaptation to alcoholic fermentation in

Drosophila suzukii

Drosophila suzukii males

- Male can be identified without microscope
- Body medium-sized, abdomen vaguely striped, terminal segments are black
- Wings with one black spot

Drosophila suzukii females

- Wings nearly unpigmented
- Body medium-large-sized, abdomen is striped, terminal segments are black
- Large, scary ovipositor with chain-saw-like appearance
Drosophila suzukii males

Drosophila suzukii females
Drosophila suzukii (Matsumura 1931)

D. suzukii, commonly called Spotted Wing Drosophila (SWD), is a medium-sized species that closely resembles D. melanogaster in body pigmentation. Males have one large black spot on each wing. The tip of the abdomen is black, while the rest is lighter in color with narrow black stripes. The wings of the males are so distinctly patterned that they can be identified in the field without a microscope. Females have a large, chainsaw-like oviscapt. Female wings have no black spot. Similar species: D. melanogaster and D. simulans males lack the black wing spot, and the females are a bit smaller and lack the chainsaw-like appearance of the ovipositor. D. suzukii is, in general, larger than either D. melanogaster or D. simulans. The darker individuals of D. suzukii, which develop during the colder parts of the season, resemble flies of the affinis subgroup – D. affinis, D. algonquin, and D. athabasca. Look for wing spots in males and a noticeably serrated ovipositor in females of D. suzukii. Tips for collecting and breeding: D. suzukii is attracted to tomato, banana, and mushroom baits and traps. This species can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast. On Instant Drosophila Medium (Carolina Biological Supply), they do well if a piece of fruit, such as strawberry, is added to the culture.

Taxonomy: Subgenus Sophophora. Species group melanogaster

D. suzukii belongs to the suzukii subgroup within the melanogaster species group, where its closest relative appears to D. biarmipes (Yang et al. 2012; Chiu et al. 2013).

Distribution: D. suzukii, a native of southeast Asia, has recently become a cosmopolitan invasive species (Walsh et al. 2011). It spread to Japan in 1916, Hawaii in 1980, North America and Europe in 2008, and South America in 2013 (Asplen et al. 2015). It is now widespread and common in the Northeast and Midwest of the United States. Among factors likely to contribute to its rapid spread are its ability to breed in a wide variety of fruits of both native plants and agricultural crops, and its being transported long distances by shipments of commercially grown fruits. The use of native plants probably helps sustain populations of D. suzukii through periods when commercial crops are unavailable.

Breeding sites: Whereas almost all frugivorous species of Drosophila will oviposit only on damaged or decaying fruit, D. suzukii frequently oviposits on fresh fruit. Females possess a remarkable serrated ovipositor with which they saw through the skin of undamaged fruit for egg deposition (Atallah et al. 2014). As mentioned above, cultivated fruits are important breeding sites for D. suzukii, and because females oviposit and larvae feed on fresh fruit, they can cause considerable agricultural losses. In California, Oregon, and Washington, losses are particularly
acute for strawberries, blueberries, raspberries, blackberries, and cherries (Bolda et al. 2009; Goodhue et al. 2011).

In both Europe and North America, where *D. suzukii* is invasive, this species utilizes as breeding sites the fruits of numerous wild, non-cultivated host species, in addition to the fruits of commercially grown crops. Among the wild hosts used as breeding sites in our region are the fruits of blackberry, dogwood, cherry, elderberry, honeysuckle, nightshade, pokeweed, and spicebush (Lee et al. 2015a, 2015b; Elsensohn and Loeb 2017). In the late summer and fall, we have captured numerous *D. suzukii* adults feeding on mushrooms in the field.

The use of numerous species of widespread non-cultivated host plants could have several effects on populations of *D. suzukii*. First, the use of wild hosts means that non-agricultural habitats are ineffective barriers to dispersal and population expansion of *D. suzukii*. Second, the use of wild host plants should increase the effective population size of *D. suzukii*, enabling it to retain more genetic variation and thus facilitating adaptation to local conditions during its range expansion. Third, the use of wild hosts gives local populations of *D. suzukii* somewhat of a head start during the season, as found in the Upper Midwest (Pelton et al. 2016). Finally, woodland habitats, with protected sites such as leaf litter, may provide superior overwintering sites for these flies (Pelton et al. 2016). Furthermore, the food resources in woodlands might be utilized by flies to enhance overwinter survival in these cold environments.

**Modes of reproductive isolation:** A molecular phylogenetic analysis suggests that *D. suzukii* split from its sister species, *D. biarmipes*, about 7 million years ago (Ometto et al. 2013). At such a divergence date, it is likely that multiple mechanisms of pre- and postmating isolation have arisen.

**Endosymbionts:** *D. suzukii* carries a strain of *Wolbachia* (*wSuz*) that is very closely related to one of the *Wolbachia* strains (*wRi*) found in *D. simulans* (Hamm et al. 2014). Populations in North America typically have a relatively low prevalence of *Wolbachia* infection - between 7% and 20%. Prevalence in this range is not consistent with expectations of a *Wolbachia* infection that is maintained by cytoplasmic incompatibility (Turelli 1994), and indeed laboratory studies find no evidence for cytoplasmic incompatibility (Hamm et al. 2014). The *Wolbachia* in *D. suzukii* experience imperfect maternal transmission, indicating that *Wolbachia* must confer some fitness benefit to be retained within natural populations of *D. suzukii*. Evidence is conflicting on whether *wSuz* increases (Mazzetto et al. 2015) or decreases (Hamm et al. 2014) offspring production by infected female flies. Cattel et al. (2016) have recently shown that adults of *D. suzukii* infected with either *Drosophila* C virus or Flock House virus survive significantly longer if they carry *Wolbachia*, indicating that *wSuz* has protective effects similar to those found in the *Wolbachia* that infect *D. melanogaster* (Hedges et al. 2008; Teixeira et al. 2008). Interestingly, Hamm et al. (2014) reported that in a population of *D. suzukii* in Winters, California, the prevalence of *Wolbachia* infection shot up from 18% in June 2012 to 58% in May 2013. They speculate that this may have been the result of a microparasite epidemic.

**Parasites and pathogens:** Because *D. suzukii* is a serious agricultural pest, there is considerable interest in developing biological control mechanisms against this species (Cini et al. 2012). In both Europe and North America, a generalist pupal parasitoid, *Pachycrepoideus vindemiae*,...
has been found to parasitize D. suzukii in the field (Stacconi et al. 2013). One difficulty with using parasitoids to control D. suzukii is that these flies have much higher hemocyte counts than does D. melanogaster, and this is associated with D. suzukii being much more resistant to a broad range of parasitoids than is D. melanogaster (Kacsoh and Schlenke 2012). However, D. suzukii is highly susceptible to attack by one parasitoid species, Asobara japonica, with which it is sympatric in Japan (Kacsoh and Schlenke 2012).

Data are not yet available about the incidence of virus infections in D. suzukii. However, the fact that the Wolbachia strain found in this species confers increased survival to virus-infected flies suggests that they are exposed to such infections in nature.

**Physiological ecology:** The cooler days of fall result in the development of dark-morph individuals of D. suzukii, with females entering a state of reproductive diapause (Shearer et al. 2016; Wallingford et al. 2016). Females in a state of diapause have a lower supercooling point and significantly greater survival following -3°C exposure (Zhai et al. 2016; Wallingford and Loeb 2016).

Given the rapidly expanding geographical range of D. suzukii, one might expect it to exhibit tolerance for a broad range of environmental conditions, such as temperature. However, in a survey of 30 species of drosophilids in Japan, Kimura (2004) found that D. suzukii was one of the least cold-tolerant species among those whose distribution extended north of Sapporo, and one of the least heat tolerant among those whose ranges extended south of Iriomote Island. Thus, although D. suzukii has a broad latitudinal range in Japan, it appears to have a relatively narrow thermal niche. It would be interesting to compare the thermal niche of D. suzukii in Japan with that in parts of North America, where it is likely to experience more extreme temperatures.

**Behavior:** Male courtship behavior includes wing displays, in which the male-specific wing spot is made evident to females, and substrate-borne vibrations, rather than airborne courtship songs, likely transmitted by the male's legs (reviewed in Hamby et al. 2016). Is the transmission of such vibrations more effective on some types of fruits (or other areas for mating) than others? If so, is this correlated with male mating success on different substrates?

We have witnessed a female D. suzukii compulsively sawing away with her oviscapt at the side of a plastic culture vial, in which she was kept. Does this mean that females don't require gustatory cues in selection of oviposition sites?

**REFERENCES:**


s12898-016-0070-3.


**Drosophila algonquin males**

- Sex comb (arrow) large (about 10 - 15 bristles)
- 1st tarsal segment (arrow) shorter than 2nd (arrow head)
- Body small and dark
- Wings uniformly grayish

**Drosophila algonquin females**

- 1st tarsal segment (arrow) longer (!) than 2nd (arrow head)
- Body small and dark, abdomen striped, only males reliably identifiable
- Wings uniformly grayish
Drosophila algonquin males

Drosophila algonquin females
The flies are small to medium-sized and the males, especially, are dark. Males have one very large sex comb on each front leg, which is easily seen under the microscope. It consists of about 10 to 15 bristles on the first tarsal segment, with the bristles oriented obliquely to the long axis of the tarsus. The first tarsal segment is shorter than the second one. Females are dark or lighter brownish and have a striped abdomen that is often white on the ventral side. Females cannot be safely identified, but they can be used to establish a culture, from which the hatching males can be identified.

Similar species: *D. athabasca, D. affinis, and D. narragansett* (see their descriptions), all of which have very different sex combs from *D. algonquin. D. paramelanica* is a larger and more flattened species without the typical white color on the ventral side of the abdomen, and males lack sex combs. Lightly colored *D. algonquin* females resemble dark *D. melanogaster* females. Culturing these individuals is the best way to identify the species, as the next generation gives rise to easily identifiable males.

Tips for collecting and breeding: These flies are abundant at banana, cantaloupe, and tomato traps, but they can also be found at mushroom baits. This species can be reared on cornmeal-sucrose-yeast medium with some grains of Baker’s yeast. It also does well on Instant *Drosophila* Medium (Carolina Biological Supply) with a cotton roll or Kimwipe added to provide pupation sites and a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Sophophora. Species group obscura; affinis subgroup

**Distribution:** From Texas and Oklahoma up through the Upper Midwest, northeastern US, and adjacent regions in Canada (Miller 1958). It is not known from the southeastern US, where *D. affinis* is the only resident member of the affinis subgroup.

**Breeding sites:** Very little is known about the primary breeding sites of this species, like other members of the affinis subgroup.

**Modes of reproductive isolation:** Miller (1939) reports that *D. algonquin* can be crossed with *D. athabasca* to yield viable hybrid progeny, although the fertility of the hybrids was not reported. The courtship behavior of males of *D. algonquin* and *D. affinis* are very similar, but the two species do not mate in the laboratory (Miller 1950). Males of these two species do not vigorously court females of the other, suggesting male discrimination against heterospecific females. Although males of *D. algonquin* have much larger sex combs than *D. affinis*, this apparently does not contribute to reproductive isolation between these species, as the males only rarely come into contact with heterospecific females (Miller 1950).

**Sex-ratio meiotic drive:** X-drive has never been found in this species, despite efforts to find
it (Sturtevant and Dobzhansky 1936; Jaenike, unpublished). However, X-drive is present in two other members of the affinis subgroup - *D. affinis* and *D. athabasca* (Eastern A and Eastern B semispecies, but not Western-northern). It is thus possible that *D. algonquin* carries suppressors of X-drive that prevent the production of ~all-female offspring sex ratios.

**Behavior:** Males of *D. algonquin* show very little interest in females of *D. affinis* and rarely come into contact with them (Miller 1950). This suggests that males detect some cue at a distance. Curtright and Miller (1978) report that *D. algonquin* is totally dependent on light for mating, suggesting the possible importance of visual cues. The two species differ substantially in relative wing length, and this might serve as a visual cue to males. Alternatively, there might be species-specific pheromones produced by females.

**Reproductive biology:** Like other members of the obscura species group, males of *D. algonquin* produce two sizes of sperm, with long sperm being 6 times longer than short sperm (Snook 1997).

**Pericentric inversion polymorphism:** *D. algonquin* was the first species of *Drosophila* found to be polymorphic for a pericentric inversion (Miller 1939). This gene arrangement is found on the B chromosome (an autosome) and differs from the standard sequence by two overlapping inversions, thus greatly suppressing recombination between the two gene arrangements, one of which includes the centromere. This pericentric inversion is widespread and common in populations of *D. algonquin* in the Northeast and Canada, though apparently missing in Texas. The selective factors maintaining the polymorphism have not been investigated.

**REFERENCES:**


**Drosophila affinis**

**Drosophila affinis males**
- Sex comb (arrow) medium-sized (about 4 bristles)
- 1st tarsal segment (arrow) shorter than 2nd (arrow head)
- Body small and dark
- Wings uniformly grayish

**Drosophila affinis females**
- 1st tarsal segment (arrow) longer (!) than 2nd (arrow head)
- Body small to medium-sized and dark, abdomen striped, only males reliably identifiable
- Wings uniformly grayish
Drosophila affinis males

Drosophila affinis females
The flies are small to medium-sized and mostly dark. Males have a medium-sized sex comb, easily seen under the microscope, consisting of about 4 bristles on the first tarsal segment oriented parallel to the long axis of the tarsus. The first tarsal segment is shorter than the second. Females are usually dark and have a striped abdomen that is often white on the ventral side. Females cannot be safely identified, but they can be used to establish a culture, from which the hatching males can be identified. Similar species: D. athabasca, D. algonquin, and D. narragansett (see their descriptions); in each of these, the male sex combs are different from those of D. affinis. D. paramelanica is a larger and more flattened species without the typical white color on the ventral side of the abdomen, and the males lack sex combs. Lightly colored D. affinis females can resemble dark D. melanogaster females. Culturing these individuals is the best way to identify the species, as the next generation gives rise to easily identifiable males.

Tips for collecting and breeding: These flies are abundant at banana, cantaloupe, and tomato baits, but they occasionally visit mushroom baits as well. For breeding purposes, we recommend either cornmeal-sucrose-yeast medium with additional Baker’s yeast grains or Instant Drosophila Medium (Carolina Biological Supply) with a cotton roll or piece of Kimwipe for pupation plus a few grains of Baker’s yeast.

Taxonomy: Subgenus Sophophora. Species group obscura; affinis subgroup

Distribution: Eastern United States, east of the 98th meridian (Patterson and Stone 1952), from Texas and Florida in the south to Maine, Minnesota and southern Ontario and Quebec in the north.

Breeding sites: Like other North American members of the obscura group, the primary breeding sites of D. affinis have not yet been discovered. Perhaps these species are broad generalists, utilizing a wide variety of substrates, but at relatively low levels. For instance, small numbers of affinis subgroup species have been bred from decaying skunk cabbage (Grimaldi and Jaenike 1983). Other resources used at low levels include mayapple and huckleberry fruits, but very rarely slime fluxes (Carson and Stalker 1951). The great abundance of affinis subgroup species in the eastern United States and Canada, including areas that completely lack skunk cabbages, mayapples, etc., suggests that they can probably utilize a wide variety of resources. However, mushrooms are not among them, as we have never reared D. affinis or other members of the affinis subgroup from mushrooms (see also Carson and Stalker 1951).

Modes of reproductive isolation: Miller (1941) found that D. affinis females occasionally mate with males of D. athabasca, but that the few hybrid male and female offspring produced are sterile. Miller (1950) examined the courtship and
mating behavior of D. affinis and D. algonquin. Although the two species have very similar mating behaviors, males of each species did not vigorously court females of the other species, and copulation was never seen. Thus, D. affinis is reproductively isolated from its closest relatives by both pre- and most-mating isolating mechanisms.

Sex-ratio meiotic drive: D. affinis has an exceptionally interesting set of polymorphisms affecting offspring sex ratio. Like several other species of Drosophila, it is polymorphic for a driving X chromosome (X^{SR}); X^{SR}Y males produce ~100% X^{SR}-bearing sperm and all-female offspring sex ratios. Unlike most species of Drosophila, XO males of D. affinis are fertile. Remarkably, X^{SR}O males sire only sons (Voelker 1972; Unckless et al. 2015). Furthermore, D. affinis is polymorphic for Y chromosome types that differ in their resistance to X-drive (Unckless et al. 2015). Finally, D. affinis carries at least two different X^{SR} chromosomes; a particular Y chromosome type that is highly resistant to one type of X^{SR} (~50% female offspring) is completely susceptible to the other (~100% female offspring) (Unckless et al. 2015). This complex and fascinating system may shed light on the maintenance of multiple Y chromosome types in natural populations.

Nematode parasitism: None known. However, Parasitylenchus diplogenus is known to parasitize related obscura group species in Europe (Welch 1959).

Pathogens: D. affinis had the second highest rate of trypanosomatid infection (13%) among eight species of Drosophila sampled from natural populations in Ohio and the highest rate of infection (7%) by the fungal pathogen Coccidiascus legeri (Ebbert et al. 2001, 2003).

D. affinis carries a species-specific strain of sigma virus (DAffSV) that causes CO₂-induced paralysis, as another strain does in D. melanogaster (Longdon et al. 2010, 2011). The virus is transmitted vertically by females and, at a lower rate, by males. Assuming that CO₂ sensitivity can be used as a measure of DAffSV infection, the infection prevalence of this virus in natural populations of D. affinis ranges from 18% - 39% (Williamson 1961). They are also infected at relatively high frequency by a species of nudivirus (R. Unckless, pers. comm.). Fungal parasites of the order Laboulbeniales (Ascomycetes) are associated with members of the affinis subgroup in our region. These fungi can be observed directly by the presence of ampule-shaped reproductive organs (thalli) protruding from the bodies (often the legs or proboscis) of infected flies (see pictures below).

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1 Terminology

X^{SR} – X chromosome type that exhibits meiotic drive in males. Manifest as female-biased offspring sex ratios.

X^{ST} – standard, non-driving type X chromosomes

SR – a male that carries an X^{SR} chromosome

ST – a male that carries an X^{ST} chromosome
In a full season’s worth of collecting in central New York, Starmer and Weir (2001) found that the infection prevalence of males (which can easily be identified to species) was 9.4% for *D. affinis* (*n* = 104), 3.4% for *D. algonquin* (*n* = 118), and 12.9% for *D. athabasca* (probably eastern A, *n* = 770). R. Unckless (pers. comm.) finds that the prevalence of infection is greatest in spring and then falls throughout the season, and that it is much greater in males than females. The fitness impact of these fungal pathogens has not been studied quantitatively.

**Wing loading:** The three members of the affinis subgroup in eastern North America show interesting variation in wing loading, although this has not been quantified. Qualitatively, it is evident that *D. affinis* has relatively small wings for its body size (high wing loading), while *D. algonquin* has larger wings (low wing loading), with *D. athabasca* appearing to be intermediate. It would be interesting to see if these differences correlated in some manner with patterns of active short-distance dispersal or passive, long-distance dispersal in these species.

**Reproductive biology:** Like other members of the obscura species group, males of *D. affinis* produce both long and short sperm, the long being 4.6 times longer (Snook 1997). Cytological studies show that only the long sperm are involved in fertilization (Snook and Karr 1998). In *D. pseudoobscura*, another member of the obscura group, the short sperm protect the fertilizing long sperm from spermicidal conditions in the female reproductive tract (Holman and Snook 2008).

**REFERENCES:**


Snook, R.R. 1997. Is the production of multiple
sperm types adaptive? Evolution 51:797-808.


**Drosophila athabasca males**

- Sex comb (arrow) small (about 4 bristles)
- 1st tarsal segment (arrow) longer than 2nd (arrow head)

**Drosophila athabasca females**

- 1st tarsal segment (arrow) longer than 2nd (arrow head)

**Wings uniformly grayish**

**Body small and dark**

**Body small and dark, only males reliably identifiable**
Drosophila athabasca males

Drosophila athabasca females
The flies are small-sized and mostly dark. Males have one small sex comb on each front leg, which can be difficult to see even under the microscope. It consists of about 4 bristles on the first tarsal segment oriented nearly parallel to the long axis of the tarsus. The first tarsal segment is longer than the second. Females are dark brown all over, except for the sternites on the ventral side of the abdomen appear white. Females cannot be safely identified, but they can be used to establish a culture, from which the males can be identified. Similar species: D. affinis, D. algonquin, and D. narragansett (see their descriptions). D. athabasca can be distinguished from D. affinis and D. algonquin by the structure of the male sex combs, and from D. narragansett by whether or not the male face (space between the eyes) has a pollinose appearance. D. paramelanica is a larger and more flattened species without the typical white color on the ventral side of the abdomen, and males lack sex combs.

Tips for collecting and breeding: These flies are abundant at banana, canteloupe and tomato baits, but they also visit mushroom baits occasionally, especially in early spring, suggesting that their normal food resources are not yet available. This species can be reared on cornmeal-sucrose-yeast medium or on Instant Drosophila Medium (Carolina Biological Supply) with a few grains of Baker’s yeast. Cultures often do well for a generation or two, but then go downhill. Perhaps these flies depend upon particular microbial species that do not persist in laboratory conditions.

Taxonomy: Subgenus Sophophora. Species group obscura; affinis subgroup

Distribution: D. athabasca comprises three “semispecies” - “western-northern”, “eastern A” and “eastern B” - between which there is little or no gene flow, even in areas where they are sympatric. The range of “western-northern” extends from Alaska down the Pacific Coast to Oregon and across the continent to Maine. “Eastern A” occurs throughout most of the Northeast and Upper Midwest, being sympatric with “western-northern” across the northern edge of its range. The range of “eastern B” extends from New Jersey west to Indiana, being sympatric with “eastern A” in much of its range. Yukilevich et al. (2016) note that “eastern B” appears to have expanded its range westward in recent years.

From data presented in Miller et al. (1975), we find that in Maine, where two of the semispecies are sympatric, “eastern A” and “western-northern” are about equally common on the mainland and very large islands, whereas “western-northern” is significantly more common on small islands ($P < 0.05$; Fisher’s exact test). This suggests that the two semispecies differ somewhat in their ecological requirements or habitat preferences. The small islands are characterized by spruce
trees, whereas the larger islands and mainland in this area more commonly harbor mixed deciduous-coniferous forests.

**Breeding sites:** *D. athabasca* is a very common species in much of its range, yet researchers have not yet identified important breeding sites for this species. Carson and Stalker (1951) report that they bred a few individuals from rotting persimmons, mushrooms (though we have not reared any from mushrooms), and slime fluxes, but the numbers bred are orders of magnitude below what would be necessary to account for the great abundance of this species.

**Modes of reproductive isolation:** Miller (1950) reported that *D. athabasca* males (most likely “western-northern” based on the origin of the strains used: Wyoming, Washington State, and Alaska) would occasionally mate with *D. algonquin* females and much more often with *D. affinis* females in no-choice situations. In reciprocal crosses involving *D. athabasca* females, there were no interspecific matings with *D. algonquin* males and extremely few with *D. affinis*. Female *athabasca-algonquin* hybrids were viable and occasionally fertile in backcrosses to *D. algonquin* males. Hybrid males, though viable, were found to be sterile. *Athabasca-affinis* hybrids have low (but nonzero) viability, with both male and female hybrids being sterile.

There is strong behavioral isolation between semispecies of *D. athabasca*, particularly those whose ranges overlap: “eastern A” and “eastern B”, and “eastern A” and “western-northern” (Miller 1958; Yukilevich et al. 2016). However, the rare hybrid offspring are fully viable and fertile. The behavioral isolation is due strong female, but not male, mating preferences.

The semispecies differ dramatically in their copulation duration (Miller 1958) and courtship songs (Miller et al. 1975; Chang and Miller 1978). Despite the potential for gene flow among the three semispecies, molecular genetic studies reveal essentially complete differentiation at certain nuclear loci between “eastern A” and “eastern B”, on the one hand, and “western-northern,” on the other (Johnson 1978; Jaenike et al. 1978; Ford et al. 1994). In addition, “eastern A” and “eastern B” carry mtDNA haplotypes different from those found in “western-northern” (Yoon and Aquadro 1994). No known diagnostic loci (i.e., those for which there are no shared alleles or haplotypes) are known between “eastern A” and “eastern B.” However, each of these two semispecies carries unique alleles or haplotypes at certain loci (Jaenike et al. 1978; Johnson 1978; Yoon and Aquadro 1994; Ford et al. 1994; Ford and Aquadro 1996). Yoon and Aquadro (1994) speculate that this pattern suggests that there is currently no gene flow between “eastern A” and “eastern B”.

Yukilevich et al. (2016) have shown experimentally that the strong behavioral isolation between “eastern A” and “western-northern” is due largely to the noticeable differences in the courtship songs of these two semispecies. In contrast, they differ little in their cuticular hydrocarbons, and experimental transfers of the cuticular hydrocarbons between the semispecies did not reduce the level of behavioral isolation between them.

**Sex-ratio meiotic drive:**¹ X-drive occurs in the “eastern A” and “eastern B” semispecies of *D. athabasca*, but not “western-northern” (Miller and Voelker 1969). The X<sup>SR</sup> chromosome differs in gene arrangement from the X<sup>ST</sup> chromosome. Interestingly, X-drive is also known in other members of the affinis subgroup, including *D. affinis* and *D. azteca*, though it is not known if drive arose independently in these different species.

¹ For terminology, see footnote for *D. affinis*. 
**Pathogens:** *D. athabasca* had the highest rate of trypanosomatid infection (17%) among eight species of *Drosophila* sampled from natural populations in Ohio, but the lowest rate of infection (0.8%) by the fungal pathogen *Coccidiascus legeri* among the 6 endemic species of *Drosophila* surveyed (Ebbert et al. 2001, 2003).

In other species of *Drosophila*, CO₂ sensitivity (death or paralysis) is associated with infection by species-specific strains of sigma virus that are vertically transmitted by both females and males (Longdon et al. 2010). Assuming that CO₂ sensitivity is indicative of infection with a sigma virus, the infection prevalence of sigma virus in natural populations of *D. athabasca* ranges from 3% - 20% (Williamson 1961). The flies that Williamson studied were collected in Minnesota and Alaska and thus were most likely the “western-northern” semispecies.

**Evolutionary history:** Based on their analysis of molecular variation at autosomal loci, Ford and Aquadro (1996) speculate that divergence between “eastern” (A and B) and “western-northern” *D. athabasca* was initiated ~23,000 years ago, a time corresponding to the last glacial maximum (~24,000 years ago). However, this estimate assumes that the flies had about 10 generations per year, which might be an overestimate, especially for more northerly populations. This divergence was accompanied by selection for differences in male courtship songs. Subsequently, “eastern A” and “eastern B” are hypothesized to have diverged very recently, perhaps 5000 years ago, with another round of selection for divergence in courtship songs.

**Reproductive biology:** Like other members of the obscura species group, males of *D. athabasca* produce both long and short sperm, with the long sperm being 13 times longer than the short in “eastern A” (Snook 1997). Cytological studies show that, at least in “eastern B,” only the long sperm are involved in fertilization (Snook and Karr 1998).

**REFERENCES:**


Drosophila narragansett

THIS FRUIT FLY JUST ATE A CARROT (APPARENTLY IN ONE PIECE!)

PLACEHOLDER - NO IMAGE AVAILABLE
ALTHOUGH BANANAS ARE SHAPED LIKE CARROTS, THEY ARE MORE CHEWABLE
"Drosophila narragansett"
Sturtevant and Dobzhansky
1936

**D. narragansett** is very similar in appearance to **D. athabasca**. It differs from **D. athabasca** in having a silvery pollinose frons (space between the eyes) in males and a mesonotum (the largest section of the thorax) with a grayish dusted appearance.

**Taxonomy:** Subgenus Sophophora. Species group obscura; affinis subgroup

Based on species descriptions, **D. narragansett** appears to be very closely related to **D. athabasca** (Sturtevant and Dobzhansky 1936; Sulerud and Miller 1966), with the space between the eyes of male (but not female) **D. narragansett** having a strongly pollinose appearance.

**Distribution:** Connecticut, Massachusetts (Woods Hole), and New York, but reported to be very rare (Sturtevant and Dobzhansky 1936). We have found one male of this species in Rochester, NY.

**Breeding sites:** Unknown.

**Modes of reproductive isolation:** Kleager (1970) examined reproductive isolation between **D. narragansett** and other species of the affinis subgroup. Week-old males or females of **D. narragansett** were placed for 7 days with a group of flies of the opposite sex of another species, after which females were dissected to determine if they had been inseminated, and culture vials were retained to rear hybrid progeny. Kleager observed a high level of behavioral isolation between **D. narragansett** and all other species, including **D. azteca**, **D. tolteca**, **D. affinis**, **D. algonquin**, **D. athabasca** western-northern, and **D. athabasca** Eastern A (based on its having been derived from a female collected in Minnesota). Of all species tested, interspecific matings were most likely between **D. narragansett** and **D. athabasca** Eastern A. Unfortunately, the closely related **D. athabasca** Eastern B was not tested.

**REFERENCES:**


Subgenus Dorsilopha

*Drosophila busckii*

*Drosophila busckii* males

- Midline *stripe* on thorax *diverges* (arrow)
- Body small to medium-sized and spotted/striped
- Wings nearly unpigmented

*Drosophila busckii* females

- Midline *stripe* on thorax *diverges* (arrow)
- Body small to medium-sized and spotted/striped
- Wings nearly unpigmented
*Drosophila busckii* males

*Drosophila busckii* females
**Drosophila busckii**
Coquillet 1901

This is a small-sized species with a flattened body. Males and females look similar. The thorax shows brown stripes, and the dorsal midline stripe diverges towards the abdomen. The abdomen is decorated with black spots that are in sharp contrast to the yellow background. The spots on the abdomen, except for those at the lateral margin, are often fused to stripes. Similar species: This striking looking species is hard confuse with any other species in our region. Tips for collecting and breeding: *D. busckii* frequently visits banana and tomato traps, and more rarely mushroom baits. We recommend breeding this species on cornmeal-sucrose-yeast medium with a few grains of Baker's yeast; it also does very well on Instant *Drosophila* Medium (Carolina Biological Supply) with a few grains of Baker's yeast added.

**Taxonomy:** Subgenus Dorsilopha. Species group busckii

Based on various morphological traits, *D. busckii* has been considered to be a member of the subgenus Dorsilopha. However, a recent molecular phylogeny clearly places this species within the subgenus Drosophila (Zhou and Bachtrog 2015).

**Distribution:** Cosmopolitan

**Breeding sites:** *D. busckii* breeds in a wide variety of substrates, including various plants, fungi, and garbage, such as rotten pigeon eggs and fish, formalin-preserved chicken, and the formalin-preserved head of a human (Sturtevant 1921; Bächli and Bural 1967; Carson 1971). Atkinson and Shorrocks (1977) found that *D. busckii* favored decaying vegetables (e.g., cauliflower, lettuce, and potato) as breeding sites in an English market. We have also bred them occasionally from decaying skunk cabbages and mushrooms (Jaenike 1978; Grimaldi and Jaenike 1983). JJ once found this species breeding in dishwater scum in a sink where the dishes had been left to soak for a couple of weeks (!).

**Modes of reproductive isolation:** The subgenus Dorsilopha contains only four species, the cosmopolitan *D. busckii*, and three species from China and Southeast Asia: *D. confertidentata*, *D. linearidentata*, and *D. neobusckii*. Although studies of reproductive isolation between these species have not yet been carried out, Toda (1986) presents data suggesting that they occupy different microhabitats (e.g., height in the forest). The species are morphologically very similar, but distinguishable by male genitalia, suggesting that they are closely related (Toda 1986).

**Parasites and pathogens:** In laboratory studies, *D. busckii* is much more (but not completely) resistant to parasitism by *Howardula aoronymphium* and *Parasylenchus nearcticus* than are the typical *Drosophila* host species of these nematodes (Perlman and Jaenike 2003). However, we have not yet found nematode-parasitized individuals of *D. busckii* in the wild.
The following parasitoid wasps have been recorded from *D. busckii*: *Asobara tabida*, *Phaenocarpa persimilis*, *Tanycarpa bicolor*, *Leptopilina heterotoma*, *Pachycrepoideus vindemiae*, and *Spalangia erythromera* (Carton et al. 1986; Davis et al. 1996).

**Life history traits:** In a comparative study of seven species of cosmopolitan “domestic” *Drosophila*, Atkinson (1979) found that body size varied positively with clutch size, larval development time, and adult survival, but inversely with egg size. Relative clutch size and egg volume for each species were determined by dividing the actual values by thorax length. Across the seven species, Atkinson (1979) found a strong negative correlation between relative egg volume and relative clutch size, with *D. busckii* having the smallest relative egg volume and the greatest relative clutch size. This combination of traits was characteristic of the larger species in Atkinson’s study, even though *D. busckii* was the second smallest. Kambysellis and Heed (1971) postulated that *Drosophila* species that utilize rare, but productive breeding sites should produce large clutches of small eggs, as *D. busckii* does. In our experience, *D. busckii* has a very sporadic occurrence among emerging flies from various resources, but when it is present, large numbers emerge.

**Chromosomal evolution:** Unlike most species of *Drosophila*, *D. busckii* lacks a dot microchromosome. Krivshenko (1955, 1959) showed cytologically that homologous regions of the X and Y in *D. busckii* are homologous to the dot chromosomes of other species *Drosophila*. This fusion of the dot to the ancestral X and Y has resulted in the origin of neo-X and neo-Y chromosomes, which Zhou and Backtrog (2015) estimate occurred less than 1 million years ago. Their transcriptional data indicate that dosage compensation has begun to evolve in the neo-X.

**Genetic variation:** Prakash (1973) reports that *D. busckii* has a low level of allozyme variation (proportion of polymorphic loci and average heterozygosity) relative to *D. melanogaster* and *D. simulans*. Prakash suggests that the low level of variation might be related to the narrow feeding niche of this species. However, as mentioned above, *D. busckii* opportunistically utilizes a wide variety of breeding sites. Thus, it seems likely that its low level of genetic variation is due to other factors.

**Behavior:** The adults of *D. busckii* run around in a frenetic manner, but the significance of this behavior is unknown.

**REFERENCES:**


Subgenus Siphlodora

Drosophila sigmoides

THIS FRUIT FLY MAMA ENJOYS A BANANA WITH HER BABY

PLACEHOLDER - NO IMAGE AVAILABLE
TIME FOR A DIAPER CHANGE
This is a medium-large-sized species with a reddish-brown thorax. The tips of longitudinal veins 2, 3, and 4, as well as both crossveins are clouded. The wings are tannish with clear or whitish spots between longitudinal veins 2 and 3 and between veins 3 and 4. According to Patterson (1943), the whitish wing spots are found only in males. The posterior crossvein is distinctly S-shaped.

**Taxonomy:** Subgenus Siphlodora

**Distribution:** *D. sigmoides* is broadly distributed across the central and eastern United States, from Texas to Georgia in the south and northwards to Illinois, New York, and New Jersey (Vilela and Bächli 2000). *D. flexa*, the only other known member of the subgenus Siphlodora, is a Neotropical endemic (Wheeler 1981).

**Breeding sites:** The only known breeding site of *D. sigmoides* are the staminate florets of eastern gamagrass (*Tripsacum dactyloides*), where its larvae feed on the anthers (Butler and Mettler 1963). This grass is native to the eastern United States. Interestingly, *D. flexa* has been bred from the tassels of maize in Brazil (Vilela and Bächli 2000). Thus, this small subgenus appears to be specialized on the anthers and pollen of Graminae. It would be interesting to examine the anthers of more plant species to get a better idea of host ranges of these species.

**REFERENCES:**


**Drosophila robusta**

**Drosophila robusta males**
- Wings grayish, posterior crossvein widely clouded
- Body large and dark, thorax not dotted

**Drosophila robusta females**
- Wings grayish, posterior crossvein widely clouded
- Body large and dark, thorax not dotted
Drosophila robusta males

Drosophila robusta females
This is a large species. Males and females appear very dark. The posterior crossvein of the wings is widely shaded. The thorax is dark, darkest along the dorsal midline. The dorsal midline of the abdomen is not dark. Similar species: D. robusta can be confused with D. americana and D. virilis, but in these two species, the abdominal pigmentation is not interrupted along the dorsal midline, as it is in D. robusta. D. nigromelanica and D. paramelanica are a bit smaller and lack the crossvein cloud on the wing. D. hydei is slightly smaller, lacks the crossvein cloud, and has numerous dark brown dots over a lighter brown thorax. D. borealis and D. lacicola are black in appearance, with black unpatterned abdominal tergites. Tips for collecting and breeding: This species frequently visits banana and tomato traps. It can be reared on cornmeal, banana, cornmeal-sucrose-yeast medium, or Instant Drosophila Medium (Carolina Biological Supply) with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group robusta

The robusta group comprises the North American D. robusta and D. colorata and about 16 species from southeastern Asia, which is considered the site of origin of the group (Narayanan 1973, Ichijo and Beppu 1990, Etges and Levitan 2004, Suwito and Watabe 2010).

**Distribution:** D. robusta is largely restricted to deciduous forest regions of the eastern United States and adjacent areas in Canada. It also occurs in riparian habitats westward to Oklahoma, Kansas, Nebraska, South Dakota, and Montana (Carson 1958, Etges and Levitan 2004).

**Breeding sites:** The principal breeding sites of D. robusta are slime fluxes (sap exudates, on which yeasts and other microbes grow) of various species of deciduous trees, including elms, maples, oaks, willows, cottonwood, and woody grape vines (Carson and Stalker 1951, Carson 1958).

**Modes of reproductive isolation:** Although D. robusta is thought to have inhabited North America for ~25 million years (Narayan 1973), it has not undergone speciation in that time - or at least speciation resulting in the persistence of two or more species. However, significant geographical variation in male courtship songs has been found, although it is not known whether this affects behavioral isolation among these flies (Arbuckle 2008). D. robusta exhibits complete behavioral isolation from other members of the robusta group (Narayan 1973).

**Chromosome-breakage system:** A strain of D. robusta was found to possess a maternally-transmitted chromosome-breakage system that targets solely chromosomes of paternal origin (Levitan and Verdnock 1986). All paternally-derived chromosomes can sustain breaks,
which are apparently randomly distributed. The chromosome-breaking factor is transmitted exclusively through the mother, but the aberrant chromosomes can be transmitted to the next generation, at which point they are transmitted in Mendelian fashion. Among the unknowns in this system are the causal agent (virus, transposable element, endosymbiont?), the possible selective advantage of paternal chromosome breakage, and the frequency of chromosome-breaking lineages in natural populations. This system appears to differ in fundamental ways from other mutator systems that have been discovered in Drosophila.

Endosymbionts: Although no heritable symbionts have been discovered in natural populations of D. robusta, Williamson (1969) transinfected this species with strains of Spiroplasma obtained from D. nebulosa and D. equinoxialis, both of which act as male killers in their native hosts. Surprisingly, both strains of Spiroplasma caused complete male-killing in D. robusta, and both were transmitted with perfect fidelity. This is quite remarkable, as D. robusta belongs to the subgenus Drosophila, which diverged from the subgenus Sophophora (to which D. nebulosa and D. equinoxialis belong) >40 million years ago.

Evolutionary response to climate change: Carson (1958) summarized the results of years of cytological studies done by him, Harrison Stalker, and Max Levitan. Two findings stand out of particular importance. First, several gene arrangements exhibit north – south clines across the range of D. robusta, suggestive of adaptation to the prevailing temperature regimes in different regions. Second, a long-term study (1946 - 1956) at a wood near St. Louis, Missouri, revealed very stable frequencies of the gene arrangements that exhibit latitudinal clines in frequency.

Levitan and Etges (2005) compiled data on gene arrangement frequencies from collections made at multiple sites around the range of D. robusta from the 1940s through 2003, finding significant increases in the frequencies of “southern” gene arrangements, i.e., those whose frequencies are positively correlated with temperature. The change is most consistently correlated with average monthly minimum temperature. Levitan and Etges (2005) attributed these evolutionary changes in D. robusta populations to adaptation to global warming. Etges et al. (2006) observed similar temporal shifts in gene arrangement frequencies in high elevation populations in the Great Smoky Mountains. Long-term changes in gene arrangement frequencies in European populations of D. subobscura have also been observed, and interpreted as an adaptive response to global warming (Balanya et al. 2004).

In addition to exhibiting clinal variation in gene arrangement frequencies, D. robusta harbors significant genetic variation in morphology. Specifically, thorax length and head width are larger in flies from southern parts of the range, while wing length and fore-femur length are larger in the north (Stalker and Carson 1947). The latter two characters were also greater in higher elevation populations in the Great Smoky Mountains (Stalker and Carson 1948). Since these flies were collected in the 1940s, it would be interesting to see if local populations of D. robusta have evolved morphologically in response to climate change.
REFERENCES:


THAT’S ENOUGH TOMATOES, LITTLE FRUIT FLY LADY (AND YOU SHOULD LOOK IN THE MIRROR)!

PLACEHOLDER - NO IMAGE AVAILABLE
DON’T EAT IT, IT’S A LADYBUG, NOT A TOMATO!
This is a large *D. robusta*-sized species. The antennae, face, and legs are reddish brown, and the thorax is grayish with reddish brown interrupted stripes and carries only 6 rows of acrostichal bristles. The abdomen is grayish with a dark brown spot on each side of each tergite, leaving a gray mid-dorsal area and narrow posterior margin on each segment. Similar species: *D. robusta* has a more dark brown appearance, in contrast to the reddish-brown *D. colorata*. In *D. robusta*, the thorax is indistinctly marked, whereas in *D. colorata* it is noticeably striped and mottled.

**Taxonomy:** Subgenus Drosophila. Species group melanica

*D. colorata* has been placed by various workers within either the robusta group (Patterson and Stone 1952) or the closely related melanica group (Beppu 1988). However, a recent molecular phylogenetic study indicates that this species might be basal to these two groups (Flores et al. 2008).

**Distribution:** There are very few records of this species, having been collected in a few places in the eastern United States, from Georgia and Mississippi in the south to Maine, Minnesota, Ontario, Quebec, and Manitoba in the north. Based on the very small number of flies collected even where it occurs, this appears to be a very rare species (Carson 1958).

**Breeding sites:** The breeding site of this species is unknown (Carson 1958).

**Modes of reproductive isolation:** Unstudied. It appears that *D. colorata* has no close relatives, making studies of isolation difficult (Flores et al. 2008).

**REFERENCES:**


**Drosophila paramelanica**

**Drosophila paramelanica males**

Body medium-large, like a small *D. robusta* without crossvein shade

Wing’s uniformly grayish, **no crossvein shade**

**Drosophila paramelanica females**

Body medium-large, like a small *D. robusta* without crossvein shade

Wing’s uniformly grayish, **no crossvein shade**
Drosophila paramelanica males

Drosophila paramelanica females
Both males and females of this medium- to large-sized species are relatively dark. Each segment of the abdomen has a transverse stripe that is interrupted at the dorsal midline. The wings have no dark posterior cross vein or vein tip shades. Similar species: *D. nigromelanica* is much darker, and the dorsal midline pigmentation on the abdomen is only interrupted on the anterior segments. *D. robusta* is darker and a bit larger with more rounded appearance than *D. paramelanica*. The posterior wing cross vein is clouded in *D. robusta* but not in *D. paramelanica*. *D. immigrans* is usually lighter in color, especially on the thorax. Females of *D. algonquin*, *D. athabasca*, and *D. affinis* are smaller, and the pigmentation on the abdominal tergites is not interrupted at the dorsal midline. In *D. funebris*, the dark dorsal midline pigmentation is interrupted only on the anterior abdominal segments. Tips for collecting and breeding: These flies come occasionally to tomato and banana traps. Cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast works well for breeding this species.

**Taxonomy:** Subgenus *Drosophila*. Species group melanica.

Based on chromosomal inversions, Stalker (1966) groups *D. melanica* as the closest relative of *D. paramelanica* within the melanica group, whereas the molecular phylogeny of van der Linde *et al.* (2010) has *D. euronotus* as sister to *D. paramelanica*, with *D. melanica* only slightly farther out.

**Distribution:** *D. paramelanica* occurs in the northeastern United States and the Upper Midwest and neighboring areas in Canada, from Nebraska and Minnesota in the west eastward to Maine and Massachusetts (Stalker 1960). According to Patterson (1943), *D. paramelanica* is replaced by *D. melanica* south of latitude 37°N.

**Breeding sites:** Though there are few unequivocal records of *D. paramelanica* breeding sites, it seems likely that they utilize slime fluxes of oak, elm, and willow (Stalker 1960).

**Modes of reproductive isolation:** Females of *D. paramelanica* will mate with males of *D. nigromelanica*, *D. melanica*, and *D. melaneura*, while males will mate with females of *D. nigromelanica*, *D. melanica*, and *D. euronotus*. The hybrid offspring are viable, with the females being fertile and the males sterile (Stalker 1966).

**Sex-ratio meiotic drive:** *D. paramelanica* possesses an exceptionally interesting sex-ratio meiotic drive system, although it has been little studied since Stalker’s (1961) original description. In this species, the driving $X^{SR}$ chromosome differs from the standard $X^{ST}$ by four inversions, two on each arm. Remarkably, there are two types of $X^{SR}$ chromosomes, which differ in their...
susceptibility to Y suppression of drive, and two types of Y chromosomes, which differ in their ability to suppress X-drive. The Southern-type $X^S_R$ is immune to Y suppression, whereas the Northern-type $X^S_R$ is susceptible to suppression, but only by Southern-type Y chromosomes. Both $X^S_R$ types are susceptible to partial suppression by autosomal genes.

Stalker (1961) presents data on the geographical distribution of the two $X^S_R$ chromosome types and the two types of Y chromosomes. Because of the expected dynamic arms race nature of interactions between driving X chromosomes and their Y chromosome targets, resampling the areas surveyed by Stalker could reveal whether any notable changes have occurred in the frequency or distribution of these chromosome types.

All members of the melanica group, except $D. \text{micromelanica}$, have an X chromosome derived by a centric fusion between the ancestral X and an autosome $\sim$8 million years ago (Flores et al. 2008). Is there a connection between X-drive in this species and its having obtained a new X chromosome arm relatively recently?

**Parasitism:** In the laboratory, at least, $D. \text{paramelanica}$ is attacked by the generalist parasitoid wasp $\text{Leptopilina heterotoma}$, although the wasps suffer a high level of egg and larval mortality, thus allowing the flies to complete development (Carton et al. 2009). Unlike $D. \text{melanogaster}$, which mounts an encapsulation response to the parasitoid, $D. \text{paramelanica}$ larvae produce elevated levels of nitric oxide (NO) almost immediately following parasitization and thus kill the wasp.

Similarly, although $D. \text{paramelanica}$ larvae do not mount an encapsulation response to another parasitic wasp, $\text{Pseudeucoila bochei}$ (Cynipidae), they are highly resistant to these parasitoids (Streams 1968). That the wasp eggs fail to hatch suggests that the nitric oxide defense might also act against this parasitoid.

**Behavior:** In a 2-dimensional setup in the laboratory, females of $D. \text{paramelanica}$ distribute themselves more evenly than expected by chance. The evenness of their distribution increases with the overall density of flies (Sexton and Stalker 1961). This even spacing is accomplished by flies extending their legs to ward off individuals that get too close to them. The ecological significance of this behavior and whether it occurs in the wild is unknown.

**REFERENCES:**


Patterson, J.T. 1943. The Drosophilidae of the Southwest. Univ Texas Publ 4313: 7-216.


Stalker, H.D. 1961. The genetic systems modifying meiotic drive in Drosophila


**Drosophila nigromelanica**

**Drosophila nigromelanica males**

Body medium-large, like a dark *D. paramelanica*

Wing’s *dusky*, especially anteriorly, no crossvein shade

**Drosophila nigromelanica females**

Body medium-large, like a dark *D. paramelanica*

Wing’s *dusky*, especially anteriorly, no crossvein shade
Drosophila nigromelanica males

Drosophila nigromelanica females
The males and females of this dark, medium- to large-sized species look similar. The abdomen is broadly striped. The dark abdominal midline pigmentation is interrupted on the anterior segments, but usually not on the posterior segments. The wings are dusky but have no dark clouds around the posterior crossveins. Similar species: *D. paramelanica* and *D. melanura* are overall lighter in color, the abdominal stripes are narrower and completely interrupted at the dorsal midline, and the wings are not dusky. *D. robusta* has a posterior crossvein shade on its wings. *D. funebris* and *D. macrospina* look similar but differ in their conspicuous outer male genital structures. Females of *D. algonquin* and *D. affinis* show a similar stripe pattern, but they are often white on the ventral abdomen and much smaller than females of *D. nigromelanica*. Tips for collecting and breeding: The flies of this species come occasionally to banana baits. They can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group melanica

**Distribution:** From spotty distribution records, Stalker (1964) infers that *D. nigromelanica* is broadly distributed in forested regions of the eastern United States, from Texas across to Florida in the south northwards to Indiana, Ohio, Pennsylvania, New York, and Massachusetts (Stalker 1964; Spiess 1949). Despite its broad range, it is reported to be quite rare in our area (Spiess 1949).

**Breeding sites:** Patterson (1943) reports finding *D. nigromelanica* feeding on various kinds of fungi. Carson and Stalker (1951) have collected adults of this species feeding at an oak slime flux, although they state that its natural breeding site is unknown. Because some other species of the melanica group breed on slime fluxes from trees (Stalker 1964), this species might do so as well.

**Modes of reproductive isolation:** Stalker (1964) attempted crosses in both directions between *D. nigromelanica* and other members of the melanica group (*D. paramelanica*, *D. melanica*, *D. melaneura*, *D. euronotus*, and *D. micromelanica*) and was unsuccessful in getting any interspecific matings. A molecular phylogenetic analysis indicates that *D. nigromelanica* does not appear to have any close relatives, even within the melanica group (Flores et al. 2008; van der Linde 2010), perhaps explaining why it will not mate with any other species.

**Parthenogenesis:** In attempted crosses between *D. nigromelanica* females and *D. euronotus* males, Stalker (1964) observed the production of three female offspring that were phenotypically and
cytologically identical to *D. nigromelanica*. One of these females was mated to *D. nigromelanica* males and produced many viable offspring. Stalker (1964) concludes that the three female offspring in the original cross were produced parthenogenetically.

**Sex chromosome evolution:** All members of the melanica group, except for *D. micromelanica*, have an X chromosome derived by a centric fusion between the ancestral X and an autosome ~8 million years ago (Flores et al. 2008).

**REFERENCES:**


Drosophila melanura

COULD SOMEONE PLEASE PICK UP THE BANANA FOR HER?

PLACEHOLDER - NO IMAGE AVAILABLE
THIS FRUIT FLY HAS ALL HANDS FULL
(OF BANANAS)
**Drosophila melanura**  
**Miller 1944**

Thorax is dull brown with paler bands running longitudinally. Broad bands on tergites interrupted at mid-dorsal. Genital region in males is pigmented dark brown, this being the original basis for description of *D. melanura* as a new species. Similar species: Miller (1944) states that, in comparison to *D. paramelanica*, *D. melanura* has lighter body coloration, more noticeable longitudinal bands on the thorax, a darker genital region in males, and bands on the 6th tergite that extend all the way to the lateral margin.

**Taxonomy:** Subgenus Drosophila. Species group melanica

**Distribution:** There are very few records of this species, with scattered collections in the Northeast from Indiana and New Jersey to Ontario and northern Maine.

**Breeding sites:** Miller (1944) collected *D. melanura*, along with far greater numbers of sympatric *D. paramelanica*, at banana baits, suggesting that they may be ecologically similar. Thus, it is probable that they utilize slime fluxes as one of their breeding sites.

**Modes of reproductive isolation:** Males of *D. melanura* will mate and produce viable male and female offspring with females of both *D. melanica* and *D. paramelanica*. Matings occurred between *D. melanura* males and *D. nigromelanica* females, but no viable hybrid progeny were produced. Hybrid *melanura × melanica* females, but not males, were fertile. Based on the lack of offspring production, it appears that both male and female *melanura × paramelanica* hybrids were sterile (Miller 1944).

**REFERENCES:**

**Drosophila virilis**

**Drosophila virilis males**
- Dark thorax stripes are less prominent anteriorly
- Stout maxillary palpus with one long terminal bristle
- Body large, abdomen uniformly dark
- Wings grayish with posterior crossvein shade

**Drosophila virilis females**
- Dark thorax stripes are less prominent anteriorly
- Stout maxillary palpus with one long terminal bristle
- Body large, abdomen uniformly dark
- Wings grayish with posterior crossvein shade
Both males and females of this large-sized species are very dark. The wings are grayish with a dark shade around the posterior crossvein. The abdomen is uniformly dark. The stout maxillary palpus has only one long terminal bristle. Similar species: *D. borealis* and *D. lacicola* are darker in overall appearance, and the thoracic stripes are more evident in them than in *D. virilis*. The pupal case in *D. virilis* is gray or black, whereas it is light brown *D. borealis* and reddish brown in *D. americana*. *D. americana* has a mahogany-brown thorax ground color (see figure below). *D. robusta* has similar wings and thorax, but the abdomen lacks dark pigment along the dorsal midline and in the anterior regions of each segment. 

**Tips for collecting and breeding:** This species is infrequently collected in our region and is likely attracted to banana and tomato traps. It can be reared on cornmeal-sucrose-yeast medium.

**Taxonomy:** Subgenus Drosophila. Species group virilis

*D. virilis* belongs to the virilis phylad, along with the North American species *D. americana*, *D. novamexicana* and the Eurasian *D. lummei* (Throckmorton 1982). Within this phylad, *D. virilis* is sister to a clade comprising the other three species (Morales-Hojas *et al.* 2012).

**Distribution:** *D. virilis* is cosmopolitan, occurring in South America, Asia, Europe, Africa, and North America, but not in Australia. In our region, *D. virilis* has been found in Manitoba, Ontario, Massachusetts, Maryland, New Hampshire, New York, Pennsylvania, and Ohio (Bächli 2016). A molecular phylogenetic analysis of mtDNA sequence variation among strains from North America, Asia, Europe, Africa, and North America.
America, Japan, mainland Asia, and Europe revealed a star-like haplotype network with no evident geographic structure to haplotype distributions (Mirol et al. 2008). This pattern is indicative of a recent and rapid global population expansion. Because of the domestic habitat of *D. virilis*, the expansion is likely to be associated with human movements around the globe.

**Breeding sites:** In his original description of *D. virilis*, Sturtevant (1916) reported that individuals of this species were bred from pineapples left out at Columbia University in New York City. According to Spieth (1979), *D. virilis* is a generalist with respect to breeding sites and has been found in breweries, markets, and other human-associated habitats, as well the rotting bark of several tree species. This last breeding site is likely to have been ancestral, as all other members of the virilis group breed in decaying bark and wood of various deciduous trees, being dependent to a significant degree on the activity of beavers to provide such resources (Spieth 1979).

**Modes of reproductive isolation:** Matings between *D. virilis* and *D. americana* occur in both directions, but far less frequently when *D. americana* females were paired with *D. virilis*

![Modes of reproductive isolation between D. virilis and other members of the virilis group.](image-url)
males than in the reciprocal pairing (Stalker 1942). \textit{D. virilis} females exhibited a rather low level of discrimination against \textit{D. americana} males in both choice and no choice situations. The same result was obtained in tests of behavioral isolation between \textit{D. virilis} and other virilis group species, including \textit{D. texana}, \textit{D. novamexicana}, \textit{D. montana}, and \textit{D. lacicola} (Patterson and Stone 1952). Thus, \textit{D. virilis} females quite readily engage in matings with males belonging to other species in the virilis group.

In all tested crosses between \textit{D. virilis} and other members of the virilis phylad (specifically, \textit{D. americana}, \textit{D. texana}, and \textit{D. novamexicana}), fertile hybrid males and females are produced in both directions, with the exception of crosses between males of \textit{D. novamexicana} and females of \textit{D. virilis}, in which case the hybrid males are almost completely sterile, due to an interaction between the \textit{D. novamexicana} \textit{Y} and the \textit{D. virilis} \textit{X} and autosomes (Patterson and Stone 1952; Heikkinen and Lumme 1998).

In crosses to members of the montana phylad (the other phylad within the virilis species group), the results are more variable, even though \textit{D. virilis} is equally divergent from all of these species. Reciprocal crosses between \textit{D. virilis} and \textit{D. littoralis} lead to fertile female and sterile male hybrids. In crosses to \textit{D. borealis} both male and female progeny are sterile. \textit{D. virilis} females mated to \textit{D. lacicola} males yield fertile female and sterile male progeny, but behavioral isolation in the reciprocal direction is so strong that offspring viability and fertility could not be assessed. In crosses between \textit{D. virilis} females and \textit{D. montana} males, both male and female progeny are fertile, but in the reciprocal cross, male progeny are sterile and females apparently die in the larval stage. Finally, crosses between \textit{D. virilis} females and \textit{D. flavomontana} males yield fertile female and sterile male offspring, but in the reciprocal cross, hybrid progeny of both sexes are sterile. A summary of these various isolating mechanisms is shown below. Orr and Coyne (1989) have dissected the genetic basis for these cases of hybrid and backcross inviability and sterility. Their results indicate that the \textit{X} chromosome alone is responsible for these effects between closely related species (specifically, between species within the virilis phylad), whereas the \textit{X} and autosomes contribute to such isolation in crosses between virilis-phylad and montana-phylad species.

It is noteworthy that \textit{D. virilis} will mate with and often produce viable and fertile progeny in crosses with rather distantly related species. Rabosky and Matute (2013) estimate the rate at which premating isolation and postzygotic isolation evolve in 9 different species groups of \textit{Drosophila}. They find that the virilis group has the second slowest rate of evolution for both types of isolating mechanisms.

**Hybrid dysgenesis:** A hybrid dysgenesis syndrome, similar to that caused by \textit{P}-elements in \textit{D. melanogaster}, has been found in \textit{D. virilis} (Lozovskaya et al. 1990). The effects of a dysgenic cross include male and female sterility, transmission ratio distortion, \textit{X} chromosome nondisjunction in hybrid females, male recombination, and elevated mutation rates. This hybrid dysgenesis results from mobilization of multiple transposable elements in dysgenic crosses (Petrov et al. 1995).

**Parasites and pathogens:** The parasitic wasp \textit{Pachycrepoideus dubius} has been reported from \textit{D. virilis} (Carton et al. 1986).

**Behavior:** Mature males of \textit{D. virilis} produce a particular hydrocarbon that serves as an aggregation pheromone for both males and females of this species (Bartelt and Jackson...
Species in the virilis phylad (D. virilis, D. americana, D. novamexicana, and D. lummei) differ in their male-specific hydrocarbons (Bartelt et al. 1986). Since these species are either allopatric or ecologically distinct, the pheromones are unlikely to play a role currently in reproductive isolation or ecological interactions.

**Physiological ecology:** Yamamoto and Ohba (1982) carried out a comparative analysis of thermal adaptation in two cosmopolitan species - D. virilis and D. immigrans - among populations in Japan. For D. virilis, they found significant geographic variation in heat resistance (the death rate of adult flies kept at 38°C or 40°C), but not in cold tolerance, as measured by recovery time from chill coma. (Their data do suggest possible geographic variation in cold tolerance, but a high level of variation among replicates may have precluded its being statistically significant.) In contrast, D. immigrans exhibited significant geographic variation in cold tolerance, but not heat resistance.

**REFERENCES:**


**Drosophila americana**

**Drosophila americana males**
- Dark thorax stripes are less prominent anteriorly
- Maxillary palpus with one long terminal bristle
- Body large, thorax ground color mahogany
- Wings grayish with posterior crossvein shade

**Drosophila americana females**
- Dark thorax stripes are less prominent anteriorly
- Maxillary palpus with one long terminal bristle
- Body large, thorax ground color mahogany
- Wings grayish with posterior crossvein shade
This is a large and dark species. Males and females look similar. The wings are grayish with a dark shade around the posterior cross vein. The ground color of the thorax is mahogany-brown, and dark brown stripes run along the thorax. The abdomen is almost black, the color of dark-roast coffee. The anterior scutellar bristles are divergent from each other, a characteristic of all members of the virilis group. The maxillary palpus has only one long terminal bristle. Similar species: D. virilis looks nearly identical, it has less prominent thorax stripes, the ground color of the thorax is less reddish, and its pupal case is gray or black, whereas that of D. americana is reddish brown. D. borealis and D. lacicola are extremely black in overall appearance. D. lacicola has two long terminal bristles on the maxillary palpus. D. borealis has a light brown pupal case, and its abdomen appears to shine (see virilis group thorax photos on page for D. virilis). D. robusta has similar wings and thorax, but the abdomen lacks dark pigment along the dorsal midline and in the anterior regions of each segment. Tips for collecting and breeding: This rare species is very likely attracted to banana and tomato traps placed near bodies of water. It can be reared on cornmeal-sucrose-yeast medium. Tips on collecting this species can be found on the web pages of Bryant McAllister (http://bioweb.biology.uiowa.edu/mcallister/bfm_files.html) and Jorge Vieira (http://evolution.ibmc.up.pt/node/11).

**Taxonomy:** Subgenus Drosophila. Species group virilis

Within the virilis group, D. americana belongs to the virilis phylad, along with the cosmopolitan D. virilis, the Eurasian D. lummei, and the North American species D. novamexicana, its closest relative (Morales-Hojas et al. 2011).

D. americana had long been thought to comprise two subspecies - a more northerly D. a. americana and a more southerly D. a. texana - that differ in a particular chromosomal rearrangement and that overlap across a broad hybrid zone (Stone and Patterson 1947). However, recent studies of sequence variation at nuclear genes reveal no differentiation between the putative subspecies at genes other than those located near the rearrangement breakpoints (McAllister 2002; Morales-Hojas et al. 2008). Consequently, the two forms are no longer regarded as subspecies, but members of a single species, D. americana.

**Distribution:** D. americana is native to North America, where it has a wide distribution, extending from Maine in the Northeast westward to Montana and south to Florida and Texas (Patterson and Stone 1952). Patterson and Stone’s distribution map for this species includes several sites in Montana and North Dakota at 48-49°N. However, it is now reported to be difficult to find this species...
north of 42°N, suggesting that the range of *D. americana* may have contracted in the past 60 plus years (B. McAllister, pers. comm.).

**Breeding sites:** As in other non-cosmopolitan members of the virilis group, the principal breeding site of *D. americana* is rotting trees (Spieth 1979). Except for the cosmopolitan *D. virilis*, the other three members of the virilis phylad, including *D. americana*, specialize on willow (*Salix* spp.). Spieth (1979) has argued that species of the virilis group (except for *D. virilis* itself) are largely dependent on beavers (*Castor* spp.), whose activities result in numerous felled trees (especially aspens, willows, and cottonwoods). The decaying bark and phloem and internal rot provide breeding sites for these flies. Black willow (*Salix nigra*) is favored by *D. americana*, as it is subject to extensive internal rot, and excavation of rotting trees by carpenter ants (*Camponotus* spp.) results in especially favorable habitats for these flies (B. McAllitser, pers. comm.). *D. americana* has also been bred from decaying bark of Sandbar Willow (*S. interior*) (Blight and Romano 1953).

**Modes of reproductive isolation:** The most detailed studies of reproductive isolation involving *D. americana* have focused on crosses with *D. virilis*. Because *D. virilis* is cosmopolitan in distribution, it is sympatric with *D. americana* in parts of the latter’s range. These species diverged ~4.1 million years ago (Morales-Hojas et al. 2011). Reproductive isolation between these species is manifest at multiple levels. There is strong behavioral isolation between females of *D. americana* and males of *D. virilis* (Stalker 1942). In addition, in cases where mating does occur, there is strong post-mating, but pre-zygotic isolation due to failure of interspecific fertilization in mated females, which results from an interaction between products of maternal and paternal genes (Sweigart 2010a). When fertilization does occur, hybrid males and females are both viable and fertile (Patterson and Stone 1952). However, male sterility arises in subsequent (F2 and backcross) generations due to a small number of interacting genes (Sweigart 2010b).

*D. americana* and its closest relative, *D. novamexicana*, are estimated to have split some time between 0.5 and 1.6 million years ago (Caletka and McAllister 2004; Morales-Hojas et al. 2011). Between these species, there is only modest behavioral isolation, and the hybrid males and females are viable and fertile (Patterson and Stone 1952; Ahmed-Braimah and McAllister 2012). However, the two species are currently allopatric, as far as is known, and thus do not have the opportunity to interbreed in nature. *D. americana* and the more distantly related *D. montana* (divergence ~9 million years ago; Morales-Hojas et al. 2011) produce sterile hybrid offspring of both sexes.

**Parasites and pathogens:** *D. americana* is subject to parasitism by the parasitoid wasps *Asobara tabida*, *Pachycrepoideus dubius*, *Spalangia erythromera*, and *Leptopilina heterotoma* (Carton et al. 1986).

**Behavior:** Mature males of *D. americana* produce aggregation pheromones, to which both male and female flies are attracted in a wind-tunnel olfactometer (Bartelt et al. 1986). Interestingly, the pheromones act synergistically with the odor of fermenting willow bark, the breeding site of this species.

**Sex chromosome evolution:** *D. americana* is one of a small number of species in which neo-sex chromosomes have evolved (McAllister 2003). The neo-X resulted from a fusion between the 4th chromosome (Muller’s element B) and the X (element A). This fusion has arisen so recently
that *D. americana* is still polymorphic for the different gene arrangements, with the frequency of the X-4 fusion (neo-X) increasing in frequency from south to north within the central United States (McAllister *et al.* 2008). In populations that are polymorphic for the fusion, the unfused 4th chromosome segregates either as an autosome or a non-recombining Y chromosome, depending on the frequency of the X-4 fusion (McAllister and Evans 2006). Furthermore, an inversion on the neo-X has been found to suppress recombination between the neo-sex chromosomes, thus leading to sequence divergence between them (McAllister 2003; Evans *et al.* 2007)

**Ecological genetics:** *D. americana* exhibits substantial variation in body color across its range, with darker forms characteristic of populations inhabiting more humid areas (Wittkopp *et al.* 2011). No comparable genetic population structure was found for presumably neutral variation, indicating that gene flow is unimpeded across the range of this species and thus that the pigmentation cline is likely to reflect adaptive evolution. The *ebony* and *tan* QTL alleles are associated with the color variation in *D. americana* (Wittkopp *et al.* 2009). These loci also contribute to variation in pigmentation between the relatively dark *D. americana* and the yellowish *D. novamexicana* (Wittkopp *et al.* 2009; Cooley *et al.* 2012).

*D. americana* is also genetically variable for lifespan under controlled laboratory conditions, with flies from central and southern populations living about 2 weeks longer than flies from northern populations. The variation in lifespan is significantly associated with the genes *hep* and *Lim3*, which have also been shown to affect lifespan in *D. melanogaster* (Fonseca *et al.* 2013).

**REFERENCES:**


Fonseca, N.A., Morales-Hojas, R., Reis, M.,


**Drosophila borealis**

**Males**
- Dark thorax stripes are very prominent anteriorly
- Maxillary palpus with one long terminal bristle
- Body large, charcoal-black, thorax ground color gray
- Posterior crossvein of wings clouded

**Females**
- Dark thorax stripes are very prominent anteriorly
- Maxillary palpus with one long terminal bristle
- Body large, charcoal-black, thorax ground color gray
- Posterior crossvein of wings clouded
Drosophila borealis males

Drosophila borealis females
This is a large species with a distinct dusky charcoal-black appearance. Males and females look similar. The thorax has black stripes on gray background. The wings are grayish with a dark shade around the posterior crossvein. The abdomen is uniformly dark. The maxillary palpus has only one long terminal bristle. Similar species: 

*D. lacicola* looks almost identical, except that it has two terminal bristles at the end of the maxillary palpus. *D. americana* has a mahogany-brown thorax ground color, and the dark thorax stripes of *D. americana* are less prominent at the anterior part of the thorax. *D. virilis* is dark gray instead of charcoal-black, its thorax stripes are overall less prominent, and the thorax ground color is a dark gray-brown (see virilis group thorax photos on the page for *D. virilis*). The pupal case in *D. americana* is reddish-brown, whereas it is light brown in *D. borealis* and gray or black in *D. virilis*. *D. robusta* lacks dark pigment along the dorsal midline and in the anterior regions of each segment. Tips for collecting and breeding: This species is rare in our region and is likely attracted to banana and tomato traps.

**Taxonomy:** Subgenus Drosophila. Species group *virilis* 

*D. borealis* is a member of the montana complex within the *virilis* group, along with *D. montana*, *D. flavomontana*, and *D. lacicola*.

Spicer and Bell (2002) constructed a molecular phylogeny of the *virilis* group based on mitochondrial rRNA genes. They found that *D. borealis* is not monophyletic, but rather includes an eastern form (from Minnesota) and a western form (from Idaho), the latter belonging to a clade that includes *D. lacicola*, *D. montana*, and *D. flavomontana*. In their phylogenetic analysis of the *virilis* group using nuclear genes, Morales-Hojas *et al.* (2011) confirm the distinctness of *D. borealis* E (eastern) and *D. borealis* W (western). Because *D. borealis* was originally described on the basis of eastern (Minnesota) specimens (Patterson 1952), the western flies represent an as yet undescribed species.

**Distribution:** Patterson (1952) reports that *D. borealis* (E and W combined) had been collected in Idaho, Colorado (where it is sympatric with *D. flavomontana*), Minnesota, and Wisconsin. Additionally, the *Drosophila* Species Stock Center has a sample from Quebec. In their discovery that *D. borealis* is not monophyletic, Spicer and Bell (2002) used *D. borealis* E from Minnesota and *D. borealis* W from Idaho. According to Spieth (1979), the species of the *virilis* group (except for the cosmopolitan *D. virilis* itself) occur in habitats near lakes and streams.

**Breeding sites:** The principal breeding site of *D. borealis* is rotting bark of aspen (*Populus*) trees. According to Spieth (1979), the species is rarely
caught, except in the vicinity of beaver ponds. The felling of aspens, willows and other trees thus provides abundant breeding sites for *D. borealis* and other virilis group species. The historically recent decimation of beaver populations for their pelts is thus likely to have caused a major population crash of these *Drosophila* species. However, beavers are abundant again, and it would be interesting to see if the presumed population crash and rebound is reflected in the patterns of molecular variation in the *Drosophila* species dependent on them.

**Modes of reproductive isolation:** Patterson (1952) reports the results of crosses to other members of the virilis group. Because the stock he used came from Minnesota, it is very likely to have been *D. borealis* E. There is strong, but not complete behavioral isolation between *D. borealis* E and *D. flavomontana* (which is allopatric to *D. borealis* E; divergence time ~4.8 million years ago [Morales-Hojas et al. 2011]) in both directions, and complete hybrid inviability or fertilization failure in the few crosses, in which mating did occur. Females of *D. borealis* E and males of *D. virilis* (a cosmopolitan species, which could be sympatric with *D. borealis* E; divergence time ~9 million years ago) show strong, but not complete, behavioral isolation, whereas in the reciprocal cross, such isolation is much weaker. In both directions, viable offspring are produced, but both male and female hybrids are sterile. There is moderate premating isolation between *D. borealis* E and the allopatric *D. montana* (divergence time ~4.4 million years ago), with a high level of hybrid inviability in one direction, and male sterility, but female fertility, in the other. Finally, there is complete premating isolation between *D. borealis* E and the sympatric *D. lacicola* (divergence time ~4.4 million years ago).

**Endosymbionts:** *D. borealis* carries a male-killing strain of *Wolbachia* that causes a 50% drop in the proportion of eggs that hatch, resulting in all-female progeny from *Wolbachia*-infected females (Sheeley and McAllister 2009). Interestingly, this strain of *Wolbachia* is closely related to a male-killing strain in the distantly related *D. innubila* (Dyer and Jaenike 2004). Because the lineages leading to *D. borealis* and *D. innubila* are estimated to have split ~40 million years ago (Itzumitani et al. 2016), this suggests that this strain of *Wolbachia* has the capacity to cause male-killing in distantly related hosts. However, the strain of *Wolbachia* that kills male embryos in *D. innubila* does not express a male-killing phenotype after transfection into *D. melanogaster* or *D. simulans* (Veneti et al. 2012), perhaps because these two species are even more distantly related to *D. innubila* than is *D. borealis*.

**Behavior:** Like some other species of *Drosophila*, mature males of *D. borealis* produce aggregation pheromones that serve to attract both male and female conspecifics, as assayed in a wind tunnel olfactometer (Bartelt et al. 1988). Most interestingly, these pheromones were much more effective in attracting flies when an extract of fermenting aspen bark (the breeding site of *D. borealis*) was added. Neither the aspen extract alone nor the pheromone blend alone was very attractive. This suggests that level of utilization of decaying aspen bark could be highly heterogeneous, being dependent on initially “chance” encounters of such bark by mature males of *D. borealis*.
REFERENCES:


**Drosophila lacicola**

**Drosophila lacicola males**
- Maxillary palpus with two long terminal bristles
- Body large, dark brown/black, thorax ground color brownish
- Posterior crossvein of wings clouded

**Drosophila lacicola females**
- Maxillary palpus with two long terminal bristles
- Body large, dark brown/black, thorax ground color brownish
- Posterior crossvein of wings clouded

Dark thorax stripes are very prominent anteriorly
Drosophila lacicola males

Drosophila lacicola females
Drosophila lacicola
Patterson 1944

This is a large species with a dark brown or black appearance. Males and females look similar. The thorax has black stripes on brownish background. The wings are grayish with a dark shade around the posterior crossvein. The abdomen is uniformly dark. The maxillary palpus has two long terminal bristles. Similar species: D. borealis looks almost identical, except that it has only one terminal bristle at the end of the maxillary palpus. D. americana has a mahogany-brown thorax ground color, and the dark thorax stripes of D. americana are less prominent at the anterior part of the thorax. D. virilis is dark gray instead of dark brown/black, its thorax stripes are overall less prominent, and the thorax ground color is a dark gray-brown (see virilis group thorax photos on the page for D. virilis). D. robusta lacks dark pigment along the dorsal midline and in the anterior regions of each segment. Tips for collecting and breeding: This species is very rare and likely attracted to banana and tomato traps.

Taxonomy: Subgenus Drosophila. Species group virilis

The virilis group comprises four subgroups (or subphylads), with D. lacicola belonging to the montana subgroup, along with D. montana, D. flavomontana, and D. borealis W (western) and D. borealis E (eastern) (Morales-Hojas et al. 2011). A multilocus analysis places D. lacicola as sister to the D. montana - D. borealis W clade, whereas an analysis based on mtDNA links D. lacicola and D. borealis W as sister species (Spicer and Bell 2002). Morales-Hojas et al. (2011) estimate that D. lacicola split from the lineage leading to D. montana and D. borealis W in the mid Pliocene, and that the montana subgroup split from the rest of the virilis group in the early Miocene ~10 million years ago.

Distribution: Patterson (1952) reports this species from Wisconsin and Minnesota, where it is sympatric with D. borealis (presumably eastern). In addition, the Drosophila Species Stock Center has samples from New York, Utah, and Manitoba. Within the virilis group, D. lacicola is replaced geographically to the south and west by D. americana (Patterson and Stone 1952).

Breeding sites: The principal breeding site of D. lacicola is rotting phloem beneath the bark of aspen (Populus tremuloides) trees, typically in association with beavers (Spieth 1951, 1979; see entry under D. borealis). Like D. borealis, D. lacicola may have experienced a substantial population crash and rebound in association with the decimation and recovery of North American beaver populations in the last couple hundred years.

Modes of reproductive isolation: D. lacicola and D. borealis E are fairly closely related (divergence time ~4.4 million years ago; Morales-Hojas et al. 2011), utilize the same type of breeding sites of
decaying aspen phloem and bark (Spieth 1979), and are sympatric in parts of their ranges. Thus, they are likely to encounter each other in nature. Patterson (1952) reported that crosses between *D. borealis* (presumably the eastern species, as the strain used was from Minnesota) and *D. lacicola* apparently exhibited complete premating isolation in both directions, as no females were inseminated.

Patterson and Stone (1952) report the outcome of various crosses between *D. lacicola* and other members of the virilis group. Viable and fertile hybrids are produced in crosses between *D. lacicola* and the closely related *D. montana* in both directions (divergence time ~3.7 million years ago; Morales-Hojas et al. 2011). Crosses in both directions between *D. lacicola* and *D. flavomontana* (divergence time ~4.8 million years ago) yield viable male and female hybrids, but only the females are fertile. Thus, premating isolation between *D. lacicola* and either *D. montana* or *D. flavomontana* may be relatively weak, but neither of the latter two species is sympatric with *D. lacicola*. No viable progeny are produced in crosses between males *D. virilis* and females of *D. lacicola* (divergence time ~9 million years ago), whereas the reciprocal cross yields viable hybrid progeny, but the females are weakly fertile and the males are sterile.

**REFERENCES:**


Drosophila repleta

**Drosophila repleta males**

- Dark dots surround the base of each thorax bristle
- Body large, thorax dotted, abdomen striped with row of yellow lateral spots (arrows)
- Wings uniformly grayish

**Drosophila repleta females**

- Dark dots surround the base of each thorax bristle
- Body large, thorax dotted, abdomen striped with row of yellow lateral spots (arrows)
- Wings uniformly grayish
**Drosophila repleta**
Woollaston 1858

This is a large species. Males and females look similar. Like in other members of the repleta group, each thoracic bristle arises from a dark spot. The dark abdominal bands include a pale yellow area laterally, forming a row of 4 - 5 yellow spots. At the lateral margin, the dark bands extend to the anterior margin of the segment. The wings are slightly grayish but otherwise unmarked. Other similar species: *Phortica variegata* is a very large species with dark speckles on the thorax. The dorsal midline of the abdomen of *P. variegata* is marked with dark brown, while both *D. repleta* and *D. hydei* are light at the dorsal midline. Tips for collecting and breeding: We collected flies over a pile of discarded beer mash outside a craft brewery in Rochester, NY. *D. repleta* can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group repleta

The repleta group is one of the most speciose groups within the genus *Drosophila*, comprising over 70 described species (Wasserman 1982). Within the group, *D. repleta* belongs to the repleta subgroup, with its closest relatives being *D. limensis, D. canapalpa, D. melanopalpa*, and *D. neorepleta* (Wasserman 1982; Oliveira et al. 2012).

**Distribution:** Cosmopolitan. *D. repleta* occurs throughout the region covered by this guide, from Minnesota to Ontario, Quebec, and Maine, and southwards to Florida, Texas, and Mexico.

**Breeding sites:** According to Patterson (1943, p. 118), *D. repleta* is “not usually found in the country, usually taken around fruit stores, and especially around toilets and urinals.” Carson and Stalker (1951) bred a single individual from an oak slime flux, suggesting that this is not an important resource. In Panama, *D. repleta* is attracted to fruit baits for purposes of feeding and oviposition (Pipkin 1965).

Because many other species in the repleta group utilize cacti as breeding sites (Wasserman 1982), perhaps *D. repleta* utilizes prickly pear (e.g., *Opuntia humifusa*, which is widely distributed in the eastern United States). A recent molecular phylogeny of the repleta group shows that *D. repleta* itself is nested within a clade of species that utilize *Opuntia* (Oliveira et al. 2012).

**Modes of reproductive isolation:** Crosses between males of *D. repleta* and females belonging to four other species of the repleta complex (*D. limensis, D. canapalpa, D. melanopalpa*, and *D. neorepleta*) yield viable progeny (Ward and Stone 1952). In crosses to *D. limensis* or *D. neorepleta*, the hybrid females are fertile, but the males are sterile, in accordance with Haldane’s Rule. Hybrids of both sexes are sterile in crosses to *D. canapalpa*. Interestingly, crosses to a strain of *D.
melanopalpa from Mexico yield fertile female and sterile male offspring, while crosses to a strain from Arizona produce sterile males and females. Thus, *D. melanopalpa* is genetically variable with respect to isolating mechanisms from *D. repleta*.

Crosses between females of *D. repleta* and males of three of its four closest relatives, including *D. limensis*, *D. canapalpa*, and *D. neorepleta*, produced no offspring. Mass crosses of *D. repleta* females to males of *D. melanopalpa*, its other close relative, produced a single female hybrid (Ward and Stone 1952). The flies were set up in mass matings with 25 males and 25 females that were kept together and transferred to fresh medium every week for 6 weeks. The virtually complete absence of hybrid progeny indicates a very high level of either behavioral isolation, post-mating pre-zygotic isolation, or hybrid inviability. With respect to behavioral isolation, species of the repleta group vary dramatically in their male courtship songs (Ewing and Miyan 1986). Ewing and Miyan (1986) postulated that one component of these songs serve as species identifiers and therefore act as behavioral isolating mechanism between species, while another component serves as a mechanism for sexual selection within species.

Crosses between females of either *D. canapalpa* or *D. melanopalpa* and males of *D. repleta* yielded a substantial fraction of female-type intersex progeny, suggesting an incompatibility in sex determination mechanisms (Wharton 1942).

**REFERENCES:**


**Drosophila hydei**

**Drosophila hydei males**
- Dark *dots* surround the *base* of each thorax bristle
- Body large, *thorax dotted*, abdomen striped
- Wings uniformly grayish

**Drosophila hydei females**
- Dark *dots* surround the *base* of each thorax bristle
- Body large, *thorax dotted*, abdomen striped
- Wings uniformly grayish
Drosophila hydei males

Drosophila hydei females
This is a large species. Males and females look similar. The thorax has small dark brown spots at the base of each bristle on a lighter grayish-brown background. At the lateral margin, the dark bands extend to the anterior margin of the segment. The wings are slightly grayish but otherwise unmarked.

Similar species: D. repleta looks very similar but has a row of yellowish spots along the sides of the abdomen. Phortica variegata looks like a large version of D. hydei, but P. variegata displays dark pigment in the dorsal midline area of the abdomen and has larger dark speckles on the thorax. D. robusta looks a bit darker and is slightly larger than D. hydei, lacks the spots on the thorax, and displays a posterior midline shade on the wing.

Tips for collecting and breeding: This species is a very rare visitor of banana and tomato traps, but can be common around compost bins. It can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

Taxonomy: Subgenus Drosophila. Species group repleta

D. hydei belongs to the hydei subgroup within the repleta group, whose phylogenetic relationships have been elucidated by Moran and Fontdevila (2007).

Distribution: Cosmopolitan. Present on all continents except Antarctica, being more common in warm regions.

Breeding sites: D. hydei utilizes a variety of fruits and can become especially common in produce storage houses (Patterson 1943). Atkinson and Shorrock (1977) report that D. hydei emerged from both discarded fruits (e.g., melon, lemon, orange, and mango) and vegetables (cabbage, lettuce, onion, yam, and tomato) collected at a Leeds fruit and vegetable market. In greenhouses and gardens in Costa Rica, D. hydei was, remarkably, the most commonly collected insect feeding on the nectar of Specklinia orchids and serving as pollinators of these plants (Karremans et al. 2015).

Modes of reproductive isolation: D. hydei can be crossed with D. neohydei to yield fertile hybrid offspring in both directions of the cross (Wasserman 1962; Schafer 1978). However, hybrid breakdown in the form of both male and female sterility occurs in backcross progeny. The backcross sterility of both males and females is due to both autosome-autosome and X-autosome interactions, while males are additionally rendered sterile by Y-autosome interactions (Schafer 1978).

Parasites and pathogens: D. hydei serves as host for the parasitic mite Macrocheles muscaedomesticae, which feeds on the eggs and
larae of the flies and on the hemolymph of adults. In addition, these mites utilize *D. hydei* as vectors to disperse away from low-quality habitats (Campbell and Luong 2016). Mite parasitism results in a substantial reduction in flight endurance of adults of *D. hydei* (Luong et al. 2015). Thus, the mites are apparently faced with a tradeoff between the dispersal and food resource services of their *D. hydei* hosts.

The parasitoid wasps *Phaenocarpa persimilis* and *Trichopria sp.* have been reported from *D. hydei* (Carton et al. 1986).

**Endosymbionts:** *D. hydei* is unique among *Drosophila* in carrying maternally transmitted *Spiroplasma* belonging to two different species, *S. citri* and *S. poulsonii* (Haselkorn 2010). The *poulsonii* strain does not cause male killing, but it is closely related to *Spiroplasma* strains that do in other species of *Drosophila*. Across five populations of *D. hydei* in Japan, the infection prevalence of this strain ranged from 23% - 66% (Kageyama et al. 2006). In a survey of *D. hydei* from Mexico and the American Southwest, about 90% of *Spiroplasma*-infected flies carried the poulsonii clade and 10% carried the citri clade, but no flies were found to carry both (Haselkorn et al. 2009).

The strain of *S. poulsonii* carried by *D. hydei* confers a high level of resistance to the generalist parasitic wasp *Leptopilina heterotoma* (Xie et al. 2010). Interestingly, the beneficial effect on *D. hydei* was greater for females, as wasp-parasitized males that survived to the adult stage were effectively sterile (Xie et al. 2011). Because *Spiroplasma* is maternally transmitted, the male sterility is of no fitness consequence to the *Spiroplasma*. It would be interesting to explore the molecular basis for this sex-specific effect.

*Osaka et al.* (2013) found that 1.4% of wild-caught *D. hydei* in Japan were parasitized by mites (*Macrocheles* sp.) and that about 25% of these mites carried *Spiroplasma poulsonii*, as determined by PCR. Laboratory studies have demonstrated the possibility that mites can vector *Spiroplasma* from one *Drosophila* host species to another (Jaenike et al. 2007). The findings of Osaka et al. (2013) indicate that mites could serve as vectors for horizontal transmission of *Spiroplasma* both within *D. hydei* and from *D. hydei* to other species of *Drosophila*.

**Behavior:** Mature males of *D. hydei* produce aggregation pheromones, to which both male and female flies are attracted, as assayed in a wind-tunnel olfactometer (Moats et al. 1987).

**Life history and reproductive biology:** Atkinson (1979) found that among seven species of “domestic” *Drosophila*, *D. hydei* had the lowest reproductive effort, as measured by the ratio of reproductive to total biomass. This species was intermediate in position in the negative tradeoff function between egg volume and clutch size.

*D. hydei* is very unusual among *Drosophila* in that females become receptive to mating at a much younger age (~3 d) than that at which males first engage in courtship (~9 d). The females are also highly unusual in that they will remate multiple times per day (Markow 1985). Males of *D. hydei* produce exceptionally long sperm, 23.4 mm on average, indicating that male gametes are costly in this species and can limit male fertility (Pitnick and Markow 1994). Across *Drosophila*, sperm length is positively correlated with male age at maturity (Pitnick et al. 1995). In many species with short sperm, such as *D. busckii* and *D. melanogaster*, males reach sexual maturity earlier than females, whereas in *D. hydei*, males take 6 days longer than females to become reproductively mature.
REFERENCES:

Atkinson, WD. and Shorrocks, B. 1977. Breeding
site specificity in the domestic species of

Campbell, E.O. and Luong, L.T 2016. Mite choice
generates sex-and size-biased infection in

Carton, Y., Bouletreau, M., Van Alphen, J.J.M.
and van Lenteren, J.V. 1986. The Drosophila
parasitic wasps. pp. 348-394 in M. Ashburner,
H.L. Carson, and J.N. Thompson Jr (eds),

Haselkorn, T.S. 2010. The Spiroplasma heritable
bacterial endosymbiont of Drosophila. Fly 4:
80-87.

Haselkorn, T.S., Markow, T.A. and Moran,
N.A. 2009. Multiple introductions of the
Spiroplasma bacterial endosymbiont into

Jaenike, J., Polak, M., Fiskin, A., Helou, M. and
Minhas, M. 2007. Interspecific transmission of
endosymbiotic Spiroplasma by mites. Biol Lett

Kageyama, D., Anbutsu, H., Watada, M.,
Hosokawa, T., Shimada, M. and Fukatsu,
T. 2006. Prevalence of a non-male-killing
Spiroplasma in natural populations of
Drosophila hydei. Appl Environ Microb 72:
6667-6673.

Karremans, A.P., Pupulin, F., Grimaldi, D.,
Beentjes, K.K., Butôt, R., Fazzi, G.E.,
Kaspers, K., Kruizinga, J., Roessingh, P.,
Pollination of Specklinia by nectar-feeding
Drosophila: the first reported case of a
deceptive syndrome employing aggregation
pheromones in Orchidaceae. Ann Bot -

Markow, T.A. 1985. A comparative investigation of
the mating system of Drosophila hydei. Anim
Behav 33: 775-781.

Moats, R.A., Bartelt, R.J., Jackson, L.L. and
Schaner, A.M. 1987. Ester and ketone
components of aggregation pheromone of
Drosophila hydei (Diptera: Drosophilidae). J

Morán, T. and Fontdevila, A. 2007. On the
phylogeny of the Drosophila hydei subgroup:
new insights from combined analyses
of nuclear and mitochondrial data. Mol
Phylogenet Evol 43: 1198-1205.

Osaka, R., Watada, M., Kageyama, D. and
Nomura, M. 2013. Detection of Spiroplasma
from the mite Macrocheles sp. (Acari;
Macrochelidae) ectoparasitic to the fly
Drosophila hydei (Diptera; Drosophilidae):
a possible route of horizontal transmission?
Symbiosis, 60: 79-84.

Patterson, J.T. 1943. The Drosophilidae of the
Southwest. Univ Texas Publs 4313: 7-216.

advantages associated with costs of sperm
production in Drosophila hydei, a species
with giant sperm. P Natl Acad Sci USA 91:
9277-9281.

Delayed male maturity is a cost of producing
large sperm in Drosophila. P Natl Acad Sci
USA 92: 10614-10618.

Schäfer, U. 1978. Sterility in Drosophila hydei x

Wasserman, M. 1962. Cytological studies of the
repleta group of the genus Drosophila: IV.
The hydei subgroup. *Univ Texas Publs* 6205, 73-84.


Drosophila bromeliae

**Drosophila bromeliae males**
- Pair of prescutellar bristles (arrows) longer than acrostichal bristles (arrow heads)
- Male front leg without sex comb
- Body small, abdomen vaguely striped
- Wings nearly unpigmented

**Drosophila bromeliae females**
- Pair of prescutellar bristles (arrows) longer than acrostichal bristles (arrow heads)
- Body small, abdomen vaguely striped
- Females resemble males (no sexual dimorphism)
- Wings nearly unpigmented
Drosophila bromeliae males

Drosophila bromeliae females
**Drosophila bromeliae**

Sturtevant 1921

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**Male**  
- Small, yellowish brown fly  
- Prescutellar bristles longer than neighboring acrostichal bristles  
- Males lack sex combs

**Female**


*Drosophila bromeliae* is a small species, whose overall body is yellowish brown. The eyes are red, and the wings are clear and unmarked. Among species in our region, a distinguishing character is the presence of a pair of prescutellar bristles that are noticeably longer than the acrostichal bristles. Similar species: at first glance, *D. bromeliae* might be mistaken for *D. melanogaster*, being similar in size and general appearance. However, a look under the microscope quickly reveals that *D. bromeliae* males lack the sex combs and abdominal pattern of *D. melanogaster*. *D. melanogaster* lacks prescutellar bristles that are longer than the acrostichals.

**Taxonomy:** Subgenus Drosophila. Species group bromeliae

**Distribution:** This is a neotropical species, whose natural distribution includes Central America, several Caribbean islands, and northern South America. *D. bromeliae* has recently been discovered in Morris County, New Jersey and Hampshire County, Massachusetts (Grimaldi 2018), so it may be in the early stages of invasion in our region. Prior to this discovery, the farthest north it had previously been documented was in Valdez, Florida (Grimaldi 2018).

**Breeding sites:** Sturtevant (1921) collected this species from pineapple. Other adult feeding resources include morning glory and squash flowers (Grimaldi 2016; Grimaldi 2018). Larval feeding sites include flowers of multiple families of plants (Schmitz 2010; cited in Grimaldi 2016). In New Jersey, adults of *D. bromeliae* were observed feeding and courting within pumpkin flowers, which also served as larval feeding sites. Like other species of flower-breeding *Drosophila*, *D. bromeliae* has low levels of ADH activity, and both larvae and adults experience high rates of mortality at low environmental concentrations of ethanol (David 1973; Mercot *et al.* 1994).

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*photo* of *D. bromeliae* flies on a squash flower.
Genetics, physiology, and behavior: Grimaldi (2016, p. 2) notes that flower-breeding species of *Drosophila* are “notoriously difficult to culture,” making it difficult to study many aspects of their biology. However, this is not true of *D. bromeliae*, as the Drosophila Species Stock Center maintains a stock on their banana food. Mercot et al. (1994) maintained a culture on killed yeast medium, and we have reared it on Formula 4-24 Instant Drosophila Medium (Carolina Biological Supply). Thus, *D. bromeliae* is a good candidate for laboratory investigations of various aspects of the biology of flower-breeding species.

REFERENCES:


**Drosophila immigrans males**

Body large, like a giant *D. melanogaster* (but lacks sex combs), dorsal midline of abdomen not dark

Wing’s crossveins an tips of longitudinal veins 2, 3, and 4 slightly clouded

**Drosophila immigrans females**

Body large, like a giant *D. melanogaster*, dorsal midline of abdomen not dark

Wing’s crossveins an tips of longitudinal veins 2, 3, and 4 slightly clouded
Drosophila immigrans males

Drosophila immigrans females
This is a large, yellowish species. Males have a dark posterior part of the abdomen, which is assembled from spots. The dorsal midline is not black. Males lack sex combs. *D. immigrans* look superficially like gigantic *D. melanogaster*. Similar species: The melanogaster group species *D. melanogaster*, *D. simulans*, and *D. suzukii* are about half the size of *D. immigrans*. The abdominal bands are interrupted at the dorsal midline in *D. immigrans*, but not in the melanogaster group species. Males of *D. suzukii* have one large spot on each wing, and males of *D. melanogaster*, *D. simulans*, and *D. suzukii* have sex combs on the forelegs. Tips for collecting and breeding: *D. immigrans* is a regular guest at banana, tomato, and occasionally also mushroom baits. This species can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group immigrans

**Distribution:** Cosmopolitan, originating from the Oriental region. Widely distributed and common throughout our area. According to Sturtevant (1921), the earliest known records of this species from the continental United States are from 1913 (New York and Massachusetts) and 1914 (Florida and California).

**Breeding sites:** Sturtevant (1921) reports that *D. immigrans* occurs around fruit in stores and markets, and in tomato gardens. Atkinson and Shorrocks (1977) bred *D. immigrans* from numerous species of decaying fruits and vegetables collected from a market in England. Atkinson (1979) notes that the survival of *D. immigrans* larvae feeding in decaying citrus fruits is substantially greater if those fruits are infected with *Penicillium* mold. Perhaps breeding sites lacking *Penicillium* harbor bacteria that are pathogenic to *D. immigrans*.

Although there are rare instances of *D. immigrans* breeding in wild mushrooms (Kimura et al. 1977; Gottschalk et al. 2009), it differs physiologically from truly mycophagous species in being susceptible to α-amanitin, ibotenic acid, and muscimol, compounds found in some species of *Amanita* mushrooms (Jaenike et al. 1983; Tuno et al. 2007). Also consistent with its utilizing decaying fruits as breeding sites, *D. immigrans* occurs in the forest floor, rather than the canopy of a beech forest in Japan (Beppu 1984).

**Modes of reproductive isolation:** A recent molecular phylogenetic study of several species of *Drosophila* found significant genetic differentiation among two clades of *D. immigrans* - one consisting of flies from Taiwan and the other comprising flies from Laos and the United States (Liu et al. 2015). Lui et al. (2015) suggest that these clades may have split ~2 million years ago. It would be interesting to study the degree to which various types of
isolating mechanisms have evolved between these groups. Spieth (1952) has presented a detailed description of the mating behavior of *D. immigrans* from the United States, noting that they have an exceptionally long copulation time (~48 minutes on average). The mating behavior of Taiwanese *D. immigrans* could be compared with Spieth’s observations.

**Parasites and pathogens:** In North America, the parasitic nematode *Howardula aoronymphium* has only been found in mycophagous species of *Drosophila*. In the Netherlands, however, Gillis and Hardy (1997) found that 2 of 378 wild-caught *D. immigrans* were parasitized by this nematode. As mentioned above, *D. immigrans* on rare occasions utilizes mushrooms as breeding sites, so perhaps these flies became parasitized as larvae feeding on mushrooms. Alternatively, *H. aoronymphium* may occasionally cycle through decaying fruits and thereby potentially parasitize frugivorous *Drosophila* like *D. immigrans*. Lab experiments indicate that *D. immigrans* is susceptible to parasitism by *H. aoronymphium* (Perlman and Jaenike 2003).

Carton *et al.* (1986) report the parasitoid wasps *Pachycerepoideus dubius* and *Leptopilina heterotoma* from *D. immigrans*.

*D. immigrans* carries a recently discovered, maternally transmitted sigma virus (DLmmSV) that renders infected flies paralyzed when exposed to CO₂ (Longdon *et al.* 2011). Interestingly, the closest known relative of DLmmSV occurs in a very distantly related *Drosophila* species, *D. obscura*. The phylogenies of the sigma viruses and their *Drosophila* hosts are incongruent, indicating that the virus jumped from one species to another some time after the split of the lineages leading to *D. immigrans* and *D. obscura*. Across several populations in Europe, the mean prevalence of infection by DLmmSV was 38%, and the low level of genetic variation within this virus suggests that it has spread very recently through *D. immigrans* populations (Longdon *et al.* 2017). Although horizontal or sexual transmission of the virus is unknown, Longdon *et al.* (2017) have discovered that it is vertically transmitted by infected individuals of both sexes, with perfect (100%) transmission by females and, on average, 50% transmission by males. Such biparental transmission can result in rapid spread of the virus, even if the virus has adverse fitness effects on its hosts (Altizer and Augustine 1997).

Using metagenomic RNA sequencing of wild-caught flies around Edinburgh and Sussex in the UK, Webster *et al.* (2016) discovered 33 different species of viruses carried by *D. immigrans*, including one that is very similar to the Iridovirus known from the isopod *Armadillidium vulgare*. *D. immigrans* was also found to carry viruses closely related *Flock House virus* and *Drosophila X virus*, which are commonly used in laboratory studies of *Drosophila*-virus interactions.

Asobara japonica is a host generalist parasitoid that attacks the larvae of various species of *Drosophila* in Japan (Mitsui and Kimura 2010). In collections of *Drosophila* pupae from multiple habitat types in the Kanto Plain near Tokyo, *D. immigrans* was the second most abundant drosophilid species, yet it was almost never parasitized, with only a single parasitized pupa found among over 10,000 that were collected. *D. immigrans* was thus found to be far more resistant to wasp parasitism than any of the other drosophilid species in that region (Mitsui and Kimura 2010).

About 10% of wild-caught *D. immigrans* from Ohio were found to be infected with trypanosomatid protozoans (Ebbert *et al.* 2001).

**Life history:** In his study of the life history variation
among seven species of “domestic” *Drosophila*, Atkinson (1979) found a negative correlation between relative clutch size (ovariole number / thorax length) and relative egg volume (egg volume / thorax length). *D. immigrans* occurred at the lower end of relative egg volume spectrum and had a large relative clutch size. Atkinson (1979) interprets this to mean that *D. immigrans* breeds on infrequently encountered breeding sites, on which many eggs can be laid.

**Physiological ecology:** *D. immigrans* of Japanese origin can complete egg to adult development at any temperature from 11°C to 26°C, but cannot do so at 29°C (Kimura and Beppu 1993). These authors found that *D. immigrans* survive <12 days at 1.5°C in the laboratory. Thus, *D. immigrans* is probably unable to overwinter in their study area, where mean temperatures less than 1.5°C occur for periods of two months or more. Kimura and Beppu (1993) conclude that the persistence of *D. immigrans* in regions with long cold winters, as in the Northeast and Upper Midwest, requires recolonization from warmer local habitats, such as houses or indoor markets.

*D. immigrans* exhibits significant geographic variation among populations in Japan in cold tolerance, as measured by recovery time from chill coma, but not in heat resistance, as measured by death rate at 38°C and 40°C (Yamamoto and Ohta 1982). Interestingly, these authors found the opposite pattern - significant geographic variation for heat resistance but not cold tolerance - in *D. virilis*.

While genetically based differences in heat resistance were not evident in *D. immigrans*, Yamamoto and Ohba (1982) found that flies acclimated at 25°C had significantly greater heat resistance at 38°C than did flies acclimated at either 14°C or 20°C. *D. immigrans* also shows an acclimation response to desiccation, as flies exposed to desiccating conditions (<10% RH) for 3-4 hours subsequently exhibited greater survival under such conditions than did flies that were not acclimated (Hoffmann 1991). The experimental flies had enhanced survival when tested up to 29 hours after the acclimation period.

**REFERENCES:**


**Drosophila funebris** males

External genitals show **many spines** of approximately equal length (arrow)

Body medium-large, dark abdominal pigment **interrupted** along dorsal midline, mainly **in anterior segments**

**Wings grayish**

**Drosophila funebris** females

Body medium-large, dark abdominal pigment **interrupted** along dorsal midline, mainly **in anterior segments**

**Wings grayish**
Drosophila funebris males

Drosophila funebris females
This is a medium- to large-sized species. The males appear somewhat darker than females due to additional abdominal pigmentation. The dark abdominal pigment of the anterior-most segments is interrupted along the dorsal midline in both sexes. In females, only the posterior half of each abdominal segment is pigmented, while the posterior segments of males are entirely dark. The wings are uniformly grayish. The thorax is dark brown. The external genitalia of males show a cluster of many spines of approximately the same length. Similar species: *D. macrospina* looks almost identical, but the male abdomen ends in one large genital spine (hence the species name). *D. nigromelanica* looks very similar but has duskier wings. In *D. paramelanica*, the dorsal midline repression of pigmentation affects every abdominal segment. Also, *D. paramelanica* has a flatter appearance. *D. hydei* has numerous dark brown spots, from which bristles arise, over a lighter brown thorax, and the dorsal midline repression of pigmentation affects every abdominal segment.

**Tips for collecting and breeding:** This species visits banana and tomato traps. It can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group funebris

The funebris group is depauperate relative to others, comprising only *D. funebris, D. macrospina*, and five other species worldwide.

Based on molecular phylogenies based on several genes, the funebris group appears to fall within the immigrans-tripunctata radiation of the subgenus *Drosophila* (Pelandakis and Solignac 1993; Amador and Juan 1999; Robe *et al.* 2005). Besides the funebris group, this radiation also includes, among others, the tripunctata, testacea, quinaria, and immigrans species groups (Robe *et al.* 2005).

**Distribution:** Cosmopolitan, being more common in cooler areas. Its range includes Asia, Africa, Australia, Europe, South America, and North America, including the area covered by this guide (Basden 1956; Jara *et al.* 2014; Patterson 1943). Its range extends as far north as arctic regions in northern Scandinavia and as far south as Tierra del Fuego, giving it a broader latitudinal range than any other species of *Drosophila* (Brncic 1970).

**Breeding sites:** *D. funebris* is a broad generalist. Sturtevant (1921) reports that it is very common in stables, and Stalker and Spencer (1939) found it breeding in walnut hulls. In Chile, the breeding sites *D. funebris* include decaying tissues of pumpkin, prickly pear, and Chilean cactus (Jara *et al.* 2014). In a UK fruit and vegetable market, *D. funebris* was bred from decaying cabbage, cucumber, celery, lemon, and orange (Atkinson and Shorrocks 1977).
In the Czech Republic, large numbers of this species have been bred from the polypore fungus *Meripilus giganteus*, a cause of white rot in a wide variety of trees (Roháček et al. 2013). In fact, *D. funebris* made up ~96% of all of the drosophilids bred from these fungi. In Ukraine, *D. funebris* has been bred from a variety of fungi, including the polypore *Ganoderma*, jelly fungus *Auricularia*, and the gilled mushrooms *Lentinula* and *Pleurotus* (Korneyev 2010).

**Modes of reproductive isolation:** Mainland (1942) attempted matings between *D. funebris* and both *D. subfunebris* and *D. macrospina*, but reported that no hybrid progeny were obtained. Mainland states that interspecific matings were very rare, indicating a high level of behavioral isolation between *D. funebris* and the other two species. In two cases, *D. funebris* males mated with females of *D. macrospina*, but none of the eggs hatched, thus indicating some kind of post-mating pre-zygotic barrier or hybrid inviability.

**Parasites and pathogens:** The parasitoid wasps *Asobara tabida*, *Aphaereta minuta*, *Pachycrepoideus dubius*, *Pachycrepoideus vindemiae*, and *Leptopilina heterotoma* have been recorded from *D. funebris* (Carton et al. 1986; Davis et al. 1996).

**Pathogens:** The fungal pathogen *Coccidiascus legeri* was first discovered in *D. funebris* (Chatton 1913). Because this pathogen has been found in natural populations of several species of *Drosophila* in Ohio, it is possible that *D. funebris* in our area can also become infected, although we are unaware of any records of this.

**Genetic anomalies:** At least two intriguing findings have been made about the genetic system of *D. funebris*. First, in referring to newly arisen visible mutations, Sturtevant (1937) states that “It has been the experience of all who have studied *Drosophila funebris* that it gives many fewer mutations than does *D. melanogaster*.” If this applies to mutations at the nucleotide level, how does this affect nucleotide diversity in natural populations? Does it affect branch lengths in genomic-scale molecular phylogenies? The phylogenetic analysis of the Drosophilidae presented in van der Linde et al. (2010) suggests that this might be the case.

In a natural population of *D. funebris* around Manchester, England in the late 1940s, all of the viable larvae of 40 wild-caught females were heterozygous for three small inversions on the 5th chromosome (Berrie and Sansome 1948). No homozygotes for these inversions were obtained in subsequent breeding. Berrie and Sansome suggest that this appears to be a balanced lethal system that is fixed in this population. It would be interesting to see if a similar situation occurs in other populations of *D. funebris*, and, if so, how this affects the molecular evolution of a chromosome that might undergo little recombination.

**REFERENCES:**


Berrie, G.K. and Sansome, F.W. 1948. Wild population studies; *Drosophila funebris* near


**Drosophila macrospina**

**Drosophila macrospina males**
- Abdomen ends in **one large terminal spine**
- Wings grayish

**Drosophila macrospina females**
- Body medium-large, dark abdominal pigment **interrupted** along dorsal midline, mainly in anterior segments
- Wings grayish
Drosophila macrospina males

Drosophila macrospina females
This is a medium- to large-sized species. The males appear darker than females due to additional abdominal pigmentation. The dark abdominal pigment of the anterior-most segments is interrupted along the dorsal midline in both sexes. In females, only the posterior half of each abdominal segment is pigmented, while the posterior segments of males are entirely dark. The wings are uniformly grayish. The thorax is dark brown. The distal tip of the male abdomen ends in a large spine. Similar species: *D. funebris* looks almost identical, but the male lacks the conspicuous terminal spine. *D. nigromelanica* looks very similar but has duskier wings. In *D. paramelanica* and *D. hydei*, the dorsal midline repression of pigmentation affects every abdominal segment. Also, *D. paramelanica* has a flatter appearance, while *D. hydei* has dark brown dots over a lighter brown thorax. In *D. robusta*, the wings have a clouded posterior crossvein, and most abdominal segments have the dark pigmentation divided by a lighter dorsal midline.

**Breeding sites:** Mainland (1942) describes *D. macrospina* as a woodland species typically found near streams or swampy areas.

**Modes of reproductive isolation:** Spencer (1940) found that the presumed subspecies *D. macrospina macrospina* and *D. m. ohioensis* mate readily and produce viable and fertile offspring. However, these forms are likely to represent endpoints of continuous geographic variation, rather than distinct subspecies. *D. limpiensis* was initially described as a western subspecies of *D. macrospina*, but it is more likely to be a distinct species (D. Grimaldi, pers. comm.). Mainland (1942) found that reciprocal crosses between *D. macrospina* and *D. limpiensis* produce viable hybrid offspring in both directions. Hybrid males and females were fertile in crosses between *D. macrospina* females and *D. limpiensis*.
males. However, among hybrids produced in the reciprocal cross, females were fertile, but males were sterile or semi-sterile. Crosses between D. macrospina and D. subfunebris yield fertile hybrid females but sterile males.

REFERENCES:


**Drosophila neotestacea**

**Drosophila neotestacea males**
- Pre-sutural bristles (arrow) present, long, and at high angle
- Wing’s posterior crossvein slightly clouded
- Body small- to medium-sized, highly variable in color but medial abdominal line pale

**Drosophila neotestacea females**
- Pre-sutural bristles (arrow) present, long, and at medium angle
- Wing’s posterior crossvein slightly clouded
- Body small- to medium-sized, highly variable in color but medial abdominal line pale
**Drosophila neotestacea**
Grimaldi, James and Jaenike 1992

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**Small brownish fly. Abdominal spots often smeared together**

**Pair of long, thin, semi-erect presutural bristles**

**Male: orange testes visible through ventral side of abdomen**

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_D. neotestacea_ is a medium-sized species. The presence and angle of the pre-sutural bristle pair on the anterior part of the mesonotum is the most helpful character in identifying this species. _D. neotestacea_ is extremely variable in body coloration. Males range from yellowish body coloration without black pigmentation to almost completely dark brown. Intermediate forms carry black spots on their abdomens, which are often smeared together into splotches. The orange testes of _D. neotestacea_ males give their abdomens a yellowish-orange tint. Females vary from yellowish without black pigmentation to dusky gray with black spots that are often smeared together. Females do not get as dark as the darkest males. The pre-sutural bristles of females are a bit less obvious than in males because they stand at a lower angle over the thorax. Be aware that the pre-sutural bristles can break off, but most specimens should have them. Similar species: Lighter colored _D. neotestacea_ can be confused with _D. recens_, _D. falleni_, and the generally smaller species _D. putrida_. Look for the absence of pre-sutural bristles, stronger wing crossvein shading, and divergent anterior scutellar bristles in _D. recens_ and _D. falleni_. _D. putrida_ males have shorter and thicker pre-sutural bristles that lie very close to the thorax surface. _D. putrida_ females show a characteristic black horseshoe pigmentation pattern around the ovipositor. The darkest _D. neotestacea_ males resemble males of the smaller species _D. athabasca_, _D. affinis_, and _D. algonquin_, all three of which lack pre-sutural bristles, have sex combs on their forelegs, and have dark orange testes visible through the ventral side of the abdomen. Tips for collecting and breeding: The flies of this species come to mushroom baits, where they can make up a large fraction of the flies present. Tomatoes (and bananas) can also attract this species, but to a lesser extent. This species can be reared on instant + mushroom food. We typically keep these cultures at 22°C.

**Taxonomy:** Subgenus Drosophila. Species group testacea

**Distribution:** _D. neotestacea_ is found across Canada and northern United States (including Alaska) in boreal and deciduous forests. Its southern limit in the eastern US is at high elevations in the Smoky Mountains.

**Breeding sites:** _D. neotestacea_ is mycophagous, being most attracted to mushrooms in which the decay process is well underway (Grimaldi 1985). In this respect, it is like _D. putrida_, the only other member of the testacea group in North America. In contrast, mycophagous members of the quinaria group are attracted to fresher mushrooms. One consequence of utilizing older mushrooms is that
the density of infective nematodes may be greater, which may contribute to the high prevalence of nematode parasitism in *D. neotestacea* (see below).

Pairs of *D. neotestacea* can frequently be found mating on mushrooms, and there is evidence that they mate quite frequently (James and Jaenike 1992). We once released several thousand recently mated individuals carrying a recessive bright red-eye mutation (obtained from that local population) in a wooded area one evening and then collected them the next morning. Most of the recaptured red-eyed females produced some offspring with bright red eyes and some with darker (wild-type) eyes, indicating that they had mated with wild flies in the ~12 hours that they had been in the field.

**Aggregation:** Like other species of mycophagous *Drosophila, D. neotestacea* exhibits high levels of intra- and inter-specific aggregation across mushrooms, even those of the same species in similar condition and within a few meters of each other (Jaenike and James 1991). The aggregation at the level of fly larvae is due to aggregation of ovipositing females and the laying of multiple eggs per mushroom by individual females (Jaenike and James 1991). Such aggregations can have several effects, including greater levels of larval competition than would be the case if larvae were randomly distributed among mushrooms.

In accordance with the aggregation data, we have shown experimentally that there is considerable heterogeneity among mushrooms in the wild in the level of competition experienced by larvae. Among other effects, larval competition results in the production of smaller adult flies (Grimaldi and Jaenike 1984). Smaller females have fewer ovarioles and thus lower potential fecundity (Grimaldi and Jaenike 1984), and smaller males have reduced mating success in the wild (James and Jaenike 1992).

Such aggregation also means that most flies have developed in mushrooms that were also bred in by many other flies, and this can facilitate transmission of parasitic nematodes from one fly species to another. Finally, a high ratio of flies to mushrooms leads to a high rate of nematode parasitism (Jaenike and Anderson 1992). Thus, aggregation probably increases the prevalence of nematode parasitism in the wild.

**Modes of reproductive isolation:** *D. neotestacea* belongs to a cluster of three very closely related and morphologically almost identical species, the others being the Palearctic species *D. testacea* and *D. orientacea* (Grimaldi et al. 1992). As far as is known, the range of *D. neotestacea* does not overlap with that of either of the other two species.

Modes of reproductive isolation between *D. neotestacea* and the other two species are complex (Grimaldi et al. 1992). In the lab, females of *D. neotestacea* will not mate with males of *D. testacea*. However, in the reciprocal set-up, females of *D. testacea* readily mate with *D. neotestacea* males. In such matings, sperm are transferred, but none of the eggs hatch. This could conceivably be due to interspecific CI, as *D. neotestacea* is infected at high frequency with *Wolbachia* (see below). This could conceivably be due to interspecific cytoplasmic incompatibility (CI) between these species. Both males and females of *D. neotestacea* willingly mate with individuals of *D. orientacea*.

In matings between *D. neotestacea* males and *D. orientacea* females, sperm are transferred, but there is complete failure of F1 egg hatch. Again, this could be due to interspecific CI, but this has not yet been tested. In matings between *D. neotestacea* females and *D. orientacea* males, we find no evidence of sperm transfer. *D. orientacea*
and *D. testacea* can produce fertile hybrid offspring, and they have recently been found to be sympatric in far eastern Eurasia (Chen et al. 1998). However, these two species exhibit very strong behavioral isolation in the lab (Grimaldi et al. 1992; Chen et al. 1998). Because these three species are very closely related, they provide an opportunity to study the early stages of the evolution of reproductive isolation between both allopatric and sympatric pairs of species.

**Sex-ratio meiotic drive:** The frequent mating mentioned above may be an adaptation to cope with X chromosome meiotic drive (Pinzone and Dyer 2013). *D. neotestacea* has one of the highest frequencies of a driving XSR chromosome in *Drosophila*, being greatest in populations on the west coast (up to 50%), intermediate in populations from the Northeast and Upper Midwest (average ≈ 20%), but much less in populations from Alberta and Manitoba (0% - 5%) (James and Jaenike 1990; Dyer 2012; Pinzone and Dyer 2013). Because multiple mating depletes the fertility of SR males more than that of ST males, frequent mating by females ensures a high level of sperm competition, thus disadvantaging the XSR chromosome. Intriguingly, Pinzone and Dyer (2013) have found that in areas where the frequency of XSR is low, females remate more frequently than in areas where it is more common, suggesting that female mating behavior can affect the dynamics of XSR chromosomes.

The spread of XSR, if unchecked, could lead to the extinction of a population or species, as it tends towards an all-female state. In addition, X-drive causes a female-biased sex ratio, thus putting a premium on the production of males (Fisher 1930) via various mechanisms, such as suppression of drive by autosomal loci. It also favors the spread of Y chromosomes resistant to drive. One theoretically possible benefit of X-drive is that a female-biased population could have greater productivity and thus be capable of more rapid population growth, as well as greater success in situations of interspecific competition (Unckless and Clark 2014). With its high frequency of XSR and high levels of larval competition, *D. neotestacea* could be an excellent species for studies of this hypothesis, which has not yet been empirically tested.

**Parasites and pathogens:** *D. neotestacea* is the most severely parasitized host of the nematode *Howardula aoronymphium* (Jaenike 1992). When parasitism was first discovered in this species in the 1980s, an average of ~25% of flies in the Northeast were parasitized, with females almost always being completely sterilized as a result. Thus, the mean productivity of the species was reduced by about 25% and occasionally by over 50% in the wild. In addition, nematode-parasitized flies experience substantially elevated rates of adult mortality in the field (Jaenike et al. 1995). The sterility of nematode-parasitized females of *D. neotestacea* contrasts dramatically with high levels of fertility of parasitized females in *D. testacea* (a Eurasian species) and *D. orientacea* (which occurs in Japan and far eastern Asia) (Perlman and Jaenike 2003). This difference in the level of tolerance could be due to a relatively recent arrival of *H. aoronymphium* in North America. Since *D. neotestacea* is not parasitized by any other species of nematodes, nematode parasitism is a recent selective agent for *D. neotestacea*, as it is for *D. putrida*. *H. aoronymphium* occurs in both Europe and Japan, with distinct genetic differences between them, suggesting that *Drosophila* populations in those areas may have been selected for tolerance (or resistance) for
much longer.

The prevalence of parasitism in mycophagous *Drosophila* is related to the most recent few months of rainfall (Jaenike 2002). Abundant rain leads to the production of numerous mushrooms, which in turn result in high population densities of *Drosophila*. The resulting high fly to mushroom ratios can lead to rapid increases in the prevalence of parasitism, which tends to be highest in the late summer and fall. Parasitism rates are also high in the spring, as *D. neotestacea* and their resident nematode parasites overwinter as adults. Thus, abundant rainfall in one year can lead to high population densities of flies that year, but to lower potential growth rates the following spring, due to the female-sterilizing effect of nematode parasitism.

Grimaldi and Jaenike (1984) reared the following parasitoid wasps from mushrooms that yielded *D. falleni*, *D. recens*, *D. putrida* and/or *D. neotestacea*: two species of *Aspilota*, one species of *Phaenocarpa*, and two species of *Kleidotoma*. The parasitoids were not matched to individual *Drosophila* species, and the ratio of emerging *Drosophila* to wasps was over 100:1.

Hamilton et al. (2015) showed that the host range of the trypanosomatid *Jaenimonas drosophilae* includes *D. neotestacea*, at least in laboratory assays. The prevalence of infection by trypanosomatids in the wild appears to be higher in *D. neotestacea* (4/59) than in *D. falleni* (0/74) in New York (Martinson et al. 2017).

**Endosymbionts:** *D. neotestacea* carries two maternally transmitted endosymbionts: *Wolbachia* and *Spiroplasma*. *D. neotestacea* and its two closest relatives (*D. testacea* and *D. orientacea*) are infected with very closely related strains of *Wolbachia* (Stahlhut et al. 2010). In *D. neotestacea*, these *Wolbachia* are present at high frequency throughout its range (80% - 95%). We have found no evidence that these *Wolbachia* cause any sort of sex-ratio distortion (male-killing, parthenogenesis, or feminization) or intra-specific CI, suggesting that they might provide some sort of direct fitness benefit, rather than being reproductive parasites (Jaenike et al. 2010a). The interspecific crossing results discussed above hint that these closely related *Wolbachia* strains might cause interspecific CI, although this has not yet been tested.

*D. neotestacea* is also infected with a strain of *Spiroplasma poulsonii* that confers a high level of resistance to the female-sterilizing effects of nematode parasitism (Jaenike et al. 2010b). Because of the high rate of parasitism experienced by *D. neotestacea*, there has been strong selection favoring *Spiroplasma* infection, which has increased in prevalence in the eastern US from 10% - 15% in the 1980s to ~70% today. *Spiroplasma* is now spreading from east to west across North America in *D. neotestacea* (Cockburn et al. 2013). Why has it spread so recently? Based on DNA sequence data, it is clear that the *H. aoronymphium* in North America are very closely related to those in Europe, suggesting that this species may have recently colonized North America. Thus, *H. aoronymphium* may represent a new selective pressure for *D. neotestacea*, especially given the high prevalence of parasitism and the complete sterilization of parasitized females. Before the hypothesized arrival of parasitic nematodes, *Spiroplasma* may have originally conferred resistance to parasitic wasps, as *Spiroplasma*-infected individuals of *D. neotestacea* are much more likely to survive parasitoid wasp attack than are uninfected individuals (Haselkorn and Jaenike 2015).

**B chromosomes:** About 60% of individuals of *D. testacea* carry supernumerary B chromosomes.
Since this species is very closely related to *D. neotestacea*, it might be worth examining the latter for B chromosomes.

**REFERENCES:**


**Drosophila putrida**

**Drosophila putrida males**
- Pre-sutural bristles (arrow) present, short, thick, and at low angle
- Wing’s posterior crossvein slightly clouded
- Body small and spotted/striped, usually pale and quite feature-less

**Drosophila putrida females**
- Pre-sutural bristles (arrow) present, short, thick, and at low angle
- Black horseshoe around the tip of the abdomen
- Wing’s posterior crossvein slightly clouded
- Body small and spotted/striped
Drosophila putrida males

Drosophila putrida females
Drosophila putrida
Sturtevant 1916

**D. putrida** is a small species. Males of **D. putrida** are often nondescript. The females have a characteristic black horseshoe-shaped tergite around the tip of the abdomen. The pair of pre-sutural bristles of both sexes lie at a very low angle to the thorax. Similar species: **D. neotestacea** is larger and has pre-sutural bristles that are longer, thinner, and stand at a higher angle from the thorax than in **D. putrida**. **D. falleni** and **D. recens** are also larger than **D. putrida**, lack pre-sutural bristles, have divergent anterior scutellar bristles, and have clouded crossveins on the wings. Tips for collecting and breeding: This species prefers mushroom traps, but it also visits tomato and banana traps. **D. putrida** grows well in the lab on instant + mushroom food, as well as on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group testacea.

**Distribution:** Eastern United States and Canada, extending as far south as Florida and Texas

**Breeding sites:** **D. putrida** breeds in a wide variety of fleshy mushrooms (Lacy 1984). It is perhaps the most abundant species of mycophagous Drosophila in the eastern United States. Whereas mycophagous members of the quinaria species group typically come to fresh mushrooms, the North American members of the testacea group (**D. putrida** and **D. neotestacea**) tend to be attracted to more decayed mushrooms (Grimaldi 1985). Field experimental evidence shows that **D. putrida** experiences significant competition for larval food in the wild, and this results in both reduced egg to adult survival and smaller adult size. Smaller size leads to reduced ovariole numbers and thus lower potential fecundity (Grimaldi and Jaenike 1984).

Among the mushrooms utilized by **D. putrida** is Amanita bisporigera, known for its extreme toxicity to humans as a result of having high levels of α-amanitin, an inhibitor of RNA polymerase II. **D. putrida** can develop with apparent impunity on such mushrooms, and lab studies show that it has a much higher tolerance of α-amanitin than do non-mycophagous species of Drosophila, such as **D. melanogaster** (Jaenike et al. 1983). While **D. putrida** can tolerate high levels of α-amanitin, Howardula aoronymphium cannot, and as a result, flies that develop on Amanita bisporigera or A. virosa in the field are almost never parasitized by nematodes (Jaenike 1985).

**D. putrida** exhibits high levels of intraspecific aggregation across mushrooms: some mushrooms yield large numbers of flies, whereas many yield few or none. This aggregation is due both to aggregation of ovipositing females and to individual females laying multiple eggs per mushroom (Jaenike and James 1991). Additionally, the number of emerging **D. putrida** per mushroom
is strongly and consistently correlated with the number of emerging \textit{D. neotestacea} and, less strongly, with the number of emerging \textit{D. falleni}. Such intra- and interspecific aggregation results in substantially higher levels of larval competition than would be experienced if larvae were randomly distributed among mushrooms. Furthermore, the interspecific aggregation means that these mycophagous species contribute to a common pool of infective stage \textit{Howardula aoronymphium} nematodes. As a consequence, there are strong and consistent correlations in the prevalence of nematode parasitism between \textit{D. putrida}, \textit{D. neotestacea}, and \textit{D. falleni} across mushrooms (Jaenike and James 1991).

**Modes of reproductive isolation:** There are no known close relatives of \textit{D. putrida}. It is estimated to have diverged from the other three members of the testacea group (\textit{testacea}, \textit{neotestacea}, and \textit{orientacea}) \textasciitilde8 million years ago (Itzumitani et al. 2016).

**Sex-ratio meiotic drive:** Unknown, despite our having reared numerous cultures of isofemale lines from wild-caught flies. Such drive would be evident in strongly female-biased offspring sex ratios.

**Nematode parasitism:** \textit{D. putrida} is commonly parasitized by the nematode \textit{Howardula aoronymphium}. Parasitized females in the wild are almost invariably rendered completely sterile, carrying no mature eggs. The ovaries are often packed with juvenile nematodes, which can be shed via the ovipositor. In addition to its effect on female fecundity, parasitism by \textit{H. aoronymphium} substantially reduces adult survival in the wild (Jaenike \textit{et al}. 1995). The effect of nematode parasitism on male mating success and virility in \textit{D. putrida} has not been studied. The highly adverse impact of \textit{H. aoronymphium} on \textit{D. putrida} might be due to the nematode having recently spread to North America, and in \textit{D. putrida} not being parasitized by any other nematodes (Perlman and Jaenike 2003). Thus, selection for resistance or tolerance of nematode infection may be evolutionarily recent.

The monthly prevalence of nematode parasitism in \textit{D. putrida} varies dramatically through time, from 0\% to >50\% (Jaenike 1992). The prevalence of parasitism is typically greatest in the spring and fall and lowest in mid-summer (Jaenike 2002). Because parasitism reduces adult survival in the wild, measures of the prevalence of parasitism, which are based on wild-caught adult flies, are probably underestimates.

As a result of the spread of \textit{Spiroplasma} into \textit{D. neotestacea}, the prevalence of nematode parasitism has dropped by about 50\% in that species (Jaenike and Brekke 2011). In addition, nematodes within \textit{Spiroplasma}-infected individuals of \textit{D. neotestacea} are smaller and much less fecund than those in uninfected flies. The combination of lower prevalence of nematode parasitism and lower reproductive output of nematodes in \textit{D. neotestacea} means that this species contributes substantially less to the pool of infective nematodes than it did previously. Around Rochester, NY, \textit{D. putrida} has replaced \textit{D. neotestacea} in recent years as the most important contributor to the pool of infective nematodes. Because of the
interspecific aggregation mentioned above, the pool of infective nematodes within a mushroom is drawn from and contributes to the infection of multiple Drosophila species.

**Parasitoids:** Grimaldi and Jaenike (1984) reared the following parasitoid wasps from mushrooms that yielded D. falleni, D. recens, D. putrida and/or D. neotestacea around Binghamton, NY: two species of Aspilota, one species of Phaenocarpa, and two species of Kleidotoma. The parasitoids were not matched to individual Drosophila species. The ratio of emerging Drosophila to wasps was over 100:1, suggesting that parasitoids did not have a major effect on the fly communities sampled.

**Pathogens:** D. putrida is susceptible to infection by trypanosomatids, but is only rarely infected in the wild, with only 1 infected fly out of 74 assayed (Martinson et al. 2016).

**Endosymbionts:** Although no heritable symbionts have been discovered in D. putrida, it is a perfectly suitable host for Spiroplasma. Several generations after artificial transinfection of Spiroplasma from D. neotestacea (the natural host) to D. putrida, both the fidelity of maternal transmission (97%) and the within-host titer of Spiroplasma reached values similar to those in D. neotestacea (Haselkorn et al. 2013). Remarkably, the newly Spiroplasma-infected individuals exhibited a much greater resistance to the sterilizing effects of nematode parasitism than flies lacking Spiroplasma. Because nematode-parasitized females are almost always completely sterile, the estimated fitness advantage in nature (taking into account the long-term mean prevalence of nematode parasitism and the potential fecundity of parasitized females) should be sufficient to overcome losses due to imperfect maternal transmission (Haselkorn et al. 2012). Thus, Spiroplasma could spread in D. putrida if it had the chance. Because mites can transmit Spiroplasma between Drosophila species in the lab (Jaenike et al. 2007) and because mites are commonly seen on wild Drosophila, including D. putrida (see photo below), it may be only a matter of time until Spiroplasma invades D. putrida.

**Behavior:** D. putrida is more tolerant of high temperature than is H. aoronymphium, and as a result, populations of D. putrida south of the 27°C July isotherm are not subject to nematode parasitism (Jaenike 1995). Furthermore, when parasitized females of D. putrida are kept at 29°C, the nematodes die and female flies regain their fertility (Ballabeni et al. 1995). However, when provided a continuous temperature gradient, these flies do not preferentially select the higher temperatures nor differ in their temperature preference from unparasitized flies, showing that they do not exhibit behavioral fever. Perhaps this is because H. aoronymphium may have recently spread to North America, and D. putrida has not evolved what would be an adaptive behavioral response to nematode parasitism.

**Phenotypic plasticity:** As mentioned above, larval competition for food in the wild often results in reduced size of adult D. putrida. Because the intensity of competition varies greatly among mushrooms (Grimaldi and Jaenike 1984), there is considerable body size variation in natural populations of this species. In addition, there is a great deal of variation in body coloration, from light yellow to dark brown, which is due to seasonal variation in temperature, with flies developing at lower temperature being darker as adults (Sabath et al. 1973). As a result of this variation in size and body color, D. putrida is perhaps the most visibly variable species in our area. Because the degree of pigmentation is associated with other traits in Drosophila, including resistance to desiccation, UV radiation, and nematode parasitism, it would
be interesting to determine whether developmental temperature-mediated variation in body color in *D. putrida* affects these other aspects of fitness.

**Chromosomal polymorphism:** Wharton (1943) discovered an unusual polymorphism in the chromosome complements of two strains of *D. putrida*, one from Texas and one from Florida. The Texas strain had two metacentric autosomes, a rod-shaped X, and a large dot chromosome, similar to *D. melanogaster*. This is likely to be independent evolution of a similar chromosome complement, as *D. putrida* and *D. melanogaster* split ~60 million years ago, and the subgenus Drosophila, to which *D. putrida* belongs, is likely to have had 6 separate chromosomes ancestrally (Patterson and Stone 1952).

The Florida strain of *D. putrida* had, in addition, an extra tiny dot chromosome, which appeared to comprise little more than a centromere (Wharton 1943). Wharton notes that this is a rare or unique increase in the number of centromeres in *Drosophila*, from the usual 4 to 5. Does this extra chromosome have any fitness effects on flies, and if so, why is the species polymorphic for it? Is this a supernumerary B chromosome? To date, B chromosomes have been found in only a handful of *Drosophila* species (Bauerly *et al.* 2014).

**Physiological ecology:** Worthen and Haney (2002) found that females of *D. putrida* are far more resistant to desiccation than are males or females of *D. tripunctata* and *D. falleni*, and this may enable them to persist better through periods of drought. *D. putrida* is also more tolerant of high temperatures than the other two species, both as measured by survival at 30°C and the critical thermal maximum, CTMax, the temperature at which half the flies cannot right themselves in a chamber in which the temperature is gradually rising (Worthen and Haney 1999). In addition, Worthen and Haney found that *D. putrida* was the only species whose CTMax increased significantly with pre-testing acclimation temperature.

**REFERENCES:**


**Drosophila falleni**

**Drosophila falleni males**
- 2nd oral bristle (arrow head) less than 1/2 as long as 1st (arrow)
- Body medium-sized, abdomen spotted/striped
- No lateral spot row (arrow)
- Wing's anterior and posterior crossveins slightly clouded

**Drosophila falleni females**
- 2nd oral bristle (arrow head) less than 1/2 as long as 1st (arrow)
- Body medium-sized, abdomen spotted/striped
- No lateral spot row (arrow)
- Wing's anterior and posterior crossveins slightly clouded
*Drosophila falleni* males

*Drosophila falleni* females
This is a medium-sized species. Males and females look similar. The ground color varies from yellowish to tan with two pairs of abdominal spot rows, which can be fused into broader stripes on each segment. Both crossveins of the wings are clouded. The second oral bristle is less than half as long as the first oral bristle. Similar species: *D. subquinaria* and *D. recens* have an additional lateral abdominal spot row, and their second oral bristle is more than half as long as the first. The crossveins on the wings of *D. falleni* are more noticeably clouded than those of *D. neotestacea* and *D. putrida*. Furthermore, *D. neotestacea* and *D. putrida* have a pair of pre-sutural bristles on the thorax, which is absent in *D. falleni*. Tips for collecting and breeding: *D. falleni* is a frequent visitor to mushroom baits and will come to bananas, particularly in later stages of ripening. *D. falleni* can be cultured on instant + mushroom food.

**Taxonomy:** Subgenus *Drosophila*. Species group *quinaria*.

For many years, *D. falleni* was incorrectly identified as *D. transversa* (a Eurasian species) until it was identified as a separate species by Wheeler (1960).

**Distribution:** Wheeler (1960) reports that *D. falleni* has been found primarily in the eastern United States and Canada, and “a single, unexpected, specimen from Robson, British Columbia.” In recent years, we have collected multiple individuals of this species in Manitoba (The Pas), Saskatchewan (Prince Albert National Park), and Alberta (Edmonton and Winston Churchill Provincial Park).

**Breeding sites:** *D. falleni* is mycophagous, utilizing a wide variety of fleshy fungi as breeding sites (Jaenike 1978a; Lacy 1984). Grimaldi (1985) found that mycophagous members in the quinaria species group, including *D. falleni*, prefer fresher mushrooms as feeding and oviposition sites than do members of the testacea group. *D. falleni* has also been bred, but in very small numbers, from skunk cabbage (*Symplocarpus foetidus*), a primary breeding site of several other members of the quinaria group, including *D. quinaria* and *D. palustris*.

*D. falleni* is a host generalist not only as a species, but also as individuals. Mark-release-recapture studies of wild flies showed that individual flies readily move from one mushroom species to another and that there is very little genetic differentiation between flies bred from different mushroom species (Jaenike 1978b; Jaenike and Selander 1979). However, there is considerable differentiation among flies bred from different individual mushrooms of the same species, suggesting that when a female fly finds a suitable mushroom, she remains there, laying many eggs. Like other mycophagous species of *Drosophila*,
D. falleni experiences significant competition in the field (Grimaldi and Jaenike 1984). In D. falleni, natural levels of larval food limitation are manifest both in reduced pre-adult survival and reduced adult body size. Because ovariole number in females is correlated with body size in this species, reduced body size results in a reduction in potential female fecundity (Grimaldi and Jaenike 1984). In addition, like other mycophagous Drosophila, D. falleni exhibits significant intra- and inter-specific aggregation in the use of individual mushrooms (Jaenike and James 1991), thus amplifying the level of competition experienced by larvae.

Ant predation can alleviate the intensity of larval competition for food in naturally occurring mushrooms. Worthen et al. (1993) set up ant exclusion and ant access cups containing field-collected boletoid mushrooms and found that the number of emerging adults to be significantly reduced in the ant access cups. However, by preying on larval Drosophila, ant predation reduced the intensity of competition, resulting in significantly larger emerging D. falleni adults from the ant access mushrooms.

D. falleni can tolerate much higher concentrations of the mushroom toxin α-amanitin than can D. melanogaster or non-mycophagous members of the quinaria group, and as a result can breed in famously toxic mushroom species like A. bisporigera (the destroying angel). Flies bred from such mushrooms are almost never parasitized by nematodes, thus raising the possibility that evolution of resistance to α-amanitin may have been in response to parasite pressure (Jaenike 1985).

Stump et al. (2011) have shown that piperonyl butoxide (PBO), an inhibitor of cytochrome P450s, does not reduce the level of tolerance to α-amanitin in D. falleni, indicating that P450s are unlikely to be responsible for this tolerance. However, they found that α-amanitin tolerance in D. phalerata, a European species, was greatly diminished by PBO. This is a very interesting result, as D. falleni and D. phalerata belong to the same section of the quinaria group, and this finding suggests that the two species have evolved α-amanitin tolerance in different ways or that D. falleni has evolved tolerance mechanisms in addition to P450s.

**Modes of reproductive isolation:**

Phylogenetically, D. falleni occurs on a sparsely populated branch of the quinaria group tree, with no very close relatives. The closest known species, D. innubila, occurs in the forested sky islands of Arizona and Mexico, and is thus not sympatric with D. falleni. We are unaware of any studies on intrinsic mechanisms of reproductive isolation between these species. If fertile hybrid females could be produced between D. innubila females and D. falleni males, it might be possible to introgress Wolbachia, a male killer in D. innubila, into D. falleni to determine the effect in this related host species. This Wolbachia strain does not cause male killing in the much more distantly related D. melanogaster and D. simulans (Veneti et al. 2012), but a closely related strain of Wolbachia does cause male killing in D. borealis (Sheeley and McAllister 2009).

**Sex-ratio meiotic drive:** There is no evidence for such drive, despite our having worked with numerous wild-derived cultures of this species over the years.

**Parasites and pathogens:** D. falleni is parasitized by two species of Howardula nematodes in North America: the generalist H. aoronymphium (Montague and Jaenike 1985) and an as yet undescribed species designated Howardula sp. F that is highly specialized on D. falleni (Perlman et al. 2003). D. falleni is much more tolerant of H.
**aoronymphium** parasitism than are *D. putrida* and *D. neotestacea*, in which females were generally rendered completely sterile prior to the spread of *Spiroplasma* in the latter species (Jaenike 1992). Based on its very close genetic similarity to European *H. aoronymphium*, we suspect that this nematode may have recently invaded North America (Perlman and Jaenike 2003). We hypothesize that *D. falleni* is less severely affected by *H. aoronymphium* parasitism because it had evolved anti-nematode defenses to cope with *Howardula* sp. *F* parasitism prior to the arrival of *H. aoronymphium*.

*D. falleni* exhibits substantial genetic variation in the number and size of abdominal spots, and artificial selection can readily extend the range of variation, yielding some lines with spots so large they merge together and other lines with very few or no spots at all (see figure above). In lab assays, the spotless flies were almost twice as likely to become parasitized by *H. aoronymphium* as were flies with normal, wild-type abdominal patterns (Dombeck and Jaenike 2004). It would be interesting to assay other aspects of fitness as a function of the abdominal spotting pattern, such as mating success, male-male interactions, crypsis, desiccation resistance, and resistance to UV radiation. *D. falleni* is susceptible to infection with a trypanosomatid parasite, *Jaenimonas drosophiliae*, which can also infect *D. neotestacea* and *D. melanogaster* in lab assays (Hamilton et al. 2015). In *D. falleni*, this infection leads to a ~1/3 reduction in female fecundity. The prevalence of infection in the wild appears to be low: at sites in Ohio, the mean prevalence of trypanosomatid infection was 2% (Ebbert et al. 2001), and in a molecularly based microbiome screen, 0/59 individuals of *D. falleni* from New York were infected (Martinson et al. 2017).

In collections from Ohio, 3.3% of wild-caught *D. falleni* were infected with the fungal pathogen *Coccidiascus legeri* (Ebbert et al. 2001, 2003).

**DNA virus infection:** The DNA virus DiNV infects several species of *Drosophila* in the wild, including *D. falleni*, suggesting that it has a potentially broad host range (Unckless 2011). Interestingly, some aspect of biogeography, perhaps climate, may play an important role in determining the prevalence of infection, as the mean infection prevalence among 5 species collected in New York was 0.011 ± 0.007, while it was much higher among 6 species collected in the Chiricahua Mountains of Arizona, 0.31 ± 0.09 (Unckless 2011). This virus dramatically reduces adult survival of both *D. falleni* and the related *D. innubila* in the lab (Unckless 2011).

Grimaldi and Jaenike (1984) reared the following parasitoid wasps from mushrooms that yielded *D. falleni*, *D. recens*, *D. putrida* and/or *D. neotestacea*: two species of *Aspilota*, one species of *Phaenocarpa*, and two species of *Kleidotoma*. The parasitoids were not matched to individual *Drosophila* species, and the ratio of emerging *Drosophila* to wasps was over 100:1.

**Behavior:** *D. falleni* exhibits both intra- and interspecific aggregation in emergence numbers from mushrooms. This could, in part, be due to a positive feedback mechanism involving aggregation pheromones (Jaenike et al. 1992). In an experimental study, hexane extracts of cuticular hydrocarbons from *D. putrida* and *D. falleni* were placed on a piece of filter paper near mushrooms in the field, and adult flies were collected by sweep netting over the mushrooms for 3-4 days. The mushrooms with either *falleni* or *putrida* extracts consistently attracted more flies of than did the control mushrooms (filter paper with pure hexane).

**Genetic population structure:** Within local
populations of *D. falleni*, there is significant differentiation among flies emerging from individual mushrooms, suggesting that individual females lay multiple eggs on a single mushroom, and that the individuals that survive to adulthood are the offspring of a small number of ovipositing females (Jaenike and Selander 1979). Hoffmann and Nielsen (1985) found similar results for *D. melanogaster*. At larger geographic scales, there is little genetic differentiation among local populations of *D. falleni*, as well as between populations in different regions (e.g., New York versus Tennessee [Lacy 1983], and New York versus Maine [Shoemaker and Jaenike 1997]). The lack of differentiation at the larger scales may be due to the essentially continuous nature of suitable habitat for *D. falleni*, woods and forests, where mushrooms can be found.

**Physiological ecology:** The elemental composition of adult *Drosophila* is correlated with that of their larval resources (Markow et al. 1999; Jaenike and Markow 2003). Because mushrooms have higher phosphorus content than many other types of *Drosophila* breeding sites, mycophagous flies tend to be higher in phosphorus as well. In a comparative study of six *Drosophila* species, Elser et al. (2006) found that *D. falleni* had the highest phosphorus and RNA contents and the greatest larval growth rate, consistent with this species feeding on the most phosphorus-rich resources. The growth rate hypothesis of Elser et al. (1996) states that species feeding on more P-rich resources can allocate more phosphorus to rRNA synthesis, which thus enables greater rates of protein synthesis required for growth.

**REFERENCES:**


Jaenike, J. 1978a. Resource predictability and


DON’T CRY ABOUT YOUR LOST TOMATO; TRY MY BANANA INSTEAD!

PLACEHOLDER - NO IMAGE AVAILABLE
ALWAYS KEEP TWO HANDS ON THE BABY!
Drosophila rellima
Wheeler 1960

D. rellima is a medium-sized species. Males and females look similar. The abdomen has one broad spot on each side of the tergites. Both crossveins of the wings are clouded. Similar species: D. subquinaria and D. recens can look similar to D. rellima, though D. rellima lacks the lateral row of small spots on each tergite found in the former two species. D. rellima differs from D. recens, D. subquinaria, and D. falleni in having one large spot on each side of the tergites, whereas the other species typically have 2-3 spots on each side. The distal portion of the aedeagus (male genitalia) of D. rellima is clearly different from those of D. falleni, D. recens, and D. subquinaria (see figures 9-12 in Wheeler 1960).

Taxonomy: Subgenus Drosophila. Species group quinaria

Distribution: Wheeler (1960) reports this species from Nebraska, Oregon, and California, and we have collected it in Minot, North Dakota. Miller et al. (2017) have recently found this species at several sites in Ontario.

Breeding sites: We have captured this species at mushroom baits in north central North Dakota. Given that it belongs to the quinaria group, which is largely mycophagous, we suspect that D. rellima is as well.

Modes of reproductive isolation: We have sequenced COI in D. rellima (GenBank accession HM436810.1). The most similar sequences (D. subquinaria, D. limbata) are only 93% identical to that of D. rellima, suggesting that the latter does not have any close relatives, with which it might hybridize.

Endosymbionts: We have found that wild D. rellima can be infected with Wolbachia. Its wsp gene (GenBank accession HM436813.1) is most similar in sequence to Wolbachia strains found in European ticks (Ixodus ricinus) and a parasitoid wasp (Odontosema anastrephae) of tephritid fruit flies that were collected in Mexico. Surprisingly, the wsp sequence of the Wolbachia in D. rellima is not similar to sequences of any Wolbachia strains found in other species of Drosophila.

REFERENCES:


**Drosophila guttifera**

**Drosophila guttifera males**

Body medium-sized, thorax striped, abdomen dark with 3 rows of black spots on each half, dorsal midline dark

Wing’s crossveins, all longitudinal vein tips, and the campaniform sensilla are intensively clouded

**Drosophila guttifera females**

Body medium-sized, thorax striped, abdomen dark with 3 rows of black spots on each half, dorsal midline dark

Wing’s crossveins, all longitudinal vein tips, and the campaniform sensilla are intensively clouded
Drosophila guttifera males

Drosophila guttifera females
This is a small- to medium-sized species. Males and females look similar. The thorax has 6 dark longitudinal stripes. The abdomen is relatively dark with 6 rows of spots and a dark dorsal midline shade. All vein termination points and campaniform sensilla of the wings carry a black spot. Similar species: The body of *D. deflecta* is lighter, and the wings lack the black wing spots on the campaniform sensilla. *D. palustris* also lacks the black wing spots on the campaniform sensilla, and its abdomen has a light dorsal midline and only 4 rows of black spots. Tips for collecting and breeding: This species visits mushroom and tomato traps. It can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Drosophila. Species group quinaria.

Although *D. guttifera* was previously placed in its own group (Patterson 1943), subsequent molecular genetic phylogenies place it squarely within the quinaria group (Perlman *et al.* 2003; van der Linde *et al.* 2010; Izumutani *et al.* 2016).

**Distribution:** *D. guttifera* is an eastern species, having been recorded from Texas to Florida and northwards to Indiana and Massachusetts, though it is much rarer in the northern part of its range.

**Breeding sites:** According to Sturtevant (1921), *D. guttifera* utilizes both gilled fungi and pore fungi as breeding sites, not distinguishing between polypores and boletes. In Ohio, *D. guttifera* has been bred from *Gymnopus* (*Collybia*) *dryophila* and *Psilocybe polytrichophila*, two species that were not used utilized by any other mycophagous insects, including the host generalists *D. falleni* and *D. putrida* (Bunyard and Foote 1990).

Stump *et al.* (2011) found that, like other mycophagous species of *Drosophila*, *D. guttifera* can successfully develop in medium containing the mushroom toxin α-amanitin.

**Modes of reproductive isolation:** Based on published molecular phylogenies, *D. guttifera* has no known close relatives within the quinaria group. Izumutani *et al.* (2016) estimate that it diverged ~10 million years ago from a clade comprising *D. recens*, *D. quinaria*, *D. palustris*, and several other species. We are not aware of any studies of isolating mechanisms between *D. guttifera* and other species.

**Wing patterning:** *D. guttifera* is one of the most striking and attractive *Drosophila* species in our region, having 6 clean, distinct abdominal spots on each tergite, 6 dark, longitudinal stripes on its thorax, and 16 spots along the wing veins and 4 shaded regions between the veins. Werner *et al.* (2010) show that both the spots and the shaded areas are produced as a result of expression of the *yellow* gene, but that the spots and shades are controlled by two different *cis*-regulatory elements.
They show that the Wingless morphogen controls one of the cis-regulatory elements of the yellow gene, leading to the generation of the black wing spots. Furthermore, transgenic manipulation of the wingless gene expression pattern in stripes along the developing wing veins changes the wild-type leopard-spotted wing pattern into a tiger-striped pattern. Thus, Wingless is sufficient and necessary for the development of the black wing spots.

The combination of wing and abdominal pigmentation patterns results in a very strikingly spotted looking fly. It would be interesting to explore the adaptive significance of this under ecologically natural conditions.

REFERENCES:


Patterson, J.T. 1943. The Drosophilidae of the Southwest. Univ Texas Publs 4313: 7-216.


**Drosophila palustris**

**Drosophila palustris males**

Body medium- to large-sized, abdomen on each side with 2 rows of spots, a dark shade, dorsal midline light.

Wing's crossveins and all longitudinal vein tips clouded, tip of longitudinal vein L5 weakly clouded, (arrow), posterior crossvein nearly straight.

**Drosophila palustris females**

Body medium- to large-sized, abdomen on each side with 2 rows of spots, a dark shade, dorsal midline light.

Wing's crossveins and all longitudinal vein tips clouded, tip of longitudinal vein L5 weakly clouded, (arrow), posterior crossvein nearly straight.
This is a medium- to large-sized species. Males and females look similar. The thorax has 2 faint stripes. The abdomen is shiny dark brown or gray with 3 broad yellow stripes running the length of the abdomen. Each tergite has a small black spot laterally and one medially, the latter partially obscured by shading in that region of the tergite. The crossveins and vein termination points of the longitudinal veins 2, 3, and 4 are moderately clouded, and the tip of vein 5 is lightly clouded. Similar species: D. palustris can be distinguished from D. subpalustris in that the latter has darker wings with heavier clouds on the crossveins and vein tips (including longitudinal vein 5) and an S-shaped posterior crossvein (Spencer 1942). D. palustris lacks a small spot on lateroventral side of the thorax that is present in D. subpalustris. The table below summarizes the differences between D. palustris and D. subpalustris. D. deflecta and D. quinaria differ from D. palustris in having lighter colored abdomens with 6 rows of black spots on the tergites. Tips for collecting and breeding: This species visits tomato, cucumber, and banana baits. It can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast. It also does well on instant + cucumber food.

**Taxonomy:** Subgenus Drosophila. Species group quinaria

**Distribution:** Widely distributed in the eastern United States, though records are very spotty. Spencer (1942) reports that D. palustris has been found in Ohio, New York, New Jersey, and Virginia, and Spieth (1957) reports it from Minnesota, all areas where the eastern skunk cabbage, an important breeding site of D. palustris, grows. T.S. collected this species in Madison, Wisconsin in 2018.

**Breeding sites:** We have found that D. palustris is one of a small set of species in the quinaria group, including D. quinaria itself, that breeds in decaying skunk cabbages (Symlocarpus foetidus). Spencer (1942) reports that they also breed in the decaying leaf stalks of broad-leaved arrowhead, Sagittaria latifolia. It has also been found feeding on decaying grasses and sedges in wetlands (Keiper et al. 2002).

**Modes of reproductive isolation:** D. palustris belongs to a rapidly diversifying clade within the quinaria group. Based on a molecular phylogeny of mtDNA, its closest relatives are D. subpalustris and D. deflecta (Perlman et al. 2003). Sears (1947) reports that D. palustris and D. subpalustris will mate reciprocally and produce viable hybrid progeny, which in turn can produce F2, indicating that both male and female hybrids are fertile. The F2 were also fertile, indicating that there is relatively little hybrid breakdown. Furthermore,
both species have been collected in the Killbuck Marsh area near Wooster, Ohio, indicating that they probably encounter each other in the wild. Thus, these two species could be informative about mechanisms that evolve in the early stages of divergence. In crosses between \textit{D. palustris} and the more distantly related western \textit{D. tenebrosa} and \textit{D. suboccidentalis}, hybrid males and females were viable, but only the females were fertile (Blumel 1949). However, \textit{D. tenebrosa} and \textit{D. suboccidentalis} occur in the western United States and Canada and are not known to be sympatric anywhere with \textit{D. palustris}.

<table>
<thead>
<tr>
<th>Trait</th>
<th>\textit{D. palustris}</th>
<th>\textit{D. subpalustris}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clouding at tip of vein L5 (the one closest to posterior crossvein)</td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td>Clouding at tips of L2-L4</td>
<td>Moderate - quinaria-like</td>
<td>Heavy - deflecta-like</td>
</tr>
<tr>
<td>Posterior crossvein</td>
<td>Straight or slightly S-shaped</td>
<td>Noticeably S-shaped</td>
</tr>
<tr>
<td>Abdominal spots</td>
<td>Lateral and median rows (the latter partially obscured by shading in that area)</td>
<td>Lateral row only</td>
</tr>
<tr>
<td>Black spot on lateroventral side of the thorax</td>
<td>Absent</td>
<td>Present</td>
</tr>
</tbody>
</table>

Morphological differences between \textit{D. palustris} and \textit{D. subpalustris}.

REFERENCES:


**Drosophila subpalustris**

**Drosophila subpalustris males**

Body medium- to large-sized, abdomen on each side with 1 row of spots, a dark shade, dorsal midline light, small spot on lateroventral side of the thorax.

Wing’s crossveins and all longitudinal vein tips heavily clouded, including tip of longitudinal vein L5 (arrow), posterior crossvein S-shaped.

**Drosophila subpalustris females**

Body medium- to large-sized, abdomen on each side with 1 row of spots, a dark shade, dorsal midline light, small spot on lateroventral side of the thorax.

Wing’s crossveins and all longitudinal vein tips heavily clouded, including tip of longitudinal vein L5 (arrow), posterior crossvein S-shaped.
Drosophila subpalustris males

Drosophila subpalustris females
**Drosophila subpalustris**  
**Spencer 1942**

This is a medium- to large-sized species. Males and females look similar. The abdomen is a shiny dark brown or gray with three broad yellow stripes running the length of the abdomen. Each tergite has a small black spot laterally. The crossveins and vein termination points of the longitudinal veins 2, 3, 4, and 5 are heavily clouded. The posterior crossvein is noticeably S-shaped. There is a small spot on lateroventral side of the thorax. Similar species: *D. subpalustris* can be distinguished from *D. palustris* in that *D. subpalustris* has darker wings with heavier clouds on the crossveins and vein tips (including longitudinal vein 5, which is only lightly clouded in *D. palustris*) and by having a distinctly S-shaped posterior crossvein (Spencer 1942). A table of differences between these two species is presented in the section on *D. palustris*. *D. deflecta* and *D. quinaria* differ from *D. subpalustris* in having lighter colored abdomens with 6 rows of black spots on the tergites. This species does well on instant + cucumber food.

**Taxonomy:** Subgenus Drosophila. Species group quinaria

**Distribution:** Spencer (1942) reported *D. subpalustris* from the Killbuck Marsh area in Holmes County, Ohio and Odell’s Lake in Holmes County, Ohio. The *Drosophila* Species Stock Center has a line that was collected in 1961 in Myrtle Beach, South Carolina, ~800 km from the Ohio sites. Thus, *D. subpalustris* appears to be widely distributed in the eastern United States, but rare.

**Breeding sites:** Given the close phylogenetic relationship between this species and *D. palustris*, which breeds in skunk cabbage and the presence of skunk cabbages at sites where *D. subpalustris* has been collected, we suspect that *D. subpalustris* also breeds in the eastern skunk cabbage, *Symplocarpus foetidus*. It has been found feeding on decaying grasses and sedges in wetlands (Keiper et al. 2002).

**Modes of reproductive isolation:** Like its close relative *D. palustris*, *D. subpalustris* belongs to a rapidly diversifying clade within the quinaria group. Sears (1947) reports that *D. palustris* and *D. subpalustris* will mate reciprocally and produce viable hybrid progeny, which in turn can produce F2, indicating that both male and female hybrids are fertile. The F2 were also fertile, indicating that there is relatively little hybrid breakdown. See entry under *D. palustris*. 
REFERENCES:


**Drosophila deflecta** males

Body medium-large-sized, thorax faintly striped, abdomen light with 3 rows of black spots on each half

Wing's crossveins and all longitudinal vein tips intensively clouded

**Drosophila deflecta** females

Body medium-large-sized, thorax faintly striped, abdomen light with 3 rows of black spots on each half

Wing's crossveins and all longitudinal vein tips intensively clouded
*Drosophila deflecta* males

*Drosophila deflecta* females
Drosophila deflecta Malloch in Malloch and McAtee 1924

This is a medium- to large-sized species that closely resembles D. subpalustris in wing pigmentation. Males and females look similar. The ground color of the body is yellowish. The abdomen is decorated with 6 rows of black spots. There is no dark dorsal midline pigmentation. The crossveins and vein termination points of the longitudinal veins 2, 3, 4, and 5 are darkly clouded. Similar species: D. quinaria is very similar in body coloration; however, the tip of the longitudinal vein 5 is not clouded, and the shading of the crossveins and wing tips is much more noticeable in D. deflecta. D. palustris and D. subpalustris have a darker abdomen and lack the dorsal-most pair of spot rows. D. guttifera wings show additional spots along longitudinal veins 3 and 5. Tips for collecting and breeding: This species can be attracted with tomato and banana traps. We recommend breeding it on cornmeal-sucrose-yeast medium with additional Baker’s yeast grains or on instant + cucumber food.

Taxonomy: Subgenus Drosophila. Species group quinaria

Distribution: This species is widely distributed in the eastern United States, but there are few records of it, having been found in Michigan, Illinois, New Jersey, the District of Columbia, and Florida (Malloch and McAtee 1924; Global Biodiversity Information Facility 2016).

Breeding sites: Keiper et al. (2002) report that larvae of D. deflecta feed on the decaying leaves of yellow water lilies (identified as Nuphar lutea; B. A. Foote, pers. comm.). In New Jersey, it was also found on water lily (probably Nuphar lutea subsp. variegata; J. A. Wilder, pers. comm.). Miller et al. (2017) report that D. deflecta also breeds in decaying arrowhead (Sagittaria).

Modes of reproductive isolation: Although D. deflecta belongs to a rapidly diversifying clade within the quinaria group (Perlman et al. 2003), we are not aware of any studies of mechanisms of reproductive isolation from closely related, sympatric species, such as D. palustris.

REFERENCES:


**Drosophila quinaria**

**Drosophila quinaria males**
Body medium- to large-sized, abdomen on each side with 3 rows of spots, dorsal midline light

Wing’s crossveins and longitudinal vein tips clouded, *except longitudinal vein 5* (arrow)

**Drosophila quinaria females**
Body medium- to large-sized, abdomen on each side with 3 rows of spots, dorsal midline light

Wing’s crossveins and longitudinal vein tips clouded, *except longitudinal vein 5* (arrow)
Drosophila quinaria males

Drosophila quinaria females
**Drosophila quinaria Loew 1866**

This is a medium- to large-sized species. Males and females look similar. The ground color of the thorax is darker than that of the abdomen. The abdomen shows 6 rows of spots and a light dorsal midline. The crossveins and vein termination points of the longitudinal veins 2, 3, and 4, but not 5, are clouded. Similar species: In *D. deflecta*, the longitudinal veins 2, 3, 4, and 5 are clouded, with stronger clouding than in *D. quinaria*. The tips of the wing veins are not clouded in *D. recens* and *D. falleni*, and *D. falleni* has only 4 rows of abdominal spots. At first glance, *D. tripunctata* resembles *D. quinaria* in terms of wing spotting and general size and coloration, but its abdominal spotting pattern is completely different. Tips for collecting and breeding: This species visits tomato and banana traps. It can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast and on instant + cucumber food.

**Taxonomy:** Subgenus Drosophila. Species group quinaria


**Breeding sites:** While most members of the quinaria group are mycophagous, *D. quinaria* and few close relatives (e.g., *D. palustris* and *D. magnaquinaria*) breed on skunk cabbages. *D. quinaria* breeds on the Eastern Skunk Cabbage (*Symplocarpus foetidus*) (Brown 1956; Jaenike 1978; Grimaldi and Jaenike 1983), which occupies swampy areas in the Northeast. In a large mesh-enclosed cage in a greenhouse, we maintained *D. quinaria* for many generations exclusively on *Amanita muscaria* mushrooms placed among small spruce trees, with no skunk cabbages present. This suggests that the specialization on skunk cabbage is due host selection behavior by the flies, rather than the unsuitability of mushrooms for larval development. Quantification of larval survival, development time, and resulting adult body size in lab culture show that *Agaricus* mushrooms appear to be just as suitable as skunk cabbage as a larval breeding site (James et al. 1988). Although mushrooms appear to be suitable for larval development, *D. quinaria* essentially never uses them as breeding sites in nature (Jaenike 1985). Perhaps this is due to competition with the guild of existing mycophagous species, of which there are at least five in Northeast (Grimaldi and Jaenike 1984). *D. quinaria* is somewhat larger than sympatric species of mycophagous *Drosophila*, which might result in its having a
longer development time (Roff 1983), something that could be disadvantageous in competition for a rapidly disappearing resource. Because mycophagy is the most likely ancestral state within the quinaria group, it is likely that *D. quinaria* itself is descended from a mycophagous ancestor, and this might explain why it can breed successfully on mushrooms. However, unlike mycophagous members of the quinaria group, *D. quinaria* is highly sensitive to the mushroom toxin α-amanitin (Spicer and Jaenike 1996). Interestingly, most mycophagous species of *Drosophila* in the Northeast occasionally breed in skunk cabbages (Jaenike, pers. obs.).

**Modes of reproductive isolation:** Sears (1947) reported that *D. quinaria* would very reluctantly mate with *D. subquinaria* in mass culture and that the offspring were sterile. Sears did not observe any matings between *D. quinaria* and eight other species of the quinaria group. Werren and Jaenike (1995) observed mating between *D. quinaria* and *D. recens* (which is very closely related to *D. subquinaria*), but no larvae were produced from any of the interspecific matings, indicating that *quinaria-recens* hybrids suffer from hybrid inviability or a post-mating pre-zygotic incompatibility. Thus, it is not known if *D. quinaria* can exchange genes with any other extant *Drosophila* species, although *D. magnaquinaria*, which breeds on yellow skunk cabbage (*Lysichitum americanum*) in the Pacific Northwest (Kibota and Courtney 1991), might be a possibility.

**Sex-ratio meiotic drive:** *D. quinaria* is polymorphic for X chromosome drive, with SR males siring 95% - 100% female offspring (Jaenike 1996). The frequency of the driving X<sup>SR</sup> chromosome is low across three populations sampled: 3% in Rochester, NY and 6% in Deer Isle, Maine and in Pymatuning, Pennsylvania. SR males exhibit reduced fertility when there are opportunities for multiple mating, and subsequent work has shown that this might be a general mechanism by which the spread of driving XSR chromosomes is held in check (Price *et al.* 2008). *D. quinaria* is also polymorphic for Y chromosome suppression of X-drive, as indicated by variation in offspring sex ratio of SR males carrying different Y chromosomes (Jaenike 1999).

**Puzzling lack of nematode parasitism:** We have never found a nematode-parasitized individual of *D. quinaria*. Nevertheless, it is readily parasitized by *Howardula aoronymphium* in laboratory culture (Perlman and Jaenike 2003). To test whether nematode parasitism is prevented by exposure of infective-stage nematodes to skunk cabbage tissue - a potentially toxic, oxalate-rich environment (in Jaenike and Perlman 2002) released nematode-infected *D. quinaria* into mesh cages enclosing undisturbed skunk cabbages in the field. Dissection of the flies emerging from the skunk cabbages revealed that several of them were parasitized, indicating that the skunk cabbage breeding site is not an insurmountable barrier to nematode parasitism. Because *D. quinaria* is a rare species, it perhaps does not attain sufficient population densities to sustain a population of nematodes (Jaenike and Perlman 2002).

**Pathogens:** *D. quinaria* had the lowest rate of trypanosomatid infection (1%) among eight species of *Drosophila* sampled from natural populations in Ohio, but it had the third highest rate of infection (4%) by the fungal pathogen *Coccidiascus legeri* (Ebbert *et al.* 2001, 2003).

**Endosymbionts:** *D. quinaria* was initially thought to lack *Wolbachia* (Werren and Jaenike 1995). However, subsequent studies of this species in western Pennsylvania showed that a small
fraction of flies do carry Wolbachia. Remarkably, the Wolbachia-infected flies carry mitochondrial haplotypes belonging to a clade distantly related to the mitochondria carried by uninfected flies. In fact, the mitochondria in the Wolbachia-infected D. quinaria fall outside a clade that includes the mitochondrial haplotypes of D. subquinaria, D. recens, Wolbachia-uninfected D. quinaria, and several other species (Dyer et al. 2011). Nuclear genes show no differentiation between the Wolbachia-infected and uninfected individuals of D. quinaria, indicating that they freely interbreed and are members of the same biological species. The mitochondria of the Wolbachia-infected flies are not closely related to that of any known Drosophila species. Dyer et al. (2011) hypothesized that these unusual mitochondria were derived from a species that is now extinct. The presence of Wolbachia in this putatively extinct species may have helped drive the associated mtDNA into D. quinaria. It is not known how the Wolbachia is currently maintained.

Behavior: Among 11 species of Drosophila assayed for patterns of daily activity in the laboratory, D. quinaria shows a higher level of midday activity than any of the others (Simunovic and Jaenike 2006). This could be because D. quinaria occurs in wet swampy areas, where there is likely to be little desiccation stress, which is typically greatest in the middle of the day in most terrestrial habitats. D. palustris, another skunk cabbage-breeding species, had the second highest level of midday activity.

Genetic population structure: D. quinaria exhibits greater genetic differentiation among local populations than do the mycophagous species D. falleni and D. recens (Shoemaker and Jaenike 1997). This is likely due to the structure of suitable habitat for these species: the skunk cabbage breeding sites of D. quinaria are patchily distributed, whereas mushrooms, the breeding sites of D. falleni and D. recens, are continuously distributed wherever woods and forests occur.

REFERENCES:


**Drosophila recens**

**Drosophila recens males**
- 2nd oral bristle (arrow head) more than 1/2 as long as 1st (arrow)
- Male genitalia (arrows point to margin of the shelf of the hypandrium)
- Wing’s anterior and posterior crossveins clouded

**Drosophila recens females**
- 2nd oral bristle (arrow head) more than 1/2 as long as 1st (arrow)
- Body medium-sized and spotted/striped, lateral spot row (arrow) exists
- Wing’s anterior and posterior crossveins clouded
Drosophila recens males

Drosophila recens females
**Drosophila recens**
Wheeler 1960

This is a medium-sized species. Males and females look similar. The ground color is usually a light orange-brown, but varies from yellowish to tan. The abdomen has three pairs of abdominal spot rows, which can be fused into stripes that are interrupted at the dorsal midline. Both crossveins of the wings are clouded. The second oral bristle is at least half as long as the first oral bristle. Similar species: *D. subquinaria* looks very similar to *D. recens*, but it has a more western distribution and is very rare in our region. Only the male genitalia can be used to reliably distinguish *D. recens* from *D. subquinaria*: the shelf of the hypandrium looks like a hummock in profile in *D. recens*, while it has two outward pointing horns in *D. subquinaria*. Other similar species are *D. falleni*, which lacks the lateral abdominal spot row and whose second oral bristle is less than half as long as the first. *D. neotestacea* and *D. putrida* have pre-sutural bristles on the thorax (lacking in *D. recens*) and convergent or parallel anterior scutellar bristles, these being divergent in *D. recens*. Tips for collecting and breeding: *D. recens* is attracted to mushroom or tomato traps, and is likely to be more common in the northern areas covered by this guide. This species can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast, or on instant + mushroom food.

**Taxonomy:** Subgenus Drosophila. Species group quinaria

**Distribution:** In the eastern United States, *D. recens* can be found from Maine in the Northeast westward to North Dakota and southward to the higher elevations of the Smoky Mountains in Tennessee (Wheeler 1960; Lacy 1982; Jaenike *et al.* 2006). In Canada, the range of this species extends from the Maritime provinces across the vast expanse of boreal forest to Alberta in the west (Jaenike *et al.* 2006).

**Breeding sites:** *D. recens* is primarily mycophagous, preferring, like *D. falleni*, fresher mushrooms than do members of the testacea group (Grimaldi 1985). *D. recens* also breeds, occasionally in considerable numbers, in the eastern skunk cabbage, *Symlocarpus foetidus*, making it less dependent on mushrooms than other mycophagous drosophilids in this region (Grimaldi and Jaenike 1983). This is perhaps not too surprising, as *D. recens* belongs to a clade that includes *D. quinaria* and *D. palustris*, for which skunk cabbage is a major breeding site.

**Modes of reproductive isolation:** Within the quinaria species group, *D. recens* belongs to a rapidly diversifying clade that includes *D. transversa*, *D. subquinaria*, *D. occidentalis*, *D. suboccidentalis*, *D. munda*, and *D. tenebrosa* (Perlman *et al.* 2003; van der Linde *et al.* 2010; Dyer *et al.* 2011; Izumitani *et al.* 2016). *D. recens* is broadly sympatric with *D. subquinaria* across
much of central Canada, and thus most studies have focused on mechanisms of reproductive isolation between these two species. At least three major mechanisms, in combination, contribute to reproductive isolation between them. First, there is strong asymmetrical behavioral isolation in areas where they are sympatric, with females of *D. subquinaria* being much more discriminating than *D. recens* females against heterospecific males (Jaenike et al. 2006). Males of *D. recens* and *D. subquinaria* differ substantially in elements of their courtship; *D. recens* males more actively engage in physical contact with females (licking and tapping), whereas *D. subquinaria* males engage more in behaviors that can be effective at a distance (circling, wing extensions, and wing vibrations) (Giglio and Dyer 2010). Through a series of experimental manipulations, Giglio and Dyer (2010) showed that females of *D. recens* rely on visual and olfactory cues for mating. In *D. subquinaria* from areas where they are sympatric with *D. recens*, females rely on olfactory cues and cues originating from a male’s wings. Females whose antennae had been removed never mated, showing an absolute dependence on olfactory cues for mating (Giglio and Dyer 2010). In a follow-up study of the olfactory cues, Curtis et al. (2013) showed that the females prefer males with specific pheromonal blends of epicuticular hydrocarbons, and that the preferred blend differs between the two species.

Second, matings between *D. recens* males (the vast majority of which are infected with *Wolbachia*) and *D. subquinaria* females (which are not infected with *Wolbachia*) result in the production of very few offspring, a result of interspecific cytoplasmic incompatibility (Shoemaker et al. 1999; Jaenike et al. 2006). We have speculated that the strong interspecific CI in this direction of the cross has selected for increased levels of discrimination by *D. subquinaria* females in areas where the two species are sympatric, as in central Canada. Interestingly, females of *D. subquinaria* from allopatric populations farther west exhibit little discrimination against *D. recens* males in laboratory assays (Jaenike et al. 2006).

Finally, hybrid males in both directions are sterile, whereas hybrid females are fertile, in accordance with Haldane’s rule (Shoemaker et al. 1999).

Despite the various mechanisms of reproductive isolation, there has been, at least historically, some gene flow between *D. recens* and *D. subquinaria*, as several individuals of *D. subquinaria* have been found carrying mtDNA haplotypes characteristic of *D. recens* (Jaenike et al. 2006).

**Sex-ratio meiotic drive:**

*D. recens* is polymorphic for X chromosome drive; males carrying the driving X<sub>SR</sub> chromosome sire 95% - 100% female offspring (Jaenike 1996). Across the range of this species, the frequency of X<sub>SR</sub> is about 3%, with no significant variation among populations (Dyer et al. 2007).

In a laboratory assay, SR and ST males did not sire significantly different numbers of offspring in their initial matings, but ST males sired nearly 3 times as many offspring in subsequent matings over the next 24 hours (*P* < 0.001), suggesting that male fertility may play a role in checking the spread of X<sub>SR</sub>, which, if left unchecked, could cause the extinction of a species (Jaenike 1996).

The X<sub>SR</sub> chromosome exhibits chromosome-wide linkage disequilibrium in comparison to the standard X<sub>ST</sub> chromosome (Dyer et al. 2007). The two chromosome types differ by a complex set of inversions, suppressing recombination between them. Furthermore, X<sub>SR</sub> / X<sub>SR</sub> females

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1 For terminology, see footnote for *D. affinis.*
are completely sterile. Consequently, X<sup>S</sup>R chromosomes cannot combine with either X<sup>S</sup>T or other X<sup>S</sup>R chromosomes, and thus are susceptible to accumulation of slightly deleterious mutations. The X<sup>S</sup>R chromosome in D. recens might currently be undergoing mutational meltdown and could ultimately be lost from the species.

**Nematode parasitism:** D. recens is one of four host species for Howardula aoronymphium in the Northeast and Midwest. The impact of this nematode on populations of D. recens is mild, because fewer than 5% of D. recens are parasitized by H. aoronymphium, and those that are parasitized suffer little reduction in potential fecundity, as measured by the number of mature eggs per ovariole (Jaenike 2002; Perlman and Jaenike 2003).

Parasitylenchus nearcticus is a parasitic nematode that specializes on D. recens and at least one very close relative, D. suboccidentalis (Poinar *et al.* 1997; Jaenike, unpublished). In D. recens, P. nearcticus has been found in the Adirondack Mountains in New York (Poinar *et al.* 1997), South Dakota, and Alberta (Jaenike, unpublished), where the prevalence of parasitism was 5% - 10%. Several individuals of D. suboccidentalis collected in Jasper National Park, Alberta were also found to be parasitized by P. nearcticus (Jaenike, unpublished). In the laboratory, this nematode is capable of infecting several other species of Drosophila, including the Eurasian species D. transversa, D. testacea, and D. limbata, and the western North American D. occidentalis, but none of these has yet been found to be parasitized by P. nearcticus in the wild (Perlman and Jaenike 2003). The impact of P. nearcticus on parasitized flies is severe, as females of D. recens (and closely related species) are rendered virtually sterile by these nematodes (Perlman and Jaenike 2003). Thus, D. recens is much more resistant to H. aoronymphium than P. nearcticus.

Grimaldi and Jaenike (1984) reared the following parasitoid wasps from mushrooms that yielded D. falleni, D. recens, D. putrida, and/or D. neotestacea: two species of Aspilota, one species of Phaenocarpa, and two species of Kleidotoma. The parasitoids were not matched to individual Drosophila species, and the ratio of emerging Drosophila to wasps was over 100:1.

**Endosymbionts:** D. recens is infected at high frequency (~98%) by maternally transmitted Wolbachia (Shoemaker *et al.* 1999, 2004). This strain of Wolbachia causes strong cytoplasmic incompatibility (CI) within D. recens, brought about by matings between infected males and uninfected females (Werren and Jaenike 1995). In addition, it causes a high level of interspecific CI in crosses between males of D. recens and females of D. subquinaria, a species in which Wolbachia is absent or very rare. This interspecific CI contributes to reproductive isolation between these species (Shoemaker *et al.* 1999; Jaenike *et al.* 2006).

Adaptation by Wolbachia following colonization of new host species involves substitutions of beneficial mutations in Wolbachia’s genome. However, because Wolbachia are strictly maternally transmitted within a species, the spread of a favored new Wolbachia mutation will drag along whatever mitochondrial haplotype it happens to be associated with, as a form of cytoplasmic hitchhiking. Consequently, the mtDNA within a host species can experience a series of severe bottlenecks as a result of adaptive evolution by Wolbachia within that host. This can result in reduced mitochondrial diversity, as has been found in D. recens in comparison with its Wolbachia-free sister species D. subquinaria (Shoemaker *et al.*
In addition, the mtDNA of D. recens appears to have experienced a greater rate of nucleotide substitution (as measured by both $d_{N}/d_{S}$ and $d_{S}$) than D. subquinaria, suggesting that purifying selection against deleterious mitochondrial mutations is less effective in D. recens (Shoemaker et al. 2004). This is consistent with the idea that adaptive substitutions in Wolbachia can drag along slightly deleterious mutations in the mtDNA of D. recens.

**Population structure:** Populations of D. recens show little genetic differentiation across the range of this species, except for a population at the very southern tip of its range in the Great Smoky Mountains (Shoemaker and Jaenike 1997; Jaenike et al. 2006). The low level of differentiation is probably due to the essentially continuous distribution of suitable habitat (woods and forests) for this species.

**REFERENCES:**


Habitat continuity and the genetic structure 
of *Drosophila* populations. *Evolution* 51: 
1326-1332.

*Wolbachia* and the evolution of reproductive 
isolation between *Drosophila recens* and 
*Drosophila subquinaria*. *Evolution* 53: 
1157-1164.

McAbee, and J. Jaenike. 2004. Molecular 
evolutionary effects of *Wolbachia* infections: 
decreased diversity but increased substitution 
rate in host mtDNA. *Genetics* 168: 2049-2058.

van der Linde, K., Houle, D., Spicer, G.S. 
and Steppan, S.J. 2010. A supermatrix-
based molecular phylogeny of the family 

and cytoplasmic incompatibility in 
mycophagous *Drosophila* and their relatives. 
*Heredity* 75: 320-326.

quinarria group of *Drosophila* (Diptera, 
**Drosophila subquinaria**

**Drosophila subquinaria males**

- 2nd oral bristle (arrow head) more than 1/2 as long as 1st (arrow)
- Male genitalia (arrows point to the horns of the margin of hypandrial shelf)
- Body medium-sized, abdomen spotted/striped, lateral spot row (arrow) exists
- Wing’s anterior and posterior crossveins clouded

**Drosophila subquinaria females**

- 2nd oral bristle (arrow head) more than 1/2 as long as 1st (arrow)
- Body medium-sized, abdomen spotted/striped, lateral spot row (arrow) exists
- Wing’s anterior and posterior crossveins clouded
This is a medium-sized western species. Males and females look similar. The ground color is usually a light orange-brown, but varies from yellowish to tan. Each abdominal segment has three spots on each side, which can be fused. Both crossveins of the wings are clouded. The second oral bristle is at least half as long as the first oral bristle. Similar species: D. recens looks very similar to D. subquinaria. D. recens is a more eastern species, although their ranges overlap across central Canada. Only the male genitalia can be used to reliably distinguish D. recens from D. subquinaria: the shelf of the hypandrium looks like a hummock in profile in D. recens, while it has two outward pointing horns in D. subquinaria.

Other similar species are D. falleni, which lacks the lateral abdominal spot row and whose second oral bristle is less than half as long as the first one. D. neotestacea and D. putrida, both of which have pre-sutural bristles on the thorax and lack noticeably clouded crossveins on the wings. D. subquinaria, being mycophagous, can be collected at mushroom baits. This species can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast or instant + mushroom food.

Taxonomy: Subgenus Drosophila. Species group quinaria

Distribution: D. subquinaria is broadly distributed in boreal forest regions of western North America, from Alaska south to British Columbia, Oregon, Colorado, Wyoming, and Utah, and eastward as far as Sault St. Marie, Ontario (Spencer 1942, Wheeler 1960; Jaenike et al. 2006). Although D. subquinaria is a western species, it overlaps across a broad swath of central Canada, from Alberta to Ontario, with its eastern counterpart, D. recens. The most reliable way to distinguish the two species is by examination of the male genitalia (see figures in Wheeler 1960).

Breeding sites: As for many other members of the quinaria group, mushrooms are an important breeding site for D. subquinaria (Heard 1998). However, D. subquinaria is closely related to D. recens, which utilizes not only mushrooms, but also, to a lesser extent, decaying eastern skunk cabbages (Symplocarpus foetidus). It would therefore be worth determining whether D. subquinaria occasionally breeds in the species of skunk cabbage, Lysichiton americanus, found in the western part of D. subquinaria’s range.

Modes of reproductive isolation: The species, with which D. subquinaria is most likely to hybridize is D. recens, as the two co-occur across much of central Canada. The two species form fertile hybrid female progeny in the lab, and there is evidence of past introgression of mtDNA from D. recens into D. subquinaria (Jaenike et al. 2006). At least three isolating mechanisms serve to reduce possible
gene flow between these species (Shoemaker et al. 1999; Jaenike et al. 2006). First, females of *D. subquinaria* from populations that are sympatric with *D. recens* strongly discriminate against *D. recens* males. However, females of *D. recens* from these areas are far less discriminating against *D. subquinaria* males. Second, *D. recens* is infected at very high frequency with *Wolbachia* that causes cytoplasmic incompatibility (CI) that acts not only within *D. recens* itself but also in crosses between infected *D. recens* males and *D. subquinaria* females, which do not carry *Wolbachia*. Finally, hybrid males, but not females, are sterile in both directions of an interspecific cross.

The three modes of reproductive isolation are expected to combine in an interesting way to limit gene flow between these species (Jaenike et al. 2006). Because of the strong asymmetry in behavioral isolation, matings are most likely to occur between *D. recens* females and *D. subquinaria* males. The vast majority of *D. recens* are infected with *Wolbachia*, so a large fraction of hybrid progeny will also be infected. Unless the *Wolbachia* infection is lost, backcrosses to *D. subquinaria* will result in *Wolbachia*-infected male offspring that in mating with uninfected *D. subquinaria* females will trigger CI and thus terminate introgression of nuclear genes into *D. subquinaria*. A comparable problem does not arise in backcrosses of *Wolbachia*-infected hybrids to *D. recens*, as a pure *D. recens* female, with which a mixed-ancestry male might mate, is very likely to be infected with *Wolbachia*; thus, their progeny will not die as a result of CI. We therefore predict that introgression of nuclear genes will be asymmetric, with greater gene flow from *D. subquinaria* to *D. recens*.

*D. subquinaria* exhibits a very strong pattern of reinforcement, as females that are sympatric with *D. recens* are far more discriminating against *D. recens* males than are females from regions where *D. recens* does not occur (Jaenike et al. 2006; Bewick and Dyer 2014). Furthermore, females of *D. subquinaria* from populations that are sympatric with *D. recens* also discriminate against males of their own species from populations, where *D. recens* does not occur. This pattern has been attributed to the process of cascade reinforcement, in which the evolution of reproductive isolation (reinforcement) between *D. subquinaria* and *D. recens* initiates the evolution of reproductive isolation among populations of *D. subquinaria* (Jaenike et al. 2006; Bewick and Dyer 2014; Rundle and Dyer 2015). In *D. subquinaria*, olfactory cues from males are very important for females to mate (Giglio and Dyer 2013), and differences among populations of *D. subquinaria* in their cuticular hydrocarbons are consistent with patterns of mating preferences of females in these populations (Dyer et al. 2014; Rundle and Dyer 2015). Thus, *D. subquinaria* appears to be in the early stages of divergence into incipient species, even though there is no obvious postzygotic isolation among flies from different populations.

**Sex-ratio meiotic drive:** X-drive has not been found in *D. subquinaria*. However, it is present in *D. recens*, a species with which *D. subquinaria* can hybridize, both in the lab and in natural populations (Jaenike 1996). If a driving X chromosome from *D. recens* could be introgressed into *D. subquinaria*, one could examine whether drive is expressed against a different Y chromosome and in a different autosomal background.

**Nematode parasitism:** We have collected individuals of *D. subquinaria* parasitized by the generalist nematode *Howardula aoronymphium* at several sites in Alberta. Although the very closely related *D. recens* can be parasitized in nature with
the nematode *Parasylrenchus nearcticus*, we have not found any individuals of *D. subquinaria* parasitized by this species. In a controlled laboratory study of nematode parasitism, we found that *D. recens* carries an average of 25 times as many *P. nearcticus* as does *D. subquinaria*. Thus, *D. subquinaria* is far more resistant to *P. nearcticus* than is *D. recens*. This resistance is nematode-species-specific, as *D. subquinaria* is slightly more susceptible than *D. recens* to parasitism by *H. aoronymphium* (Perlman and Jaenike 2003). *D. recens* could conceivably evolve resistance to *P. nearcticus* via introgression of the appropriate genes from *D. subquinaria* genes in the region, where the two *Drosophila* species, as well as *P. nearcticus*, are sympatric in central Canada.

**Endosymbionts:** Although *D. subquinaria* does not carry any heritable endosymbionts, as far as is known, it could obtain *Wolbachia* from *D. recens* (in which it causes strong cytoplasmic incompatibility) via hybridization between a *Wolbachia*-infected female of *D. recens* and a *D. subquinaria* male. Through subsequent backcrossing of the hybrid females to *D. subquinaria* males, *Wolbachia* could be introgressed into *D. subquinaria*. This appears to have happened in the past, as a small fraction of *D. subquinaria* individuals carry mitochondrial haplotypes characteristic of *D. recens*, evidence of past cytoplasmic introgression (Jaenike et al. 2006). Since *Wolbachia* infects >90% of the individuals in *D. recens*, it is likely that *Wolbachia* accompanied the mtDNA in this introgression event(s). However, this cytoplasmic lineage in *D. subquinaria* does not carry *Wolbachia*, perhaps due to imperfect maternal transmission coupled with insufficient selection to maintain the infection. Surprisingly, if *Wolbachia* from *D. recens* were to spread in populations of *D. subquinaria*, it would cause male killing in coastal, but not central, populations of this species (Jaenike 2007). The *Wolbachia* from *D. recens* does not cause CI in *D. subquinaria*, although it does so in its native host.

**REFERENCES:**


**Drosophila tripunctata**

**Drosophila tripunctata males**

Wing’s anterior and posterior crossveins and the tips of longitudinal veins L2, L3, (arrows) and to some extend L4 (arrow head) clouded

Body medium-sized, three dorsal midline spots on the abdomen

**Drosophila tripunctata females**

Wing’s anterior and posterior crossveins and the tips of longitudinal veins L2, L3, (arrows) and to some extend L4 (arrow head) clouded

Body medium-sized, three dorsal midline spots on the abdomen
Drosophila tripunctata males

Drosophila tripunctata females
The tripunctata group is one of the most diverse species groups of Drosophila. Diversity is greatest in the Neotropics (Robe et al. 2010), with only D. tripunctata having colonized the United States and Canada.

**Distribution and range expansion:** D. tripunctata is widespread in eastern North America from Texas to Florida in the south northwards to the Upper Midwest and Northeast. This species has been expanding its range northward in recent decades. According to the range map in Patterson and Wagner (1943), the northern limit of D. tripunctata’s range did not extend beyond 40°N latitude. Since then, Spiess (1949) collected three individuals in Cambridge, Massachusetts, and Lacy (1984) bred a total of 42 from mushrooms collected around Ithaca, New York (both sites at ~42.4°N). In recent years, D. tripunctata has been one of the most abundant species in late summer in Rochester, NY (43.2°N), and we have collected several individuals of this species in the Upper Peninsula of Michigan (47°N) and one in Wawa, Ontario (48.0°N). This represents a ~900 km northward expansion of the range of D. tripunctata in recent decades. Because this species is so easy to identify, it is unlikely to have been overlooked by earlier Drosophila researchers. It seems plausible to us that the expansion could be due to anthropogenic climate change.

D. tripunctata was found for the first time in Europe in 2012. The individuals were collected in a botanical garden greenhouse in Prague, but there is concern that it could spread to become a pest in Europe (Máca et al. 2015). Brake and Bächli (2008) report that D. tripunctata has also been found in Columbia and Brazil. The facts that: 1) the tripunctata group is Neotropical in origin, 2) D. tripunctata is the only member of this group found in the United States and Canada,
3) it has also been found in South America, 4) it has recently colonized Europe, and 5) it has been rapidly expanding its range northwards in recent years, suggest that *D. tripunctata* may have colonized North America in recent times. A molecular phylogenetic comparison of North and South American populations of this species could resolve this question. 

**Breeding sites:** *D. tripunctata* is unusual among *Drosophila* in that it commonly breeds in both fruits (*e.g.*, mayapples and tomatoes) and numerous species of mushrooms (Carson and Stalker 1951; Collins 1956; Lacy 1984). Among the mushrooms, it utilizes as breeding sites is *Amanita bisporigera*, a deadly poisonous species that contains α-amanitin (Lacy 1984). It is likely that such toxic mushrooms are a regular part of the diet of *D. tripunctata*, as laboratory studies show that this species exhibits a high level of resistance to α-amanitin (Jaenike et al. 1983; Stump et al. 2011).

*D. tripunctata* harbors substantial genetic variation in its preference for mushrooms versus fruits as feeding and breeding sites (Jaenike and Grimaldi 1983). Two strains, both of which were established from single females collected in the Great Smoky Mountains, exhibited distinct preferences when released in the wild and then recaptured at mushroom versus tomato baits (Jaenike 1986). For one strain, 74% of recaptured flies (*n* = 387) were collected at mushrooms, while for the other strain, only 18% (*n* = 303) were collected at mushrooms. The two strains had been crossed to yield F2 flies, which were released and recaptured simultaneously with the two parental strains, and 51% of these (*n* = 750) were collected at mushrooms. Such genetic variation in preference may enable this species to respond rapidly to changing availabilities of different resource types. 

**Modes of reproductive isolation:** This has not been studied. According to published molecular phylogenies (Hatadani et al. 2009; Robe et al. 2010), *D. tripunctata* has no close relatives among species studied. 

**Sex-ratio meiotic drive:** Over the course of several years of work on numerous isofemale strains of *D. tripunctata*, we have never found distorted offspring sex ratios, suggesting that *D. tripunctata* is not polymorphic for X-linked meiotic drive. However, a related species in the tripunctata group, *D. mediopunctata*, is polymorphic for both X chromosome drive (resulting in female-biased offspring sex ratios) and autosomal and Y-linked suppression of drive (Carvalho and Klaczko 1993; Carvalho et al. 1997).

**Nematode parasitism:** Although *D. tripunctata* is sympatric with other species of *Drosophila* that can be infected with the host generalist nematode *Howardula aoronymphium*, we have never found a nematode-parasitized individual of *D. tripunctata* among flies collected in New York, Pennsylvania, Virginia, and Tennessee (Jaenike and Perlman 1992). In laboratory experiments, *D. tripunctata* is highly, but not completely, resistant to parasitism by *H. aoronymphium* (Perlman and Jaenike 2003). Such resistance to a parasite that can infect and sterilize other species of mycophagous *Drosophila* probably gives *D. tripunctata* a competitive edge in communities where they co-occur.

**Community ecology:** *D. tripunctata* larvae are susceptible to predation by *Aphaenogaster* and *Iridomyrmex* ants at field sites in South Carolina (Lewis and Worthen 1992). A field experiment using ant-exclusion cups showed that ant predation reduced pre-adult survival of these flies from 35 ± 3% to 22 ± 2%.

A variety of other predators, such as toads, staphylinid beetles, and spiders, are commonly
seen on or near mushrooms in the field. To our knowledge, no one has quantified the effects of predators other than ants on either adult or pre-adult survival in the field. The skittishness of some species of *Drosophila* certainly suggests that they are wary of predators.

**Physiological ecology:** As assayed in the laboratory, the temperature preference of *D. tripunctata* adults is affected by both genetic and environmental variation (McDaniel et al. 1995). The longer a line has been kept in the lab at 20°C, the greater its preferred temperature, varying from 18.8°C in a strain derived from recently collected flies to 20.3°C in a strain that had been kept in the lab for 7 years. This suggests an adaptive evolutionary response to laboratory culture and could be relevant to the ongoing range expansion of this species. In addition, *D. tripunctata* exhibits an acclimation response for temperature preference, as the preference of recently collected flies increased from 18.8°C to 20.5°C after a two-day acclimation period at 26°C prior to testing (McDaniel et al. 1995).

There is also an acclimation effect on the critical thermal maximum (CTMax) of *D. tripunctata*, where CTMax is defined as the temperature at which half of the flies are unable to right themselves. Flies that had acclimated for five days at 15°C had a significantly lower CTMax than did flies acclimated at higher temperatures (Worthen and Haney 1999). If such acclimatization occurs in the wild, it could facilitate greater survival at high temperature, thereby facilitating evolutionary changes in temperature tolerance and preference (a physiological Baldwin effect; Crispo 2007).

**REFERENCES:**


Sci USA 83: 2148-2151.
**Mycodrosophila dimidiata**

**Mycodrosophila dimidiata males**
Body small-medium sized, thorax shiny dark brown, abdomen high in contrast (almost black and white in appearance). The abdominal bands are **interrupted** by the midline (arrow). Spot on 5th segment is often isolated (arrow head).

Wings uniformly light tan, **black marking at costal vein break** (arrow)

**Mycodrosophila dimidiata females**
Body small-medium sized, thorax shiny dark brown, abdomen high in contrast (almost black and white in appearance). The abdominal bands are **interrupted** by the midline (arrow). Spot on 5th segment is often isolated (arrow head).

Wings uniformly light tan, **black marking at costal vein break** (arrow)
**Mycodrosophila dimidiata**
(Loew 1862)

This small-sized species lives on shelf mushrooms. Males and females look similar. The thorax is shiny dark brown. The abdomen appears almost white with black stripes and spots. The stripe on the 4th abdominal segment does not cross the dorsal midline, and the spot on the 5th abdominal segment is often isolated. Similar species: *Mycodrosophila stalkeri* is very similar, but the spot on the 5th abdominal segment is more connected to the lateral pigmentation bands. *Mycodrosophila claytonae*’s stripe on the 4th abdominal segment crosses the dorsal midline, and the spot on 5th abdominal segment is isolated. Tips for collecting and breeding: Collect flies with an aspirator or net from fresh shelf mushrooms. We recommend rearing this species on cornmeal-sucrose-yeast medium with the addition of a few grains of Baker’s yeast and a piece of fresh white bottom mushroom inserted into the food. Later, add a small piece of Kimwipe to provide a pupation site.

**Distribution:** Eastern United States (and probably Canada), from Texas to the Upper Midwest east to Florida and the Northeast (Wheeler and Takada 1963). It is broadly sympatric with the other two species of *Mycodrosophila* known from the United States and Canada, *M. claytonae* and *M. stalkeri*.

**Breeding sites:** Wheeler and Takada (1963) state that all species of *Mycodrosophila* around the world breed primarily in shelflike polypore fungi. However, through extensive breeding records of flies from field-collected mushrooms in Tompkins County, NY and Great Smoky Mountains in Tennessee over the course of several years, Lacy (1984) found that *M. dimidiata* utilizes a much greater diversity of mushroom species as breeding sites, utilizing not only polypores, but also gilled mushrooms and coral, jelly, and cup fungi. In fact, he found that only 13 of 293 individuals bred from fungi were obtained from species of Polyporaceae.

**Modes of reproductive isolation:** Junges et al. (2016) present a COI-based phylogeny showing that *M. dimidiata* and *M. claytonae* are sister species. Given that they are broadly sympatric, there is likely to be behavioral isolation, as well as other barriers to gene flow, between them. However, this has not been studied.
REFERENCES:


**Mycodrosophila claytonae**

**Mycodrosophila claytonae males**

Body small-medium sized, thorax shiny dark brown, abdomen high in contrast (almost black and white in appearance). The abdominal band on the 4th segment continues through the midline (arrow). Isolated spot on 5th segment (arrow head).

**Wings uniformly light tan, black marking at costal vein break (arrow)**

**Mycodrosophila claytonae females**

Body small-medium sized, thorax shiny dark brown, abdomen high in contrast (almost black and white in appearance). The abdominal band on the 4th segment continues through the midline (arrow). Isolated spot on 5th segment (arrow head).

**Wings uniformly light tan, black marking at costal vein break (arrow)**
Mycodrosophila claytonae males

Mycodrosophila claytonae females
This small-sized species lives on shelf mushrooms. Males and females look similar. The thorax is shiny dark brown. The abdomen appears almost white with black stripes and spots. The stripe on the 4th abdominal segment crosses the dorsal midline, and the spot on the 5th abdominal segment is isolated. The 6th tergite has pale regions laterally. The costal index is ~1.7. Similar species: Mycodrosophila stalkeri, which is occasionally found in our region, is very similar, but the spot on the 6th abdominal segment is more connected to the lateral pigmentation bands. The costal index of M. stalkeri is ~2.0. Mycodrosophila dimidiata is similar, but the stripe on the 4th abdominal segment does not cross the dorsal midline. Tips for collecting and breeding: Collect flies with an aspirator from underneath shelf mushrooms (e.g., Ganoderma applanantum after a rain). We recommend rearing this species on cornmeal-sucrose-yeast medium with the addition of a few grains of Baker’s yeast and a piece of fresh white bottom mushroom inserted into the food. Later, add a small piece of Kimwipe for the larvae to form pupae.


Taxonomy: Electrophoretic evidence indicates that M. claytonae consists of two species, which have been referred to as M. claytonae A and M. claytonae B (Lacy 1982). Both species are known to occur in both New York and Tennessee, where they use similar types of mushroom breeding sites (Lacy 1984).

Distribution: Eastern United States and Canada, from Florida and the Northeast west to the Rocky Mountains (Wheeler and Takada 1963). M. claytonae is broadly sympatric with the other two species of Mycodrosophila known from the United States and Canada, M. dimidiata and M. stalkeri.

Breeding sites: Like most species of Mycopdrosophila other than M. dimidiata, M. claytonae shows a similar pattern of specialization on polypores, with over 90% individuals bred from fungi collected in New York and Tennessee having developed on various species of Polyporaceae (Lacy 1984). This relative specialization stands in contrast to the generalization exhibited by mycophagous species that utilize more ephemeral
mushroom species (Lacy 1984).

**Modes of reproductive isolation:** Given that there are two morphologically similar or identical species of *M. claytonae* (A and B) that are sympatric, there must be some kind of reproductive barrier between them, but this has not been studied.

**REFERENCES:**


Mycodrosophila stalkeri

THIS FRUIT FLY HAS A BUG ON HIS FACE
(HE OBVIOUSLY LOVES BUGS!)

PLACEHOLDER - NO IMAGE AVAILABLE
THESE TWO FRUIT FLIES JUST LOVE THEIR LITTLE BABY
Mycodrosophila stalkeri
Sturtevant 1969

Distribution: *M. stalkeri* is widely distributed in the eastern United States and southern Canada, being found from Florida to Texas across the south and northwards to Ohio and southern Ontario (Wheeler and Takada 1963).

Breeding sites: We are unaware of breeding site records for this species, although, like other species of *Mycodrosophila*, it is likely to utilize bracket fungi.

Modes of reproductive isolation: *M. stalkeri* is broadly sympatric with *M. claytonae* and *M. dimidiata*, suggesting that they may come into contact regularly at their breeding sites. However, Wheeler and Takada (1963) note that *M. stalkeri* is easier to raise in the lab than are the other two species, suggesting that it may use somewhat different breeding sites.

**REFERENCES:**


*M. stalkeri* is very similar in appearance to *M. claytonae*. Wheeler and Takada (1963), who described both species, note that the 6th tergite is mostly black of *M. stalkeri*, but has pale regions laterally in *M. claytonae*:

They also state that the costal index is 2.0 in *M. stalkeri* and 1.7 in *M. claytonae*.
Zaprionus indianus

Zaprionus indianus males

Body medium-sized, thorax tan with four white stripes, which are framed in black, abdomen yellow

Wings nearly unpigmented

Zaprionus indianus females

Body medium-sized, thorax tan with four white stripes, which are framed in black, abdomen yellow

Wings nearly unpigmented
Zaprionus indianus males

Zaprionus indianus females
This is a medium-sized species. Both sexes have four white stripes with black borders on the thorax. The two dorsal stripes extend to the head. The abdomen is yellow or tan. Similar species: *Z. ghesquierei* has an additional white spot at the tip of the scutellum and between the antennae, but it does not occur in our region. Tips for collecting and breeding: *Z. indianus* is attracted to banana traps. This species can be reared on cornmeal-sucrose-yeast medium with a few grains of Baker’s yeast.

**Taxonomy:** Subgenus Zaprionus. Species group armatus

A molecular phylogenetic analysis indicates that the genus *Zaprionus* falls within *Drosophila* (a paraphyletic genus), being most closely related to the genera *Liodrosophila* and *Hypselothyrea* and the *Drosophila repletoides* species group, and fairly close to the *immigrans-tripunctata* radiation within the subgenus Drosophila (Yassin 2013; van der Linde *et al.* 2010). Yassin *et al.* (2008a) have shown that what has been called *Z. indianus* is actually a complex of three species - *Z. indianus* itself, *Z. africanus* (from Uganda), and *Z. gabonicus* (from Gabon) - that differ in subtle aspects in morphology, as well as in being reproductively isolated.

**Distribution:** The genus *Zaprionus* is believed to have arisen relatively recently (~10 million years ago) in the Oriental region and from there to have spread to Africa about 7 million years ago (Yassin *et al.* 2008b). *Z. indianus* itself is native to tropical Africa, where it has apparently undergone more or less continuous population expansion over the past 100,000+ years (Bouiges *et al.* 2013). It has very recently spread to many other parts of the world, being first recorded in the Palearctic region in the late 1980s, the Neotropics (Brazil) in 1998, and Florida in 2005 (Chassagnad and Kraaijeveld 1991; Vilela 1999; van der Linde *et al.* 2006). In our region, it reached Pennsylvania in 2011 and New York, Michigan, and Wisconsin in 2012 (Joshi *et al.* 2014; Van Timmerman and Isaacs 2014; Gibert *et al.* 2016). Molecular data indicate that populations of *Z. indianus* now present in Central America and the United States were derived from South America, with perhaps an additional, independent introduction from elsewhere (Markow *et al.* 2014).

**Breeding sites:** Lachaise and Tsacas (1983) report that *Z. indinaus* utilizes fruits of ~30 families of plants in Africa, suggesting that it is a broad generalist. However, because of past confusion of this species with close relatives (Yassin *et al.* 2008a), some of these records might not be valid for *Z. indianus*. Among its known breeding sites are figs, citrus, guava, banana, apricot, and date palms (Yassin *et al.* 2009). Surprisingly, but perhaps reflective of its being a host generalist, *Z. indianus* has also been bred from wild fungi (*Phallus* sp.) in Brazil (Gottschalk *et al.* 2009).
The common name of *Z. indianus*, the fig fly, reflects one of its more important breeding sites. According to van der Linde *et al.* (2006), most fruit species require some kind of damage before larvae can gain access to food resources. However, the ostiole of figs (the opening by which fig wasps access the interior of a fig) provides an entrance for fly larvae; thus, females of *Z. indianus* lay their eggs near the ostiole. Soon after colonizing Brazil, *Z. indianus* became a major pest of commercial figs there (Gomes *et al.* 2003). In our region, *Z. indianus* has been bred from grapes in Michigan (Van Timmerman and Isaacs 2014) and collected in areas where cherries, grapes, raspberries, or blackberries are grown in Pennsylvania (Joshi *et al.* 2014). Thus, it may have the potential to become a pest of certain fruit crops in our area.

**Modes of reproductive isolation:** Sympatric species of *Zaprionus* differ in their courtship behavior and songs, with males and females having sex-specific songs (Bennet-Clark *et al.* 1980). Muller *et al.* (2012) showed experimentally that wingless males were rejected by females, suggesting that courtship songs were essential for mating. It is likely that the behavioral variation between species contributes to their reproductive isolation, but this has not yet been directly tested. Muller *et al.* (2012) report that if a female *Z. indianus* is receptive, then mating will take place “immediately,” suggesting that elaborate courtship rituals are unimportant. However, males whose wings were experimentally removed were always rejected by females. Males actually have two song types that differ in interpulse interval, one produced prior to copulation and one produced during copulation. Females also produce two types of sound in response to males, one produced in response to a male’s courtship song to signal acceptance, and the other to signal rejection of the male. Most other species of *Zaprionus* that have been studied also have two types of male song and two types of female song (Bennet-Clark *et al.* 1980).

Based on crossing experiments and a molecular phylogenetic analysis, Yassin *et al.* (2008a) conclude that *Z. indianus* comprises two reproductively isolated phylads. They placed groups of virgin females from one phylad together with males of the other for three weeks and then scored the cultures for production of viable offspring. For none of the between-phylad crosses were any offspring produced. However, it is not known if the failure to produce inter-phylad hybrids was due to behavioral isolation, fertilization failure, or hybrid inviability.

**Parasites and pathogens:** Although the natural parasites and pathogens of *Z. indianus* have apparently not yet been studied, Svedese *et al.* (2012) show that two species of entomopathogenic fungi - *Beauveria bassiana* and *Metarhizium anisopliae* - increase both pre-adult and adult mortality of these flies. Thus, these fungi could play a part in biological control programs against *Z. indianus*.

**Physiological ecology:** As an invasive species that has spread to regions far different from those in its native range, *Z. indianus* faces physiological, ecological, and evolutionary challenges. Ecological niche modeling was used to compare the climatic niche of this species in its native range in Africa with that in India and the Americas, which *Z. indianus* has recently colonized (Da Mata *et al.* 2010). The populations in Africa and India experience substantially different environmental conditions, particularly in temperature seasonality, elevation, and minimum temperature of the coldest month of the year. The ecological niches of the
American populations have diverged significantly from those in Africa, but less so than have the Indian populations. The American and African niches differ in mean annual temperature, annual precipitation, and minimum temperature of the coldest month of the year. *Z. indianus* is estimated to have colonized India >30 years prior to arriving in South America (Yassin et al. 2008a), thus giving it more time to adapt to conditions in India. Since the publication of the paper by Da Mata et al. (2010), *Z. indianus* has spread to northern states in the United States (see above). Thus, the ecological niche of the American populations probably continues to diverge from that in Africa. Across a latitudinal gradient in India, Karan et al. (1998) found a negative correlation between desiccation resistance and starvation resistance among populations of *Z. indianus*, as well as among populations of *D. melanogaster* and *D. ananassae*. In all three species, desiccation resistance increased with latitude, which is perhaps not surprising, given the year-round humid conditions in southern India. Starvation resistance, on the other hand, decreased with latitude in each species. These findings indicate that starvation and desiccation resistance are to some degree genetically independent in these species, even though genetic correlations between them are often found in selection experiments. The effect of temperature on egg to adult development in *Z. indianus* from Brazil has been examined by Nava et al. (2007). They find lower temperature thresholds of 9.7°C, 9.2°C, and 10.7°C for development through the egg, larval, and pupal stages, respectively. For a strain collected in a Brazilian tropical forest, male fertility drops precipitously in flies kept at temperatures below 17°C (Araripe et al. 2004). Given the much cooler climates in the recently invaded northern parts of the United States, *Z. indianus* may be under selection to complete development at lower temperatures in our region.

**Racing stripes:** Members of the genus *Zaprionus* have sharp-looking white “racing stripes” extending longitudinally across the head and thorax. Remarkably, these stripes are produced by two completely different mechanisms. In Oriental species of the subgenus Anaprionus, they arise via white pigmentation (Yassin et al. 2010). The stripes of *Z. vittiger* and *Z. indianus*, which are especially striking, are produced by a central stripe of trichomes, which either reflect or refract light, surrounded on each side by dark stripes produced by epidermal pigment granules (Walt and Tobler 1978). The trichomic stripes are found in African species of the subgenus Zaprionus (Yassin et al. 2010).

**Sex-comb like structures:** In *Zaprionus*, males, but not females, possess a brush of bristles on the foreleg that may be homologous to the male-specific sex combs in species of the obscura and melanogaster groups, which are distantly related to *Zaprionus*. Tanaka et al. (2011) show that the development of these male-specific structures may be under similar genetic control in these groups.

**REFERENCES:**


Microdrosophila quadrata

THIS FRUIT FLY IS ABOUT TO TRY A LEMON (STILL SMILING)
THESE FRUIT FLIES ARE IN LOVE
(HOLDING HANDS AND TOMATOES)
This is a very small species, superficially resembling *D. melanogaster*, but smaller. Most bristles on the head are large, including one pair of very large vibrissae. There is a wide brown stripe running along each side of the yellowish thorax, starting at the neck and ending underneath the halteres. The abdomen is brownish, darkest at the posterior edges of each segment. The wings are clear (Sturtevant 1916; Okada 1985). This species rarely visits traps and baits and has not been reared in the laboratory.

**Taxonomy:** Subgenus Microdrosophila

**Distribution:** Eastern Canada and United States, west to Texas (Sturtevant 1916; McAlpine 1981). Of the 59 species of Microdrosophila (Zhang 1989), *M. quadrata* is the only species known from North America. Of the remaining species, a few are known from Europe, Africa, and Australia, with the great majority being known from eastern Asia and Oceania (Okada 1985).

**Breeding sites:** Unknown

**REFERENCES:**


Scaptomyza spp.

Scaptomyzas are small, dull yellow, brown or grayish flies, with 2 or 4 rows of acrostichal bristles (in contrast to *Drosophila* species, which have either 6 or 8), and often with a striped thorax, including one narrow median stripe and a broader lateral stripe on each side. They are generally more slender in appearance than *Drosophila*. Although they are typically yellowish or grayish in color, they can exhibit considerable intraspecific variation. Some species are leaf miners; others are saprophagous and thus rarely come to typical *Drosophila* baits.

**Phylogeny and biogeography:** Molecular phylogenetic analysis of both mitochondrial and nuclear DNA sequences indicates that the genus *Scaptomyza* is a sister group to the Hawaiian *Drosophila* and therefore phylogenetically within the subgenus *Drosophila*. It is therefore believed to have arisen in the Hawaiian Islands and from there dispersed to the rest of the world ~20 million years ago (O’Grady and DeSalle 2008; Lapoint et al. 2013).

**Identification:** At least five species of *Scaptomyza* occur in our region. The following key can be used in conjunction with the sketches below and the cheat sheet on the preceding page to distinguish among these species.

**Key to *Scaptomyza* species of our region**

1a Wing with terminal dark spot................. 2
1b Wing without such a spot....................... 3
2a One prominent humeral bristle................. *S. adusta*
2b Two prominent humeral bristles.............. *S. terminalis*
3a Four rows of acrostichal bristles........... *S. graminum*
3b Two rows of acrostichal bristles........... 4
4a Maxillary palpi brownish black............... *S. paravittata*
4b Maxillary palpi yellowish.................... *S. pallida*
REFERENCES:


Scaptomyza adusta

Scaptomyza adusta males

Wings clear with apical wing spot (arrow)

Scaptomyza adusta females

Body slender and medium-sized, thorax striped, abdomen dull and somewhat striped.
Scaptomyza adusta males

Scaptomyza adusta females
Scaptomyza adusta microscopic features summary

- Apical wing spot: YES
- Rows of acrostichal bristles: 4
- Ventral branches below fork of arista (not counting terminal fork): 2
- Prominent humeral bristles: 1
- Ratio of apical to basal scutellar bristle length: ~2/3
Scaptomyza adusta (Loew 1862)

The males and females of this slender, light brownish-gray, medium-sized species look similar. The thorax displays two light longitudinal bands that flank a darker dorsal midline. The abdominal pigmentation pattern is usually dull. The wings display one apical wing spot. The maxillary palpi are light. Two ventral branches exist below the fork of the arista (not counting the fork). The thorax has four rows of acrostichal bristles and one prominent humeral bristle. The ratio of apical to basal scutellar bristle length is 2/3. The apical scutellar bristles are crossed and stand at a higher angle than the basal scutellar bristles. Similar species: S. terminalis has two prominent humeral bristles but looks otherwise identical. Tips for collecting and breeding: The flies of this species can be reared or collected with a net from skunk cabbage.

Taxonomy: Subgenus Parascaptomyza. Species group adusta

Distribution: S. adusta is common and widely distributed in eastern North America (Wheeler 1952). This species, which is native to North America, has recently colonized Europe (Bächli et al. 2004).

Breeding sites and ecology: In the northeastern United States, adults of S. adusta are reported to be moderately common in piles of rotting green grass and on the stems and roots of chickweed, Stellaria media, which is an introduced species in this region (Stalker 1945; Batra 1979). It has also been bred from rotting cactus in Texas and mulberry tree sap in Illinois (Wheeler 1952). This species will feed on field-grown tomatoes (Collins 1956).

REFERENCES:


Scaptomyza pallida

**Scaptomyza pallida males**

- Maxillary palpi (arrow) light (compare to *S. paravittata*)
- Body medium-sized, thorax with two lighter stripes flanking a darker midline, abdomen yellowish to graybrown, somewhat striped
- Wings nearly unpigmented

**Scaptomyza pallida females**

- Maxillary palpi (arrow) light (compare to *S. paravittata*)
- Body medium-sized, thorax with two lighter stripes flanking a darker midline, abdomen yellowish to graybrown, somewhat striped
- Wings nearly unpigmented
Scaptomyza pallida males

Scaptomyza pallida females
Scaptomyza pallida microscopic features summary

- Apical wing spot: NO
- Rows of acrostichal bristles: 2
- Ventral branches below fork of arista (not counting terminal fork): 1
- Prominent humeral bristles: 1
- Ratio of apical to basal scutellar bristle length: 1
Scaptomyza pallida (Zetterstedt 1847)

The males and females of this slender, light brownish-gray to darker brown, medium-sized species look similar. The thorax displays two light longitudinal bands that flank a darker dorsal midline. The abdominal pigmentation pattern is usually dull. The wings are clear. The maxillary palpi are light. One ventral branch exists below the fork of the arista (not counting the fork). The thorax has two rows of acrostichal bristles and one prominent humeral bristle. The ratio of apical to basal scutellar bristle length is 1. The apical scutellar bristles are crossed and stand at the same angle as the basal scutellar bristles. Similar species: S. paravittata has dark maxillary palpi and an apical to basal scutellar bristle length ratio of 2/3. S. graminum has light maxillary palpi and four rows of acrostichal bristles. Some males of Hirtodrosophila ordinaria can look almost exactly like S. pallida males, with the exception that H. ordinaria has eight rows of acrostichal bristles and their testes are lemon-yellow. Tips for collecting and breeding: The flies of this species can be reared or collected with a net from skunk cabbage. The flies are also occasional visitors of banana, tomato, and mushroom baits as well as compost bins (especially when they contain grass clippings).

**Taxonomy:** Subgenus Parascaptomyza

**Distribution:** Holarctic, now cosmopolitan (Wheeler 1981; Bächli et al. 2004), including Indiana in our region (Sabath 1975)

**Breeding sites and ecology:** S. pallida feeds on decaying vegetation (Bächli et al. 2004). In Japan, this species breeds in decaying herbaceous vegetation, including cow parsley and parsnip (Apiaceae), anemone (Ranunculaceae), and white clover (Fabaceae) (Toda and Kimura 1978). In addition, they occasionally breed in decaying mushrooms and fruits, and adults are common in patches of white clover (Kimura et al. 1977). In the northeastern United States, adults of S. pallida are common on the stems and roots of chickweed, Stellaria media (Batra 1979).

**Endosymbionts:** Wolbachia has been found in the only strain of S. pallida that has been examined (Mateos et al. 2006). We are unaware of any studies of the phenotypic effect of this infection or of its prevalence of infection in natural populations.

**Parasites and pathogens:** S. pallida is parasitized by the widely distributed fungus Stigmatomyces scaptomyzae (Laboulbeniales) (Rossi and Maca 2006).

**Physiological ecology:** Where it has been studied in Japan, S. pallida overwinters as adults, nestled under snow-covered fallen leaves in a state of reproductive diapause (Toda and Kimura 1978). Overwintering females were found to be uninseminated, but mate soon after emergence in the spring.
**P-elements:** S. pallida has been shown to possess two different P-elements, one of which undergoes active transposition after experimental transfer to D. melanogaster (Simonelig and Anxolabehere 1991). Moreover, these P-elements are closely related to those found in other, distantly related drosophilids, including Drosophila bifasciata, indicating horizontal transfer of these elements between these fly species (Hagemann et al. 1996; Clark and Kidwell 1997).

**REFERENCES:**


THIS FRUIT FLY IS CRYING BECAUSE IT DROPPED ITS TOMATO
THIS FRUIT FLY MAMA IS HAVING A GREAT TIME WITH HER BABY
THIS FRUIT FLY IS ABOUT TO EAT A TOMATO AND A BANANA
Scaptomyza graminum (Fallen 1823)

The males and females of this slender, light brownish-gray to darker brown, medium-sized species look similar. The thorax displays two light longitudinal bands that flank a darker dorsal midline. The abdominal pigmentation pattern is usually dull. The wings are clear. The maxillary palpi are light. One ventral branch exists below the fork of the arista (not counting the fork). The thorax has four rows of acrostichal bristles and one prominent humeral bristle. The ratio of apical to basal scutellar bristle length is 1. Similar species: S. paravittata has dark maxillary palpi, two rows of acrostichal bristles, and an apical to basal scutellar bristle length ratio of 2/3. S. pallida has four rows of acrostichal bristles. Some males of Hirtodrosophila ordinaria can look almost exactly like S. graminum males, with the exception that H. ordinaria has eight rows of acrostichal bristles and their testes are lemon-yellow.

**Taxonomy:** Subgenus Scaptomyza. Species group graminum

This species has been described multiple times and therefore has numerous synonyms, including S. borealis Wheeler 1952.

**Distribution:** Holarctic, and possibly cosmopolitan (Wheeler 1981). In North America, S. graminum is most common in the eastern United States, occurring throughout our region (Stalker 1945; Wheeler 1952). Other areas where it has been found include Japan, the Canary Islands (28°N), Egypt, Taiwan (24°N), and much of Europe (Stalker 1945; Toda 1979). S. graminum is one of the very few drosophilid species found in Iceland (Heimaey, 63°N; Messersmith 1982).

**Breeding sites:** Like most species of the subgenus Scaptomyza s. str., S. graminum is a leaf-miner (Máca 1972). Stalker (1945) found adults as well as pupal cases of S. graminum on piles of rotting green grass, the presence of pupal cases indicating use of this resource as a breeding site. Other breeding sites for S. graminum include giant chickweed (Caryophyllaceae), watercress and several species of mustards (Brassicaceae), butterbur (Asteraceae), columbine (Ranunculaceae), winter squash and cucumber (Cucubitaceae), tomato (Solanaceae), and occasionally mushrooms (Fronk 1956; Ostrauskas et al. 2005; reviewed in Grimaldi and Jaenike 1983). Máca (1972) has bred this species in the former Czechoslovakia from plants belonging to the Caryophyllaceae, Chenopodiaceae, Amaranthaceae, and Fabaceae. Stalker (1945) states that adults of S. graminum are very common in patches of red clover, but that larval mines are rare, suggesting that the flies might ovipositing on a plant associated with clover. In the past, there was confusion between S. graminum and S. pallida, so some of these breeding site records for S. graminum might not
be correct.

**Parasites and pathogens:** *S. graminum* can serve as a vector of *Erwinia carotovora*, a bacterium that causes celery heart rot (Leach 1927).

**Physiological ecology:** The distribution of *S. graminum* from sub-tropical to tundra biomes indicates that this species has an exceptionally broad thermal niche. As far as we know, no one has investigated the genetic or physiological basis for this. Like *D. putrida* and some other drosophilids, *S. graminum* exhibits considerable temperature-related seasonal variation in color, with flies collected in early spring being much darker than those collected in mid-summer (Stalker 1945).

**Genetics:** Stalker (1945) examined the F2 of 152 wild-caught females for the appearance of visible mutant phenotypes. Stalker found 52 mutants affecting numerous traits, including bristle morphology, wing shape and venation, and eye color and texture, but only 60% of these showed complete penetrance. Stalker notes that *S. graminum* resembles *D. funebris* in having a substantial fraction of mutants with incomplete penetrance.

**REFERENCES:**


Scaptomyza terminalis

THIS FRUIT FLY HAS QUITE A MOUTH FULL OF TEETH!
THIS FRUIT FLY IS GETTING READY FOR VALENTINE’S DAY
DON’T THESE FRUIT FLIES LOOK LIKE MADE FOR EACH OTHER?
The males and females of this slender, light brownish-gray, medium-sized species look similar. The thorax displays two light longitudinal bands that flank a darker dorsal midline. The abdominal pigmentation pattern is usually dull. The wings display one apical wing spot. The maxillary palpi are light. Two to three ventral branches exist below the fork of the arista (not counting the fork). The thorax has four rows of acrostichal bristles and one prominent humeral bristle. The ratio of apical to basal scutellar bristle length is 2/3. The apical scutellar bristles are crossed and stand at a higher angle than the basal scutellar bristles. Similar species: S. terminalis has two prominent humeral bristles but looks otherwise identical.

Tips for collecting and breeding: The flies of this species can be reared or collected with a net from skunk cabbage.

**Taxonomy:** Subgenus Hemiscaptomyza. Species group terminalis

**Distribution:** Wheeler (1952) reports this species from Alaska, northwest Canada, and Pacific Northwest. It is therefore somewhat surprising that he also collected it in central and southern Arizona, as well as in southern California.

**Breeding sites:** In southern California S. terminalis has been bred from watercress (Brassicaceae; Wheeler 1952).

**REFERENCES:**

**Scaptomyza paravittata**

**Scaptomyza paravittata males**
- Maxillary palpi (arrow) dark (compare to *S. pallida*)
- Body medium-sized, thorax with two lighter stripes flanking a darker midline, abdomen yellowish to graybrown, somewhat striped
- Wings nearly unpigmented

**Scaptomyza paravittata females**
- Maxillary palpi (arrow) dark (compare to *S. pallida*)
- Body medium-sized, thorax with two lighter stripes flanking a darker midline, abdomen yellowish to graybrown, somewhat striped
- Wings nearly unpigmented
Scaptomyza paravittata microscopic features summary

Apical wing spot: NO

Rows of acrostichal bristles: 2

Ventral branches below fork of arista (not counting terminal fork): 2-3

Prominent humeral bristles: 1

Ratio of apical to basal scutellar bristle length: 2/3
**Scaptomyza paravittata**  
Wheeler 1952

The males and females of this _slender_, light brownish-gray, medium-sized species look similar. The _thorax_ displays two light longitudinal bands that flank a darker dorsal midline. The abdominal pigmentation pattern is usually dull. The _wings_ are nearly unpigmented. The _maxillary palpi_ are dark. Two to three _ventral branches_ exist below the fork of the arista (not counting the fork). The thorax has two rows of acrostichal bristles and one prominent humeral bristle. The ratio of _apical to basal_ scutellar bristle length is \( \frac{2}{3} \). The apical scutellar bristles are crossed and stand at a higher angle than the basal scutellar bristles. Similar species: _S. pallida_ has lightly colored maxillary palpi and parallel-standing apical and basal scutellar bristles of equal length. _S. graminum_ has light maxillary palpi and four rows of acrostichal bristles. Tips for collecting and breeding: The flies of this species can be reared or collected with a net from skunk cabbage.

**Taxonomy:** Subgenus Mesoscaptomyza. Species group vittata

**Distribution:** Reported from the southwestern United States (Wheeler 1981), although we have collected a few individuals in the Northeast (Grimaldi and Jaenike 1983).

**Breeding sites:** We have bred a few _S. paravittata_ from the leaves and petioles of the eastern skunk cabbage, _Symplocarpus foetidus_, in New York (Grimaldi and Jaenike 1983). Wheeler (1952) reports that the larvae feed as leaf miners in watercress (Brassicaceae).

**REFERENCES:**


Cladochaeta inversa

‘I AM VERY CUTE!’
‘LET’S CELEBRATE!’
**Cladochaeta inversa**
Wheeler and Takata 1971

This is a small to medium-sized fly with extensive shading on the anterior part of the wing. The thorax is yellowish brown, and the abdomen is darker, uniformly brown.

**Taxonomy:** Based on shared morphological features, Grimaldi (1990) has placed the genus *Cladochaeta* and sister group *Diathoneura* in the tribe Cladochaetini within the subfamily Drosophilinae.

**Distribution:** The genus *Cladochaeta* is restricted to the western hemisphere. *C. inversa* is widespread in the eastern United States and southeastern Canada, and as far west as Wisconsin and Manitoba (Wheeler and Tanaka 1971; Grimaldi and Nguyen 1999).

**Breeding sites:** *Cladochaeta inversa* is associated with nymphs of *Clastoptera* spittlebugs, most notably the Alder Spittlebug, *C. obtusa* (Ashburner 1981; Grimaldi and Nguyen 1999). The larvae of *C. inversa* insert their mouthparts between the tergites of their spittlebug hosts, suggesting that they are ectoparasites feeding on the hemolymph of the spittlebugs (Wheeler 1952; Grimaldi and Nguyen 1999).

**Modes of reproductive isolation:** *C. inversa* is the only member of its genus in our region, and therefore it is unlikely to encounter individuals of other species, with which it might mate. However, in the Neotropics, there may be over 800 species of the genus *Cladochaeta* (Grimaldi and Nguyen 1999), suggesting that reproductive isolating mechanisms among them must be important.

**REFERENCES:**


About the authors
IV. About the authors

Thomas became interested in the question “What is life?” as a four-year old child in his parent’s garden in former East Germany. By the age of 10, he began to develop a life-long interest in the biology of butterflies and moths. He has been breeding and collecting them ever since. For his Master’s thesis at Friedrich-Schiller-University Jena in Germany, Thomas decided to shift his focus to molecular biology and studied the human heart disease-causing virus Coxsackie B3 at the molecular level. His mentors were Dr. Werner Reichardt, Dr. Carola Leipner, and Dr. Andreas Henke. After the fall of the Berlin Wall, Thomas made one of his childhood dreams come true and moved to Sweden to spend seven years in Umeå, where he earned his Ph.D. in cell and molecular biology, working on fruit fly immunity. This was his first encounter with Drosophila melanogaster in the laboratory. From 2005 to 2010, Thomas worked as a postdoctoral fellow at the University of Wisconsin-Madison in Dr. Sean B. Carroll’s lab, where he established the fruit fly Drosophila guttifera as a new transgenic model organism to investigate how complex animal color patterns evolve. In 2010, Thomas started as a tenure-track assistant professor at Michigan Technological University, where he has been working on mushroom toxin resistance, color pattern evolution, and this species identification guide since then.
Tessa has been interested in science since a very young age because one of her brothers has Down Syndrome, and she always wanted to explain to her peers why and how her brother is different. She is originally from the Netherlands and has lived in the United States since she was 12 years old. Tessa realized that one can do great research using fruit flies when she visited Thomas' lab in spring 2017 during Open House at Michigan Tech. Thomas told her if she e-mailed him, he would send her a copy of his book “Drosophilids of the Midwest and Northeast” (Version 1.0). A couple of days later, Tessa typed up a short e-mail, asking for a copy of the book and maybe a spot in Thomas' lab. An hour and a half later, she received an e-mail back with a promise for a copy of the book and a request to join his research team. Tessa has been working in Thomas' lab since day one of her undergraduate experience at Michigan Tech. She rose in quick steps from a dishwashing help to a research assistant, then to the lab manager, and finally became the new co-author of Version 2.0 of this book.
John has been interested in all aspects of natural history for as long as he can remember. He was first introduced to serious ecological research as an undergraduate doing a senior thesis with Lincoln Brower at Amherst College. As a graduate student at Princeton University, being advised by Robert MacArthur and Henry Horn, he focused on ecological genetics of natural populations of *Drosophila*. Unfortunately, the obscura group species he was working on turned out to be rather poor subjects for field ecology. One day, on an uninhabited island off the coast of Maine, he saw swarms of *Drosophila* feeding on mushrooms and decided then and there to shift his research focus to those species when his dissertation was complete. Mycophagous *Drosophila* and their relatives have kept him amused from his postdoctoral days with Robert Selander (then at the University of Rochester) to the present day.
V. A bedtime story for kids
V. A bedtime story for kids

The idea to add a bedtime story to version 2 of our book came from John, partly as a joke. Thomas immediately liked the idea, having three kids of his own: Natalia (7 years, the illustrator of this book), Oliver (4 years), and Oscar (2 years).

After months of fruitless attempts to come up with a story that is cute, educational, funny, and heartwarming, Thomas finally asked his very talented undergraduate student, Tessa Steenwinkel, for help. She recollected some of her childhood adventures and carved out a story line within ten minutes. Thomas was amazed, and on their second meeting, Tessa sketched the story, totalling 13 pages. Our illustrator Natalia then used Tessa’s sketches as templates to draw her own pictures, using colored pencils.

We hope that this bedtime story will spark an interest and appreciation for nature’s wonders and science in our young readers. What made us passionate about science were beautiful moments outdoors; a beautiful butterfly visiting flowers in a garden in former East Germany, or hungry fruit flies sitting on a mushroom on a beautiful island in Maine.

Dear parents, uncles, aunts, school teachers, etc., please enjoy this story with the kids you know, and please let them have a good look at the real fly images in the main part of the book! Thank you!

Tessa, Natalia, Thomas, and John
Fruit fly adventures in the Midwest and Northeast: A walk to make new friends
Look, mom!

Oliver, get down!

Come say hi to the new neighbors! Let's invite them on a walk!

Mine!
And so the two families went on a walk

Look at all these berries, dad!

Natalia, Jasper, don’t go too far!

Yes, mom!
Don't eat too many, Nick! You will feel sick!
Three whole steps later ...

Can we go play?

Yes, you can!

Yay!
See how high I can climb!
Oh no, I'm stuck!

Ahh, what is that brown thing?!

That brown thing is a pupa.

Watch out for that larva on the stem!

Om nom nom
Help!

Crack!

Wham!

Snap!
I'm here, it's going to be alright, Oliver!

My wing hurts, Tessa!
Here is a bandaid for your wing.

Thank you, you are so nice, Tessa!
Look, now I have spots on my wing, too!
Who would like some ice cream to recover from that accident?

Me, me, me, me!

Me!

Me, too!

Me, three!
Here you go, Oscar.

Thank you!

And two scoops for the brave Oliver.

Oh, look at your face!

Yum!

I got chocolate!

Yay!

Me, too!