Journal of Integrated Pest Management, (2022) 13(1): 19 1–14
https://doi.org/10.1093/jipm/pmac015
Profile

Eye Gnat (*Liohippelates*, Diptera: Chloropidae) Biology, Ecology, and Management: Past, Present, and future

Kier D. Klepzig,[1,3] Jessica A. Hartshorn,[2] Alexandra Tsalickis,[2] and Thomas N. Sheehan[1]

[1]The Jones Center at Ichauway, 3988 Jones Center Drive, Newton, GA, 39870, USA, [2]Department of Forestry and Environmental Conservation, Clemson University, Lehotsky Hall 272F, Clemson, SC, 29634, USA and [3]Corresponding author, e-mail: kier.klepzig@jonesctr.org

Subject Editor: Dawn Gouge

Received 20 April 2022; Editorial decision 16 June 2022

Abstract

Eye gnats (mainly *Liohippelates pusio* and *Liohippelates collusor*) are pest species that have been the subject of considerable research and extension activity in the United States since the 1930s. They cause considerable discomfort and stress—and may transmit pathogens—to humans and animals. We reviewed the abundant literature on biological, ecological, and management aspects of *Liohippelates* eye gnats. Eye gnat biology and life cycles have been well studied in agricultural systems. However, their ecology, roles in trophic cascades, and functions in natural ecosystems, particularly forests, are not well documented. Additionally, there remain opportunities to improve traps, repellents, deterrents, and controls for eye gnats. The substantial and substantive early work on these insects provides a strong foundation for future investigations and extension.

Key words: Chloropidae, fall line, agricultural pest, disease transmission, vector

Eye gnats are true flies in the family Chloropidae (from the Greek *clorops*, meaning 'swarm'), so named for their propensity to hover around mucous membranes, especially the eyes (Machtinger and Kaufman 2011, Hendrix 2013). This behavior was first noted in literature in the journals of Lewis and Clark (1805, as cited in Mussulman 2011):

> "Musquitors very troublesome, and in addition to their torments we have a Small Knat which is as disagreeable… does not sting but attacks the eyes in swarms and compels us to brush them off or have our eyes filled with them."

They have since been described as 'justly dreaded' in the southeastern United States, noted for their potential to transmit pathogens like *Haemophilus aegyptius* (the causal agent of pink eye) and for bodies so hard that 'a slap with the hand which would be sufficient to crush any mosquito or house fly does not hurt them in the least' (Schwarz 1895). Much later, a return to the sites described by Lewis and Clark (the portage route of 1805 in Montana) led to a report of considerable reduction in populations of eye gnats since the early 20th century. This was attributed to reduced herd size of large ungulates like bison, deer, and antelope—with which large swarms of gnats are frequently associated (Mussulman 2011). Nevertheless, in many areas of the United States, eye gnats remain numerous and troublesome. Fifty years ago, Biery (1977) reviewed eye gnats specifically in the context of population control. Herein, we review the current knowledge on–and identify critical research gaps in—the biology, ecology, and management methods of this pest.

Pest Species and Disease Vectors

Eye gnats are not host-specific; humans, livestock, and other animals are all susceptible to being bothered by this pest. Their impacts may be especially bothersome near irrigated agricultural lands (Burgess 1950). Female eye gnats require a food source rich in protein (e.g., mucus, blood, scabs) to produce young. Humans and other animals near prime breeding areas for eye gnats may suffer. Keeping the gnats away as they swarm mucous membranes, exposed skin, and wounds, requires constant effort (Schwarz 1895). Because of this, eye gnats may also impact tourism, outdoor recreation, and land development (Bethke et al. 2013). Workers in agricultural areas within in affected areas, as well as nearby residents, become irritated with abundant gnats and may develop eye irritations or allergies (Nigh et al. 1997).

Beyond these annoyances, eye gnats have received attention for their potential as vectors of disease causing microbes, including those responsible for pink eye (aka conjunctivitis), the spirochete bacterium (*Treponema pallidum*) that causes yaws, the virus that causes vesicular stomatitis, and the bacterium (*Staphylococcus agalactiae*) that causes bovine mastitis (Herms and Burgess 1930, Bengston 1933, Kumm and Turner 1936, Sanders 1940, Bigham 1941, Burgess 1950, Mulla and Barnes 1957, Dow and Hutson

1958, Harrison et al. 1989, Day and Sjogren 1994, Bradley 2002, Jiang and Mulla 2006, Harrison et al. 2008, USDA APHIS 2019). Some of these pathogens are spread by mechanical transmission (i.e., pathogen transfer from any surface to an infection site on a human or other animal). It is likely and widely accepted that when eye gnats feed on pathogen-infected fluids and subsequently feed on a different host with an open wound, they transmit the pathogen (Machtinger and Kaufman 2011). Eye gnats are also suspected vectors of the pathogen that causes anaplasmosis (a typically tick-transmitted bacterial pathogen, *Anaplasma phagocytophilum*) in cattle due to observations of adults ingesting blood from wounds created by horse flies (Roberts 1968, Roberts et al. 1969). Follicular conjunctivitis (a bacterial disease of the eye and eyelid) is documented in young children from the Coachella Valley in association with *Liohippelates pusio* activity (Herms and Burgess 1930, Burgess 1950). Twenty species of bacteria were isolated from both laboratory-reared and wild-caught eye gnats (Snoddy et al. 1974), and eye gnats were found to transmit *H. aegyptius* (the bacterial causative agent of conjunctivitis) to rabbits in laboratory settings (Payne et al. 1977). Likewise, eye gnats transmitted the pathogen that causes yaws from human to rabbit in experimental settings (Burgess 1950). Other eye diseases are also associated with high abundance of gnats (Schwarz 1895, Herms 1926, Mulla and Barnes 1957, Buehrle et al. 1983) and eye gnats likely spread mites and other parasites (Mulla 1958, Eskafi and Legner 1974a,b,c).

Taxonomy

The family Chloropidae, commonly called 'frit flies' or 'grass flies,' contains 188 genera worldwide and more than 2,000 described species (Sabrosky 1987), some of which are known from the Oligocene, with examples *Protoscinella* (extinct) and *Tricimba* (extant) found in Baltic amber (Nartshuk 2014). *Liohippelates* consists of at least 31 described species with greatly variable regional densities of each (GBIF Backbone Taxonomy 2021). In this review, we focus on two species at the center of the most research, especially concerning impacts on humans and livestock: *L. pusio* (Loew, 1872) and *L. collusor* (Townsend, 1895). *L. pusio* and *L. collusor* were originally placed in different, but still extant, genera (*Hippelates* and *Oscinis*, respectively). *Liohippelates pusio* subsequently became the type species of the genus (Duda 1929). *Hippelates* is derived from the Greek for 'horse drivers' referring to the ability of this insect to bother livestock, and humans. The Latin prefix *lio* means 'plain' or 'smooth.' The specific epithets *pusio* and *collusor* derive from Latin for 'little boy' and 'playmate,' respectively. Invalid synonyms of *L. pusio* include: *Hippelates pusio* Loew, 1872; *H. splendens* Adams, 1904; and *H. lituratus* Becker, 1912. Invalid synonyms of *L. collusor* include: *Oscinis collusor* Townsend, 1895 and *Hippelates collusor* (Townsend, 1895). Invalid synonyms of *Liohippelates* include *Stenoprosopon* Duda, 1930; *Stratiomicroneurum* Duda, 1933; and *Neohippelates* Roberts, 1934. The type specimen of *L. collusor* was destroyed in a fire in the early 20th century (Herms 1928). Unless otherwise stated, we will refer to these two species (*L. pusio* and *L. collusor*) as 'eye gnats.' Other aspects of eye gnat taxonomy may be found in Machtinger and Kaufman (2011).

Morphology of Adults

Eye gnats are approximately 1.5–2 mm long, and black or gray in color (Fig. 1, Machtinger and Kaufman 2011). The legs of adult eye gnats have extensive black markings and are never pale yellow,

Fig. 1. Adult eye gnats (*Liohippelates pusio*), about 1.5–2 mm in length, on human skin. Photograph: Matt Bertone, NC State University.

though they can sometimes be entirely deep yellow to orange with only the coxae and middle femora being basally blackened. They also have a hind tibial spur that exceeds the apex of the tibia by ¼ to ⅓ the tibial length (Sabrosky 1941). Their mouthparts have small tooth-like structures, as well as large labella with pseudotracheal rings tipped with spines (Russell et al. 2013). These spines enable them to scrape the conjunctival surface of the eye, causing irritation, and increasing the flow of secretions, attracting even more gnats. The mouthparts cause particular concern to human and animal health as these structures can scrape scabs open and release pus and other exudates from wounds (Graham-Smith 1930).

Distribution

Liohippelates pusio can be found throughout much of the continental United States, as well as Hawaii, Puerto Rico, and the U.S. Virgin Islands (Fig. 2; Table 1). This eye gnat may also be found as an abundant nonnative species, in some places dominating collecting efforts (Amprako et al. 2020). Most research, however, has focused on sandy agricultural areas where the gnats are abundant enough to become nuisance pests. For example, in the Southeast, their greatest abundance is south of the so-called 'Gnat Line,' which approximates the Fall Line where the Piedmont meets the Coastal Plain (Fig. 3, Mackie 2017). This includes sandy soil portions of Alabama and southwestern Georgia and agricultural areas of Louisiana, Mississippi, and Texas (Bigham 1941). Multiple areas of Florida contain high populations of eye gnats including agricultural areas, organic soils of Florida near citrus groves, rural communities, and recreational and tourist areas (Williams and Kuitert 1974), which has led to gnat research in this state (e.g., Schwarz 1895, Sanders 1940, Bigham 1941, Flint 1965, Williams and Kuitert 1974). Likewise, southwestern Georgia hosts the highest abundance of gnats in the state, likely associated with the extensive agriculture in sandy, irrigated soils in this region (Bengston 1933, Bigham 1941, Dow and Hutson 1958). Eye gnats are most active here in summer and fall months (Bigham 1941, Lyman and Dow 1948). The Carolinas host significant populations of eye gnats as well. The eastern half of South Carolina contains dense populations of eye gnats where soil is sandy and friable (Gaydon and Adkins 1969), and North Carolina has been home to gnat research as well (Axtell 1967, DuBose and Axtell 1968, Karandinos and Axtell 1972). Perhaps the most affected and most studied gnat affected area is The Coachella Valley in California. This extensive agricultural area on disturbed, sandy soils has been the center of extremely high eye gnat

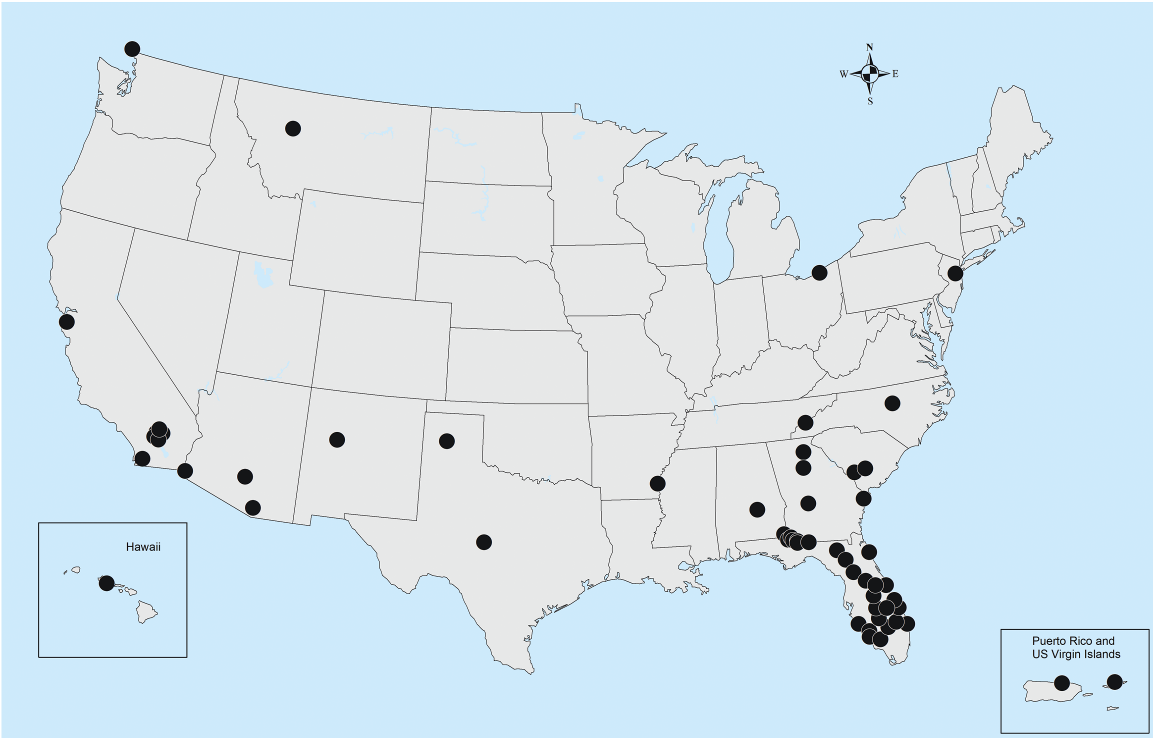

Fig. 2. Map of locations in the United States of eye gnats mentioned in reviewed literature.

populations, and concomitant research activity (Herms 1926, Herms 1928, Herms and Burgess 1930, Hall 1932, Parman 1932, Burgess 1950, Mulla and Barnes 1957, Mulla et al. 1960b, Georghiou and Mulla 1961, Mulla 1962a,d, 1963b; Mulla et al. 1973, Hwang et al. 1976, Day and Sjogren 1994, Bethke et al. 2013).

Biology and Life History

Life Cycle and Description of Immature Stages

On average, *Liohippelates* develop from egg to reproductive adult (Fig. 4) in about 28 d in natural conditions (i.e., not incubated) (Burgess 1950, Mussulman 2011), but the life cycle can take anywhere from 11 d to as long as 3 mo (Machtinger and Kaufman 2011) depending on environmental conditions (Hall 1932, Mussulman 2011). For example, females ovipositing in rainy seasons tend to have more fully developed eggs than those found during dry conditions (Mulla and Chansang 2007). Mature males may inseminate as many as four mature females in a 24-hour period, and 6–14 females in a 10-day period (Schwartz 1965). Both sexes require 36 h after eclosion to reproduce; no sperm is present in the ejaculatory duct for 1–2 days after emergence (Schwartz 1965).

Eye gnat eggs are about 0.5 mm long, pearlescent white, and banana-shaped (Herms and Burgess 1930). Eggs and larvae are sensitive to the amount of moisture surrounding them and even a short period (i.e., hours) of insufficient moisture can be fatal (Hall 1932). Eye gnats prefer to deposit eggs in disturbed, sandy soil containing organic matter (Mulla 1963b). They may also be associated with areas where large animals—such as bison *Bison bison*—graze (Mussulman 2011). Females may lay eggs on excrement as well as decaying meat, fruit, and vegetables (Hall 1932). They require three factors for oviposition: 1) friable soil, 2) sufficient moisture, and 3) decaying vegetable material (Gaydon and Adkins 1969). Eggs eclose at a sex ratio of 1:1 in cool, shady conditions; larvae then grow to about 3 mm long, turn opalescent white, and grow both a pair of mouth hooks and a small pair of ocular tubercles (Herms and Burgess 1930). Larvae feed on organic material such as rotten vegetation or dung (Burgess 1950, Russell et al. 2013, Wiesenborn 2016). Larvae occur at the base of stems of rotting vegetation and overwinter as deep as 12.5 cm below the soil surface (Burgess 1950). In winter conditions, larvae move sluggishly in a state of semihibernation, though they can survive on artificial media down to freezing temperatures, and anywhere from arid conditions to immersion in water (Burgess 1950). As high as 97% of developing gnats die from physical and biotic factors in noncultivated fields during the summer (Legner and Bay 1970).

Behavior and Activity

Adult activity varies by environmental conditions such as season, location, and climate. Differences in activity occur between the western and southeastern United States. In the Coachella Valley of California (western United States), adults are most commonly active in relatively moderate, wet weather (e.g., spring and fall) with significant reductions in activity in the heat of summer and cold of winter (Hall 1932, Burgess 1950). The attraction of eye gnats to moisture is evident by their abundance around lawn sprinklers, perspiring humans, or even a person using a hose to wash a car (Hall 1932). In California, adult gnats seek hosts upon which to feed most actively between 25 and 27°C (Mulla and Chansang 2007). In the Coachella Valley, *L. collusor* populations increase in March and reach a peak in August or September before decreasing in numbers (Mulla 1964). In longleaf pine forests near Thomasville, GA, response to traps baited with liver was moderate in March, lower in April and May, higher in June, reaching peak attraction in July and August, but declining in September and October and reaching their lowest levels in November (Dow and Hutson 1958). Gnats are generally diurnal, active from dawn until dusk, and are especially active during the

Table 1. A selection of digital records of eye gnats

Location Collected	Species	Year Collected	Source
AZ: Pinal Co.	*Liohippelates pusio*	2010	GBIF
AZ: Santa Cruz Co.	L. *pusio*	1993	GBIF
BC: Vancouver	*L. pusio*	2001	LEMQ
CA: Merced Co.	*L. pusio*	2011	GBIF
CA: San Diego Co.	*Liohippelates* sp.	2019	iNat
CO: Weld Co.	*Liohippelates* c.f. *pusio*	2009	GBIF
FL: Collier Co.	*Liohippelates* c.f. *pusio*	2011	GBIF
FL: Higlands Co.	*Hippelates* sp.	1989[a]	ABS
FL: Highlands Co.	*L. pusio*	1970	AMNH
FL: Highlands Co.	*L. pusio*	2000	ABS
FL: Palm Beach Co.	*L. pusio*	1932	UHIM
GA: Baker Co.	*L. bishoppi*	1947	AMNH
GA: Baker Co.	*L. pusio*	2018	iNat
GA: Chatham Co.	*L. bishoppi*	1952	USNM
GA: Montgomery Co.	*L. pusio*	1968	USNM
GA: Peach Co.	*L. pusio*	1945	AMNH
GA: Thomas Co.	*L. bishoppi*	1948	AMNH
GA: Thomas Co.	*L. bishoppi*	1952	AMNH
HI: Honolulu Co.	*L. collusor*	1961	UHIM
HI: Honolulu Co.	*L. collusor*	1995	UHIM
MB: Gardenton	*L. pusio*	1992	GBIF
MS: Bolivar Co.	*L. pusio*	2012	CUAC
NC: Wake Co.	*Hippelates* sp.	1965	UHIM
NJ: Middlesex Co.	*L. pusio*	1995	CLEV
NM: Bernalillo Co.	*L. pusio*	1963	NMSU
NM: Luna Co.	*L. collusor*	1960	NMSU
NM: Roosevelt Co.	*L. pusio*	1993	LEMQ
NM: San Miguel Co.	*L. pusio*	1961	NMSU
NM: Sandoval Co.	*Hippelates* sp.	1988[a]	NMMNHS
OH: Geauga Co.	*Liohippelates* sp.	2004	iDigBio
Puerto Rico	*H. incipiens*	1926	AMNH
Puerto Rico	*H. lutzi*	1926	AMNH
SC: Orangeburg Co.	*L. pusio*	1964	CUAC
TN: Blount Co.	*L. pallipes*	2003	CUAC
TX: Atascosa Co.	*L. pusio*	1989	TAMU
TX: Cameron Co.	*L. pusio*	1995	LEMQ
TX: Concho Co.	*L. pusio*	n.d.	MCZC
TX: Randall Co.	*L.* cf. *pusio*	2011	GBIF
US Virgin Islands	*L. collusor*	1926	AMNH
VA: Falls Church Co.	*L. bishoppi*	n.d.	MCZC

ABS, Archbold Biological Station; AMNH, American Museum of Natural History; CLEV, Cleveland Museum of Natural History Invertebrate Zoology Collection; CUAC, Clemson University Arthropod Collection; GBIF, Global Biodiversity Information Facility; iDigBio, Integrated Digitized Biocollections; iNat, iNaturalist.org; LEMQ, Lyman Entomological Museum; MCZC, Museum of Comparative Zoology, Harvard University; NMMNHS, New Mexico Museum of Natural History and Science; NMSU, New Mexico State University Arthropod Collection; TAMU, Texas A&M University Insect Collection; UHIM, University of Hawaii Insect Museum.

[a]Collected at a light source at night.

warmest hours of the afternoon (Schwarz 1895, Hall 1932, Mulla and Chansang 2007), and are largely inactive at temperatures below 21°C (Hall 1932). They are not attracted to lights at night (though see Table 1 for records of nocturnal collections in UV light traps) but do move towards daylight within darkened traps and cages (Hall 1932, Burgess 1950, Mulla et al. 1960a, Dorner and Mulla 1961, Rogoff 1978b). In laboratory settings, they have been found to prefer 29°C when humidity is low and 39°C when humidity is high (Dorner and Mulla 1962a). Adults rest on trees, shrubs, other plants, and the ground when not in flight (Schwarz 1895, Mulla and March 1959). They also often shelter in clods of soil or manure when temperatures drop suddenly and can withstand considerably low temperatures this way (Burgess 1950).

Mating Behavior

Adults mate in cool, shady conditions. Females lay up to 50 eggs (Schwarz 1895, Burgess 1950, Mulla and Chansang 2007) in low light or shady conditions on disturbed, sandy soils. Females especially prefer soil mixed with organic matter (e.g., cut grass, dung) (Nartshuk 2014). Oviposition can be induced, perhaps as needed for research studies, by placing females in a jar in the sun until they are near exhaustion from the heat, and then quickly placing them in dark and cool conditions (Burgess 1950). After larvae feed for approximately 1–2 wks, pupae develop for a week before emerging as adults. Gnats pupate in the top 0–10 cm of soil; the type of crop has no effect on development, nor does the type of loose and friable soil, as long as sufficient and ample decaying organic matter is present

Fig. 3. The area south of the Fall Line delineating the edge of the Piedmont and Coastal Plain, also known colloquially as the 'Gnat Zone', contains sandy soils that provide habitat for high abundances of eye gnats.

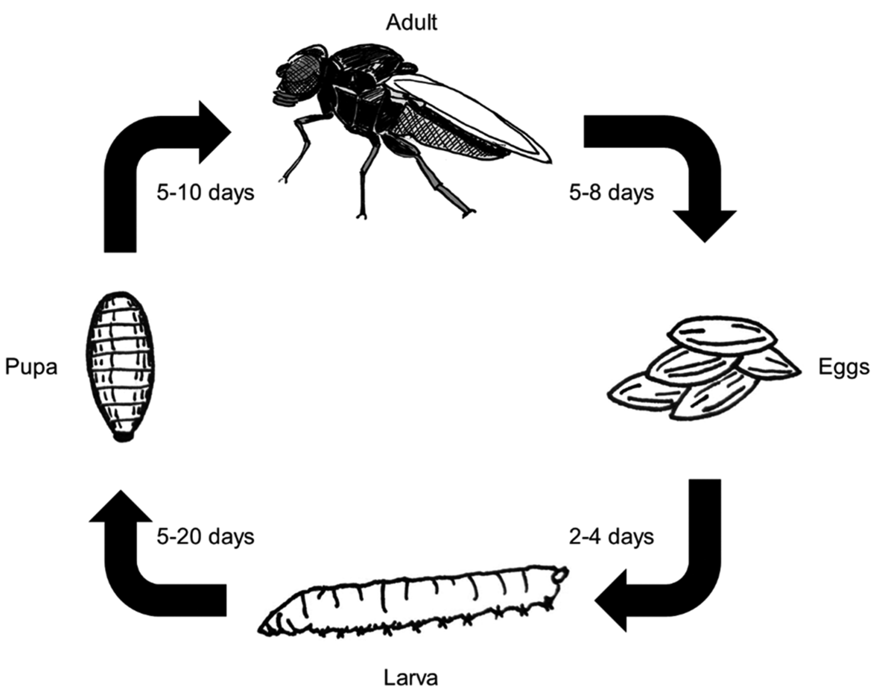

Fig. 4. Life cycle of eye gnats, *Liohippelates pusio*. Modified from Bethke et al. (2013).

(Mulla 1962a). Puparia are about 2.25 mm in length, and the color of light straw when young, darkening over time (Herms and Burgess 1930). Adult density apparently does not affect hatch success of *L. pusio* (Karandinos and Axtell 1972), but this species is not totally density independent. Larval competition and parasitism affect population growth rates (Legner 1966, Legner et al. 1966a, Karandinos and Axtell 1972).

Dispersion

Adults are generally strong fliers (Hendrix 2013) and can disperse several kilometers (Mulla and March 1959, Russell et al. 2013), though winds likely aid in dispersing these very small bodied insects (Bethke et al. 2013). Mark-recapture studies in an area of agricultural cultivation mixed with forests found farthest adult dispersal to be up to 1.1 km 10 d after release (Williams and Kuitert 1974) and 6.9 km with the wind (Mulla and March 1959). Another study collected 15 gnats over 1.6 km from their release point in just 3.5 h (Dow 1959a). However, they seem to be weak flyers upwind, with *L. collusor* unable to fly against wind speeds over 3.2 km/h in laboratory settings (Dorner and Mulla 1962a), and *L. pusio* unable to fly against windspeeds above 4.0 km/h in the field (Gerhardt and Axtell 1972). Population density estimates range from 5,000 to 12,500 gnats/ha (Mulla and March 1959, Williams and Kuitert 1974).

Feeding

Eye gnats do not bite, though adults do use their rasping mouthparts (Graham-Smith 1930) (Fig. 1) to pierce scabs and scar tissues to feed on exudates, wounds, lacerations, and fluids from mucous membranes from a wide variety of animals including humans, livestock, domestic pets, and wildlife, even frogs (Legner and Bay 1970, Machtinger and Kaufman 2011). Eye gnat larvae feed on both living herbaceous plants (Stegmaier 1966) and decomposed plant material. They may also feed on immature insects, decomposing wood, and fungi (Nartshuk 2014). In laboratory settings, eye gnats may feed on sugar water, fruit juice, meat juice, and decaying vegetable matter (Hall 1932). Adults may not be widespread pollinators or necessarily attracted to flowers, though *L. pusio* was frequently collected on blooms of common elderberry *Sambucus simpsonii* (Frost 1979) and *Bidens pilosa* (Needham 1948). In addition, eye gnats do carry mistletoe *Phoradendron coryae* pollen and have been found to carry more pollen than some other fly species (Wiesenborn 2016).

Substrate Preference

Adult eye gnats prefer loose, sandy soils with high amounts of organic matter and moisture (Mulla et al. 1960b, Jiang and Mulla 2006, Machtinger and Kaufman 2011), which are common in agricultural land. Elevated populations of eye gnats are frequently, almost invariably, associated with soil disturbances such as irrigation, plowing, discing of cover crops, and other farming practices in sandy, friable soils (Bigham 1941, Burgess 1950, Mulla et al. 1960b, Mulla 1962a, Mulla 1962d, 1963b; Gaydon and Adkins 1969, Jiang and Mulla 2006). Gnats are most frequently captured from freshly disturbed sandy soils, and not pine duff, grass, weed sod, leaf mold (compost produced by fungal breakdown of shrub and tree leaves), rotting fruit or vegetables, aquatic vegetation (Bigham 1941), or riparian environments (Bethke et al. 2013). After hatching, larvae tunnel downward into the soil to find moist areas and pupate at the interface between moist and dry areas of the soil (Hall 1932).

Field and Laboratory Study Methods

Collection

Gnats may be collected using a variety of techniques (Herms and Burgess 1930, Hall 1932, Burgess 1950, Mulla 1962d, Rogoff 1978a,b; Bethke et al. 2013). Washing soil samples in a large water tank with an overflow outlet opening 2.5 cm from the top separates pupae from the substrate and causes them to float to where they can be filtered through a series of mesh screens (Mulla 1962d). Square screen cages can be used to capture flying adult gnats and measure use of breeding niches (Mulla 1961, 1962a, 1963b). Such traps collect high numbers of gnats which can be counted by separating out several samples of 100 gnats, oven drying, and immediately weighing them to derive a constant for gnats per unit mass (Dow and Hutson 1958). Others have noted the potential utility of attraction of gnats to humans for collection, though attempts at gnat count estimates on humans are difficult (Herms and Burgess 1930).

Additional methods for collecting eye gnats include sieving small soil cores (20 cm long), using aspirators (including some with a battery powered vacuum), and hand nets (Rogoff 1978b). A copper pipe may be driven several cm into the ground to remove a plug of soil to collect gnat eggs. The collected soil can then be screened into a pan mixed with water containing magnesium sulfate (3:1 by volume) and briefly allowed to settle. The supernatant can be then decanted through a sieve, and the eggs and debris washed to remove the scum. Any eggs collected in this manner are then transferred to another pan with water and magnesium sulfate. Larvae in the top 4 cm of soil may be collected in this way as well. A screen of milling grade stainless steel wire cloth (24 × 24 mesh) screen may also be added into the extension tube of a handheld vacuum to retain adult insects (Rogoff 1978b). The density of eye gnat adults may also be assessed by suction sampling grass and weed ground cover where the gnats rest at night (Rogoff 1978b).

Lab Methods (Mass Rearing)

Hippelates and *Liohippelates* have both been successfully reared in laboratories (Mulla and Barnes 1957, Mulla 1962a,b; Karandinos and Axtell 1972). There are four cage considerations for mass rearing: 1) ventilation, 2) light, 3) space, and 4) depth of the larval breeding medium (Mulla and Barnes 1957). Photoperiod affects eclosion rhythm in laboratory-reared populations of eye gnats (Scherer 1964). A suitable larval medium may be made from alfalfa meal and dry vermiculite creating a 20% organic matter mixture along with 150–200 g of brewer's yeast (Mulla and Barnes 1957). Hall (1932) found human excrement to best support eye gnat larval development (compared to figs, oranges, dead flies, tomatoes, liver, peppers, cantaloupes, potatoes, onions, squash, lawn clippings, blood meal, dog, goat, chicken, or cow manure). Mulla and Barnes (1957) also developed an adult gnat rearing medium which included honey, protein, yeast, human blood, macronutrients, and micronutrients. This rearing technique was successfully used for at least eight generations in the lab. Initial populations of 300–400 male and female gnats may develop into as many as 5,000–6,000 emerging gnats. Supplementation of casein and yeast do not increase rearing yield, but diets containing a carbohydrate or honey support gnat life for 30 d (Schwartz and Turner 1965). Mass rearing techniques (including feeding adult gnats split prunes soaked in honey and blood) have been refined to the point of making it possible for a single technician to care for 50 colonies of *L. collusor* and produce two million eye gnats during an average work week (Bay and Legner 1963). A vacuum powered aspirator can assist in sorting and sexing adult gnats, at a rate up to 1,000 gnats/h (Schwartz 1964). To replicate field conditions, larvae are successfully grown on millet seedling roots (Legner and Bay 1964, Legner et al. 1966b, 1971).

Monitoring and Management

Monitoring and management have been the focus of considerable research on eye gnats. A diverse array of traps have been developed for monitoring eye gnats (Figs. 5–10, Herms 1928, Parman 1932, Bigham 1941, Burgess 1950, Dow and Hutson 1958, Mulla et al. 1960a, Mulla and Axelrod 1974, Snoddy 1974, Williams and Kuitert 1974, Rogoff 1978a,b; Day and Sjogren 1994, Bethke et al. 2013). All the traps are based around having an attractive substance in a darkened entryway or bait chamber, with a brighter and higher light chamber. One early effort at trapping

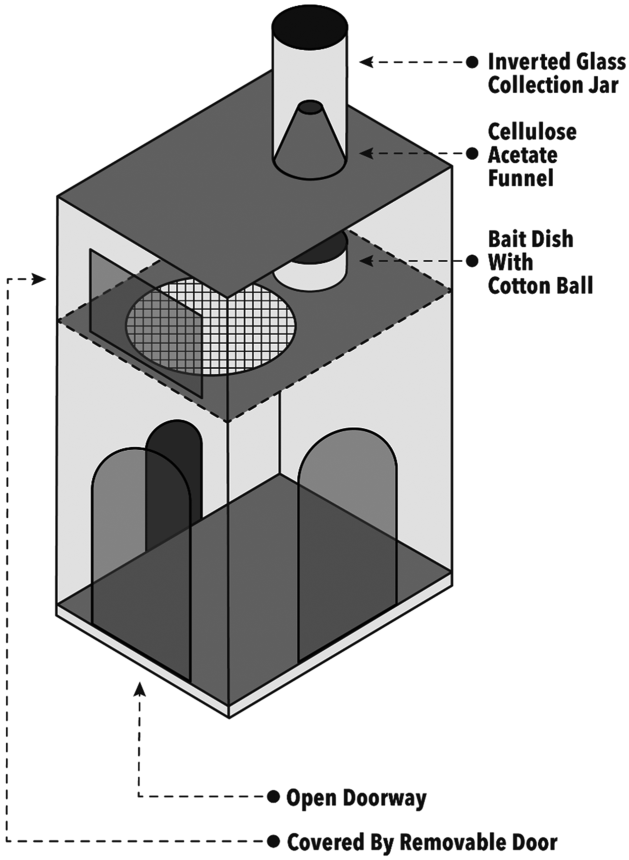

Fig. 5. Original drawing of an eye gnat trap design from a photograph in Dow and Hutson (1958) (Artist: Jamie Hammond). Gnats drawn to an odiferous bait on the second level fly into openings on the bottom and end up in a collection jar atop the trap.

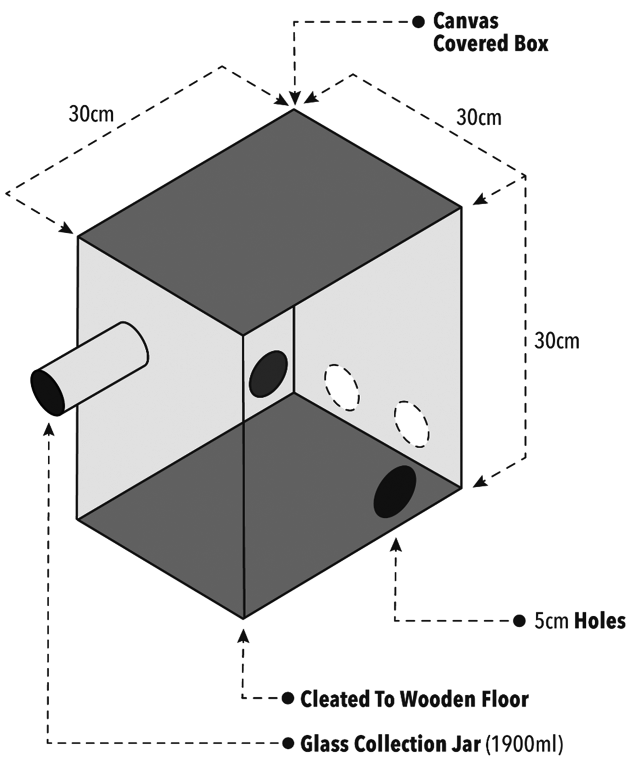

Fig. 6. Original drawing of an eye gnat trap design from a description in Burgess (1950) (Artist: Jamie Hammond). Gnats attracted to bait within the darkened canvas box are then drawn to the clear collection jar on the side of the box.

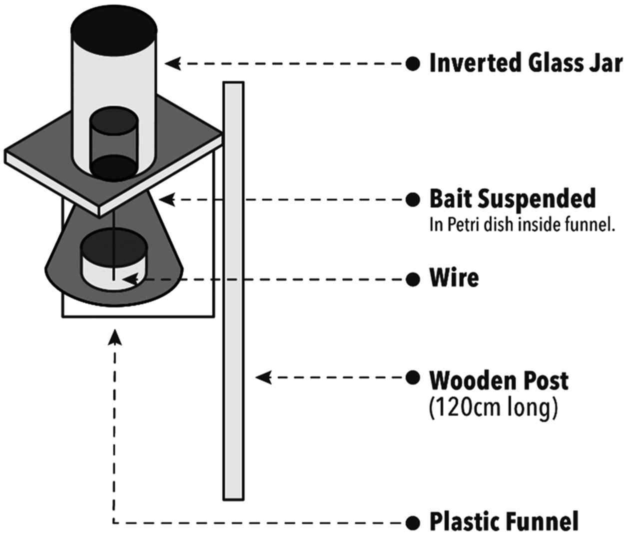

Fig. 7. Original drawing of an eye gnat trap design from a photograph in Mulla et al. (1960a) (Artist: Jamie Hammond). Gnats drawn to an odiferous bait within the inverted funnel end up flying into the collection jar atop the spout of the funnel.

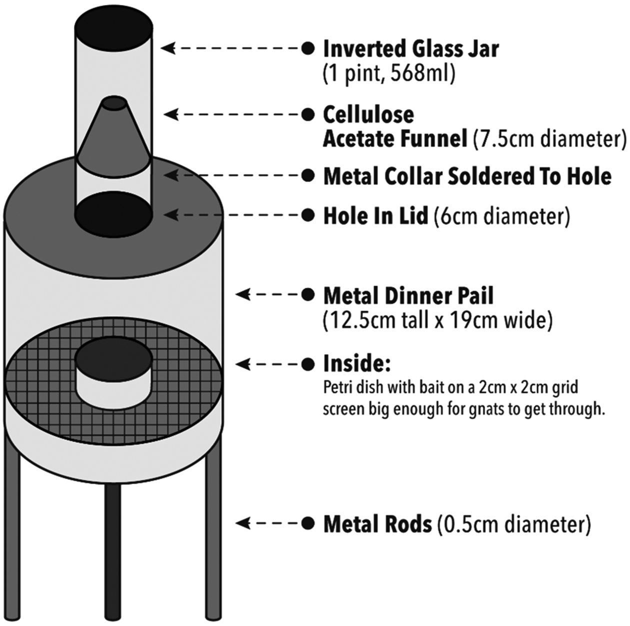

Fig. 8. Original drawing of an eye gnat trap design from a photograph in Dow and Hutson (1958) (Artist: Jamie Hammond). Gnats drawn to an odiferous bait on the wire mesh platform are attracted to the light coming from the collection jar atop the trap and prevented from escaping by the inverted funnel.

out gnats used a large eye gnat trap (1.2 m wide × 1.85 m long × 2.57 m tall) constructed from a large barrel containing a windmill agitator to stir bait mixtures and evenly distribute odors (Parman 1932). These traps attracted only gravid females which oviposited in the mixture, becoming trapped along with their offspring. This effort at mass trapping reportedly 'decimated' eye gnat populations after two seasons of use. Bigham (1941) later used traps baited with liver, with one trap catching 80,000 gnats in one week. Ultimately, the materials used for trap construction do not matter as long as the traps include a bait, a darkened chamber, and have a jar or other light chamber at the top of the trap (Figs. 5–10). Dry ice traps can be constructed from an insulated container. This trap releases carbon dioxide through a small hole on each side of a large cone with basal openings and a small opening at the top through which flies can enter, and a catch chamber which traps the flies. Although designed for other flies, these traps can also be effective in trapping eye gnats (DeFoliart and Morris 1967). Despite this extensive research, 'the long search for the perfect eye gnat attractant continues and emphasizes how difficult it is to identify a perfect attractant, incorporate it into a removal trapping program for eye gnats where no other control strategy presently exists' (Mulla et al. 1990). Most recently, pest control agencies in Yuma County, Arizona, and Coachella Valley, California are using manufactured traps using a collar with holes, threaded to accept a bait jar below and collection jar above (Fig. 10). These traps are serviced weekly, with additional liquid attractant added from a service vehicle. The lower jars are replaced when attraction declines. These traps work best when mounted on to a vertical pole, close to—but not touching—the ground.

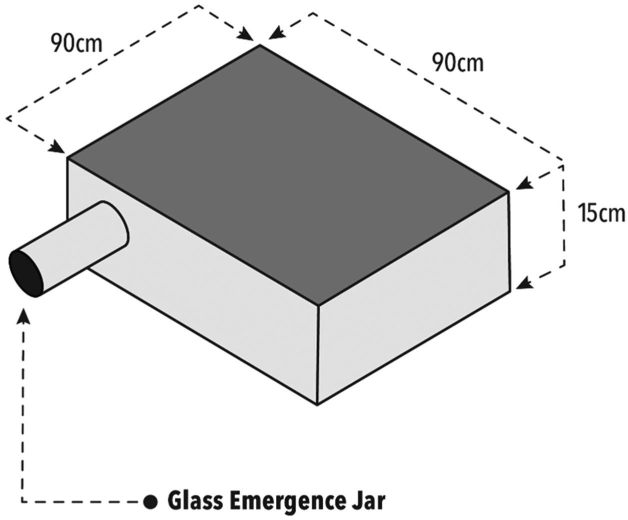

Fig. 9. Original drawing of an eye gnat emergence trap design from a photograph in Mulla (1963b) (Artist: Jamie Hammond). Gnats emerging from soil substrate are drawn to light from the collection jar on one side of the trap.

Fig. 10. Photograph of an eye gnat removal trap (permission granted by Yuma County Pest Abatement District). A black molded collar (with 6x1cm holes radially penetrating the collar) is threaded to accept a 32oz PET jar into the top and bottom. The bottom jar contains fermented egg in water. The top jar contains a funnel to prevent gnats from escaping.

Likewise, investigators have tested a variety of baits including hog liver, kidneys, beef 'slime', blood and 'sundry chemicals' (Herms 1928) (Table 2). Extensive investigations in the Coachella Valley have also used a variety of other methods to capture gnats (Burgess 1950). Adults were studied using direct observations and sweep nets, larvae were sampled with shovels and soil sieves. They also found that red and green traps collected significantly more gnats than blue and black traps, which collected more gnats than yellow traps (Snoddy 1974).

Beginning in the late 1960s, several possible attractants were identified, isolated, formulated, and tested as possible baits for gnats (Table 2). However, baits are difficult to standardize, and some can be corrosive, and all are malodorous.

Controls

Protective Materials and Repellents

In his early investigations, Schwarz (1895) noted that a close-fitting veil could protect eyes from gnats but also stated that wearing a veil in the summer in Florida was 'a torture almost equal to that of the flies.' He also observed that sprinkling clothing with eucalyptus oil (and perhaps other strong-smelling oils) could deter gnats. These types of essential oils are the active ingredients of various cottage industry gnat repellents (e.g., Homie Juice, No Gnats, etc.) currently sold in gas stations and other stores throughout the gnat prone areas of the southeastern United States (K.D.K., personal observations).

Mulla (1963a) tested 15 materials (though none of them contained DEET or other current products). In both olfactometer and skin tests, dimethyl carbate, ethyl hexanediol, and Triple Mix [64% dimethyl phthalate, 17% ethyl hexanediol, and 19% Indalone (butyl 3,4 dihydro-2,2-dimethyle-4-oxo-2-II-pyran-6-carboxylate)] showed the greatest effect. The remaining materials tested manifested moderate to very little repellency. Axtell (1967) also used a turntable mechanism to evaluate repellents, most of which are no longer available for use. They found the greatest repellency from Triple Mix, MGK Formula 5780, MGK repellent 11, butyl acetanilide, and butyl ethyl propanediol. Repellents containing DEET can provide some temporary protection (Axtell 1967, Machtinger and Kaufman 2011). A screen fence, or other barrier that is higher than ~2.5 m high, can exclude over 90% of the eye gnats in an area since they fly close to the ground (Bethke et al. 2013), however one individual *L. pusio* adult was collected from an airplane flying ~300 m over Illinois (Glick 1960).

Table 2. Baits used in gnat monitoring and management

Bait	Attractant activity	Reference
Liver secretions and excretions, ground beef, kidneys	Feeding but not oviposition	Herms 1928
Bermuda grass	Oviposition but not feeding	Herms 1928
Onions, cotton, dates, tamarisk, saltbush, ditch 'ooze'	No activity	Herms 1928
Hog liver + urea + table salt + adobe soil + water	Attracted gravid females	Parman 1932, Dow 1959b
Homogenized gnats, aged 2d	Modest attractancy	Dorner and Mulla 1962b
Lursect: whole chicken egg solids fermented in water. Other egg and water baits.	Highly attractive, combined with toxicant for spot control	Mulla et al. 1973 Bethke et al. 2013
Trimethylamine + ammonia + linoleic acid + acetic acid + indole	Highly attractive, similar to fermented eggs in water	Hwang and Mulla 1971, Hwang et al. 1976
Fermented liver and egg	Attractive, used in 'killing stations'	Day and Sjogren 1994

Table 3. Gnat controls and repellents

Compound	Uses and effects	Reference
DDT	Effective control of gnats	Mulla 1960a,b Mulla et al. 1960a
Aldrin	Moderate control, did not reduce breeding	Mulla et al. 1960a
Heptachlor		
Dieldrin and Thiodan	No control	Mulla et al. 1960a
Parathion	Most to least effective	Georghiou and Mulla 1961
Dicapthon	Effective knockdown	
Ronnel	Effective knockdown	
Diazinon		
Dichlorvos		
Dibrom		
Trithion		
Methyl trithion		
Malathion		
Guthion		
Dylox		
Phostex		
DDT		
Dieldrin		
Isolan		
3-ter-butylphenyl N-methylcarbamate		
Dicapthon, Malathion, Parathion	Effective knockdown	Mulla et al. 1960b
With Lursect: Dichlorvos, Naled, Trichlorfon, Isolan	Effective knockdown/killing	Mulla and Axelrod 1974
Thiamethoxam	Good contact activity	Jiang and Mulla 2006
Imidacloprid, Spinosad	Low contact activity	Jiang and Mulla 2006
Pyrethrins, Piperonyl Butoxide	Provide some relief to livestock	Machtinger and Kaufman 2011

Pesticides and Other Controls

There are currently no effective area-wide chemical controls for eye gnats (Machtinger and Kaufman 2011). Tests of insecticides, fogs, and soil treatments have had varying degrees of success (Table 3). Effects range from moderate control to quick knockdown of flying gnats to some degree of relief for besieged livestock. However, many of the more effective compounds are not labeled for gnat control or not in use at all in the United States.

The development of resistance to chemical treatments is a risk that must be considered. Mulla (1962d) documented a Coachella Valley strain of eye gnat exhibiting approximately 1,000-fold resistance to dieldrin and heptachlor. This same strain developed tolerances to DDT five times stronger than unexposed gnats in only four years of large-scale gnat control treatments.

In addition to chemical treatments, other integrative methods can reduce populations. Limiting cultivation can reduce population densities, as can limiting soil cultivation to essential activities and to times when temperatures are below 18°C or winds above 3 km/h (Legner 1970). Eliminating weeds with herbicide can drastically reduce eye gnat breeding (Mulla 1963a), though weed destruction and frequent tilling may only result in low levels of areawide gnat control (Mulla 1963b).

Biological control has been explored to varying degrees and effects as well. The entomopathogenic fungus *Beauveria bassiana* can cause up to 100% mortality in both adults and larvae of *L. collusor* (Hall et al. 1972). Many species of Hymenoptera parasitize *L. collusor*, but may not be very effective as biological control agents (Table 4, Bay et al. 1964, Legner 1967, Eskafi 1976). Some parasitoids, such as species of *Hexacola* may use blades of grass as landmarks to locate the larval gnats below the soil surface (Legner and Bay 1964, Legner 1968, Eskafi 1976). *Hexacola* sp. nr. *websteri* are parthenogenetic (producing only females) at 27°C but will produce males at 32°C (Eskafi and Legner 1974c). *Ooencyrtus submetallicus* (Howard) (Hymenoptera: Encyrtidae), an egg parasite of the southern green stink bug *Nezara viridula* (L.) (Hemiptera: Pentatomidae), also parasitizes pupae of *L. pusio* (Legner and Bay 1965a). Methods to collect eye gnat parasitoids

Table 4. Predators and parasitoids of *Liohippelates* eye gnats

Parasitoid/predator			Gnat species	Location	Reference
ARANEAE	Theridiidae	*Anelosimus studiosus* (Hentz)	*Liohippelates*	FL	Brach 1977
COLEOPTERA	Carabidae	*Amara californica* DeJean	*L. collusor*	CA	Legner and Bay 1970
		Anisodactylus californicus DeJean	*L. collusor*	CA	Legner and Bay 1970
		Stenolophus maculatus (LeConte)	*L. collusor*	CA	Legner and Bay 1970
	Staphylinidae	*Aleochara* sp.	*L. collusor*	CA	Legner and Bay 1970
		Platystethus sp.	*L. collusor*	CA	Legner and Bay 1970
		Philonthus sp.	*L. collusor*	CA	Legner and Bay 1970
		Aleocharine gn. sp.	*Liohippelates*	CA	Moore 1965
DERMAPTERA	Anisolabididae	*Euborellia annulipes* (Lucas)	*L. collusor*	CA	Legner and Bay 1970
DIPTERA	Asilidae	*Atomosia puella* (Wiedemann)	*Liohippelates*	FL	Bromley 1950
		Efferia cressoni (Hine)	*L. pusio*	WY	Dennis et al. 1986
HEMIPTERA	Reduviidae	*Phymata pennsylvanica* Handlirsch	*Liohippelates*	IL	Balduf 1943
HYMENOPTERA	Crabronidae	*Lindenius columbianus* (Kohl)	*L. bishoppi*	MA	Miller and Kurczewski 1975
		Oxybelus emarginatus Say	*Liohippelates*	GA	Snoddy 1968
	Encyrtidae	*Ooencyrtus submetallicus* Howard	*L. pusio*	CA, PR	Legner and Bay 1965a,b, Zuparko 2015
	Figitidae	*Hexacola* sp.	*Liohippelates*	CA	Mulla 1962c, Legner and Bay 1970
		Hexacola nr. *websteri* (Crawford)	*L. collusor*	CA	Eskafi 1976, Eskafi and Legner 1974a,b,c
		Trybliographa sp.	*Liohippelates*	PR	Legner and Bay 1964, 1965b
	Formicidae	*Monomorium pharaonis* (L.)	*Liohippelates*	PR	Legner and Bay 1965b
		Solenopsis geminata (F.)	*Liohippelates*	PR	Legner and Bay 1965b
		Solenopsis invicta Buren	*L. pusio*	FL	Williams et al. 1990
		Tapinoma melanocephalum (F.)	*Liohippelates*	PR	Legner and Bay 1965b
		Tetramorium guineense (F.)	*Liohippelates*	PR	Legner and Bay 1965b
		Wasmannia auropunctata (Reg.)	*Liohippelates*	PR	Legner and Bay 1965b
	Ichneumonidae	*Trichopria occidentalis* (Fouts)	*L. collusor*	CA	Bay et al. 1964, Legner and Bay 1970
	Pteromalidae	*Eupteromalus nidulans* (Thomson)	*L. collusor*	CA	Bay et al. 1964
		gn. sp.	*Liohippelates*	PR	Legner and Bay 1965b
		Spalangia drosophilae Ashmead	*Liohippelates*	CA, PR	Bay and Legner 1963, Bay et al. 1964, Legner and Bay 1964, 1965b, 1970
		Spalangia nov. sp.	*Liohippelates*	PR	Legner and Bay 1965b
		Trichomalopsis hemiptera	*L. collusor*	CA	Legner and Bay 1970
ISOPODA	Armadillidiidae	*Armadillidium vulgare* (Latreille)	*L. collusor*	In vitro	Edney et al. 1974
ODONATA	Aeshnidae	*Anax junius* (Drury)	*Liohippelates*	FL	Neal and Whitcomb 1972
SARCOPTIFORMES	Histiostomatidae	*Anoetus* sp.	*L. collusor*	In vitro	Mulla 1958
SQUAMATA	Dactyloidae	*Anolis grahami*	*L. pusio*	Bermuda	Simmonds 1958
TROMBIDIFORMES	Pyemotidae	gn. sp.	*L. collusor*	In vitro	Mulla 1958
TRYPANOSOMATIDA	Trypanosomatidae	*Herpetomonas muscarum* Saville-Kent	*L. pusio*	In vitro	Bailey and Brooks 1972a,b
[various]	[various]	[various]	*L. collusor*	CA	Legner et al. 1971

vary but generally involve burying immatures in cups filled with larval growth medium (Legner and Bay 1964, Moore 1965, Legner et al. 1966b, Legner 1968). Predators include ants (Hymenoptera: Formicidae) and larger wasps (Hymenoptera: Crabronidae) (Legner and Bay 1965b, Snoddy 1968, Miller and Kurczewski 1975).

In addition to hymenopterans, other arthropods predate or parasitize eye gnats, including ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), earwigs (Dermaptera: Anisolabididae), assassin bugs (Hemiptera: Reduviidae), cobweb spiders (Araneae: Theridiidae), terrestrial isopods (Isopoda: Armadillidiidae), mites, darner dragonflies (Odonata: Aeshnidae), and robber flies (Diptera: Asilidae) (Table 4, Balduf 1943, Bromley 1950, Moore 1965, Legner and Bay 1970, Neal and Whitcomb 1972, Edney et al. 1974, Brach 1977, Dennis et al. 1986, Mulla 1958). Legner et al. (1971) collected over 100 different species of predatory and scavenger arthropods in the habitat of *L. collusor*. Eggs and first stage larvae of eye gnats are significantly more susceptible to predation than later larval stages, pupae, and adults (Legner et al. 1971). In addition, one instance of a lizard in Bermuda eating two gnats has been reported (Simmonds 1958). One attempt to control eye gnats using a nematode was unsuccessful (Nigh et al. 1997). Finally, eye gnat pupae may serve as effective—albeit expensive—kill bait for red imported fire ant when dipped in acetone solutions of fenoxycarb, even more effective than commercial formulations (Williams et al. 1990).

Critical Knowledge Gaps

Research on eye gnats in the past century has been extensive, yet numerous gaps still exist. The position of eye gnats within trophic food web interactions remains poorly defined. Little research exists documenting what wildlife species consume eye gnats or if any wildlife species rely on eye gnats for survival—as we suspect gnats are an easy prey species for animals in forested ecosystems (birds, small mammals, amphibians, reptiles, as well as larger predatory and parasitic arthropods) to catch. The genetic diversity of eye gnats has not been assessed and could provide important information such as roles in trophic cascades, dispersal mechanisms, range, and movement between populations.

Few have attempted areawide management of eye gnats. The development of effective techniques could allow for larger scale reductions in eye gnat abundance, however, the ecological impacts and cost of implementation of such efforts should be considered. The Yuma County Pest Abatement District operates approximately 8,800 chicken egg baited traps per week to reduce populations of *L. collsuor* in Yuma County, Arizona. These traps effectively reduce populations but do not eliminate eye gnats in the area (E. MacAdam, personal communication). Effective repellents are also needed for humans, cattle, and other outdoor livestock. Repelling eye gnats could greatly improve quality of life for many animals.

Finally, eye gnat ecology—especially in natural systems—has been less studied, leaving their primary ecological roles unknown. We suspect eye gnats may play an important role in decomposition, nutrient movement, and trophic interactions in forested ecosystems. Even with the substantial and substantive body of knowledge on these gnats, we have much to learn about their biology, ecology, and management in different ecosystems, land uses, and environmental conditions.

Acknowledgments

We thank the Jones Center at Ichauway and Clemson University for providing funding and supporting advancement in eye gnat research. We also thank iNaturalist for providing creative commons licensing on images. We acknowledge the utility of the Symbiota Collections of Arthropods Network, the Global Biodiversity Information Facility, and the Integrated Taxonomic Information System for cataloging records and taxonomic authorities of eye gnats and other arthropods. Finally, we thank the reviewers and editors for very useful comments, additional information, and even sample traps.

References Cited

Amprako, L., K. Stenchly, M. Wiehle, G. Nyarko, and A. Buerkert. 2020. Arthropod communities in urban agricultural production systems under different irrigation sources in the northern region of Ghana. Insects 11: 488. doi:10.3390/insects11080488

Axtell, R. C. 1967. Evaluations of repellents for *Hippelates* eye gnats. J. Econ. Entomol. 60: 176–180.

Bailey, C. H., and W. M. Brooks. 1972a. Effects of *Herpetomonas muscarum* on development and longevity of the eye gnat, *Hippelates pusio* (Diptera: Chloropidae). J. Invertebr. Pathol. 20: 31–36.

Bailey, C. H., and W. M. Brooks. 1972b. Histological observations on larvae of the eye gnat *Hippelates pusio* (Diptera: Chloropidae), infected with the flagellate *Herpetomonas muscarum*. J. Invertebr. Pathol. 19: 342–353.

Balduf, W. V. 1943. Third annotated list of *Phymata* prey records (Phymatidae, Hemiptera). Ohio J. Sci. 43: 74–78.

Bay, E. C., and E. F. Legner. 1963. Quality control in the production of *Hippelates collusor* (Tsnd.) for use in the search and rearing of their natural enemies. Proc. N. J. Mosq. Exterm. Comm. 1963: 403–410.

Bay, E. C., E. F. Legner, and R. Medved. 1964. *Hippelates collusor* (Diptera: Chloropidae) as a host for four species of parasitic Hymenoptera in southern California. Ann. Entomol. Soc. Am. 57: 582–584.

Bengston, I. A. 1933. Seasonal acute conjunctivitis occurring in the southern states. Public Health Rep. 48: 917–926.

Bethke, J. A., B. Vander Mey, and L. M. Bates. 2013. Eye gnats: integrated pest management for home gardeners and landscape professionals. *In* M. L. Fayard (ed.), Pest Notes Publication 74164. University of California Agriculture and Natural Resources, Davis, CA.

Biery, T. L. 1977. *Hippelates* eye gnats: a review and bibliography. U.S. Air Force School of Aerospace Medicine, Brooks Air Force Base, TX.

Bigham, J. T. 1941. *Hippelates* (eye gnat) investigations in the southeastern states. J. Econ. Entomol. 34: 439–444.

Brach, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution. 31: 154–161.

Bradley, A. 2002. Bovine mastitis: an evolving disease. Vet. J. 164: 116–128.

Bromley, S. W. 1950. Florida Asilidae (Diptera) with description of one new species. Ann. Entomol. Soc. Am. 43: 227–239.

Buehrle, J. W., J. T. Holloway, R. A. Goodman, and R. K. Sikes. 1983. Gnat sore eyes: seasonal, acute conjunctivitis in a southern state. South Med. J. 76: 587–589.

Burgess, R. W. 1950. The life history and breeding habits of the eye gnat, *Hippelates pusio* Loew, in the Coachella Valley, Riverside County, California. Am. J. Epidemiol. 53: 164–177.

Day, J. F., and R. D. Sjogren. 1994. Vector control by removal trapping. Am. J. Trop. Med. 50: 126–133.

Defoliart, G. R., and C. D. Morris. 1967. A dry ice–baited trap for the collection and field storage of hematophagous Diptera. J. Med. Ent. 4: 360–362.

Dennis, D. S., R. J. Lavigne, and S. W. Bullington. 1986. Ethology of *Efferia cressoni* with a review of the comparative ethology of the genus (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 88: 42–55.

Dorner, R. W., and M. S. Mulla. 1961. Response of the eye gnat *Hippelates collusor* to light of different wave lengths. Ann. Entomol. Soc. Am. 54: 69–72.

Dorner, R. W., and M. S. Mulla. 1962a. Laboratory study of wind velocity and temperature preference of *Hippelates* eye gnats. Ann. Entomol. Soc. Am. 55: 36–39.

Dorner, R. W., and M. S. Mulla. 1962b. On the nature of the eye gnat attractant chemical contained in ground-up eye gnats, *Hippelates collusor*. Ann. Entomol. Soc. Am. 55: 33–35.

Dow, R. P. 1959a. Dispersal of adult *Hippelates pusio*, the eye gnat. Ann. Entomol. Soc. Am. 52: 372–381.

Dow, R. P. 1959b. A method of testing insect traps and attractants, and its application to studies of *Hippelates pusio* and *Culex tarsalis*. J. Econ. Entomol. 52: 496–503.

Dow, R. P., and G. A. Hutson. 1958. The measurement of adult populations of the eye gnat, *Hippelates pusio*. Ann. Entomol. Soc. Am. 51: 351–360.

DuBose, W. P., Jr, and R. C. Axtell. 1968. Sensilla on the antennal flagella of *Hippelates* eye gnats. Ann. Entomol. Soc. Am. 61: 1547–1561.

Duda, O. 1929. Die ausbeute der deutschen Chaco-Expedition 1925/6 (Diptera). VI. Sepsidae, VII. Piophilidae, VIII. Cypselidae, IX. Drosophilidae und X. Chloropidae. Konowia. 8: 33–50.

Edney, E. B., W. Allen, and J. McFarlane. 1974. Predation by terrestrial arthropods. Ecology. 55: 428–433.

Eskafi, F. M. 1976. Host instar, habitat, and host exposure affecting parasitization by *Hexacola* sp. near *websteri* of *Hippelates collusor*. Ann. Entomol. Soc. Am. 69: 42–44.

Eskafi, F. M., and E. F. Legner. 1974a. Descriptions of immature stages of the cynipid *Hexacola* sp. near *websteri* (Eucolinae: Hymenoptera), a larval-pupal parasite of *Hippelates* eye gnats (Diptera: Chloropidae). Can. Entomol. 106: 1043–1048.

Eskafi, F. M., and E. F. Legner. 1974b. Fecundity, development, and diapause in *Hexacola sp*. near *websteri*, a parasite of *Hippelates* eye gnats. Ann. Entomol. Soc. Am. 67: 769–771.

Eskafi, F. M., and E. F. Legner. 1974c. Parthenogenetic reproduction in *Hexacola* sp. near *websteri*, a parasite of Hippelates eye gnats. Ann. Entomol. Soc. Am. 67: 767–768.

Flint, H. M. 1965. The effects of gamma radiation on the fertility and longevity of *Hippelates pusio*. J. Econ. Entomol. 58: 555–559.

Frost, S. W. 1979. A preliminary study of North American insects associated with elderberry flowers. Fla. Entomol. 62: 341–355.

Gaydon, D. M., and T. R. Adkins. 1969. Effect of cultivation on emergence of eye gnats (*Hippelates* spp.) in South Carolina. J. Econ. Entomol. 62: 312–314.

GBIF Backbone Taxonomy. 2021. *Liohippelates pusio* (Loew, 1872) in GBIF Secretariat. Checklist dataset https://doi.org/10.15468/39omei. Accessed 22 February 2022.

Georghiou, G. P., and M. S. Mulla. 1961. A method and results of screening insecticides against adult *Hippelates* eye gnats. J. Econ. Entomol. 54: 264–267.

Gerhardt, R. R., and R. C. Axtell. 1972. Flight of the eye gnat, *Hippelates pusio* (Diptera: Chloropidae): effect of temperature, light, moisture and wind velocity. J. Med. Ent. 9: 425–428.

Glick, P. A. 1960. Collecting insects by airplane, with special reference to dispersal of the potato leaf-hopper. U.S. Department of Agriculture Technical Bulletin, number 1222, Washington, DC.

Graham-Smith, G. S. 1930. The Oscinidae (Diptera) as vectors of conjunctivitis, and the anatomy of their mouth parts. Parasitology. 22: 457–467.

Hall, D. G. 1932. Some studies on the breeding media, development, and stages of the eye gnat *Hippelates pusio* Loew (Diptera: Chloropidae). Am. J. Hyg. 16: 854–864.

Hall, I. M., H. T. Dulmage, and K. Y. Arakawa. 1972. The susceptibility of the eye gnat *Hippelates collusor* to entomogenous bacteria and fungi. J. Invertebr. Pathol. 19: 28–31.

Harrison, I. H., G. A. Da Silva, M. Pitman, D. W. Fleming, A. Vranjac, and C. V. Broome. 1989. Epidemiology and clinical spectrum of Brazilian purpuric fever. J. Clin. Microbiol. 27: 599–604.

Harrison, L. H., V. Simonsen, and E. A. Waldman. 2008. Emergence and disappearance of a virulent clone of *Haemophilus influenzae* Biogroup *aegyptius*, cause of Brazilian Purpuric Fever. Clin. Microbiol. Rev. 21: 594–605. doi:10.1128/CMR.00020-08

Hendrix, C. M. 2013. Eye gnats. The Merck Veterinary Manual, Merck & Co., Whitehouse Station, NJ. https://www.merckvetmanual.com/integumentary-system/flies/eye-gnats. Accessed 22 February 2022.

Herms, W. B. 1926. *Hippelates* flies and certain other pests of the Coachella Valley, California. J. Econ. Entomol. 19: 692–695. doi:10.1093/jee/19.5.692a

Herms, W. B. 1928. The Coachella Valley (California) *Hippelates* fly project. J. Econ. Entomol. 21: 690–693. doi:10.1093/jee/21.5.690

Herms, W. B., and R. W. Burgess. 1930. A description of the immature stages of *Hippelates pusio* Loew and a brief account of its life history. J. Econ. Entomol. 23: 600–603. doi:10.1093/jee/23.3.600

Hwang, Y., and M. S. Mulla. 1971. *Hippelates* eye gnat attractants. 1. Isolation and identification of ether-soluble coattractants produced by fermentation of whole-egg solids. Ann. Entomol. Soc. Am. 64: 1086–1091.

Hwang, Y. S., M. S. Mulla, and H. Axelrod. 1976. Identification of attractants and coattractants for *Hippelates* eye gnats (Diptera: Chloropidae). J. Agr. Food Chem. 24: 164–169.

Jiang, Y., and M. S. Mulla. 2006. Susceptibility of the adult eye gnat *Liohippelates collusor* (Diptera: Chloropidae) to neonicotonoids and spinosad insecticides. J. Vector Ecol. 31: 65–70. doi:10.3376/1081-1710(2006)31[65:SOTAEG]2.0.CO;2

Karandinos, M. G., and R. C. Axtell. 1972. Population density effects on fecundity of *Hippelates pusio* Loew (Diptera: Chloropidae). Oecologia 9: 341–348.

Kumm, H. W., and T. B. Turner. 1936. The transmission of yaws from man to rabbits by an insect vector, *Hippelates pallipes* Loew. Am. J. Trop. Med. 16: 245–262.

Legner, E. F. 1966. Competition among larvae of *Hippelates collusor* (Diptera: Chloropidae) as a natural control factor. J. Econ. Entomol. 59: 1315–1321.

Legner, E. F. 1967. Two exotic strains of *Spalangia drosophilae* merit consideration in biological control of *Hippelates collusor* (Diptera: Chloropidae). Ann. Entomol. Soc. Am. 60: 458–462.

Legner, E. F. 1968. Parasite activity related to ovipositional responses in *Hippelates collusor*. J. Econ. Entomol. 61: 1160–1163.

Legner, E. F. 1970. Advances in the ecology of *Hippelates* eye gnats in California indicate means for effective integrated control. Proc. Pap. Annu. Conf. Calif. Mosq. Contr. Assoc. 38: 89–90.

Legner, E. F., and E. C. Bay. 1964. Natural exposure of *Hippelates* eye gnats to field parasitization and the discovery of one pupal and two larval parasites. Ann. Entomol. Soc. Am. 57: 767–769.

Legner, E. F., and E. C. Bay. 1965a. *Ooencyrtus submetallicus* Howard in an extraordinary host-relationship with *Hippelates pusio* Loew. Canad. Ent. 97: 556–557.

Legner, E. F., and E. C. Bay. 1965b. Predatory and parasitic agents attacking the *Hippelates pusio* complex in Puerto Rico. J. Agric. Univ. P.R. 49: 377–385.

Legner, E. F., and E. C. Bay. 1970. Dynamics of *Hippelates* eye gnat breeding in the Southwest. Calif. Agric. 24: 4–6.

Legner, E. F., E. C. Bay, and R. A. Medved. 1966a. Behavior of three native pupal parasites of *Hippelates collusorin* controlled systems. Ann. Entomol. Soc. Am. 59: 977–984.

Legner, E. F., G. A. Olton, and F. M. Eskafi. 1966b. Influence of physical factors on the developmental stages of *Hippelates collusor* in relation to the activities of its natural parasites. Ann. Entomol. Soc. Am. 59: 851–861.

Legner, E. F., L. Moore, and R. A. Medved. 1971. Observations on predation of *Hippelates collusor* and distribution in southern California of associated fauna. J. Econ. Entomol. 64: 461–468.

Loew, H. 1872. Diptera Americae septentrionalis indigena, centuria decima. Berl. Entomol. Zeitschr. 16: 49–124.

Lyman, F. E., and R. P. Dow. 1948. Something about those eye gnats. Ga. Rev. 2: 428–433.

Machtinger, E., and P. E. Kaufman. 2011. Eye gnats, grass flies, eye flies, fruit flies *Liohippelates* spp. (Insecta: Diptera: Chloropidae). University of Florida, Gainesville, FL. EENY-485.

Mackie, M. 2017. Climate change means more gnats bugging Middle Georgians. WGXA. https://wgxa.tv/news/local/climate-change-means-more-gnats-bugging-middle-georgians. Accessed 9 March 2022.

Miller, R. C., and F. E. Kurczewski. 1975. Comparative behavior of wasps in the genus *Lindenius* (Hymenoptera: Sphecidae, Crabroninae). J. N. Y. Entomol. Soc. 83: 82–120.

Moore, L. D. 1965. A coleopterous parasite of *Hippelates* eye gnats of the family Staphylinidae. Proc. Calif. Mosq. Contr. Assoc. 33: 61–62.

Mulla, M. S. 1958. Control of mites in laboratory cultures of the eye gnat, *Hippelates collusor* (Townsend). J. Econ. Entomol. 51: 461–462. doi:10.1093/jee/51.4.461

Mulla, M. S. 1960a. Chlorinated hydrocarbon insecticides as soil treatments against the eye gnat *Hippelates collusor* (Townsend) in the laboratory. J. Econ. Entomol. 53: 367–372.

Mulla, M. S. 1960b. Effectiveness of granular insecticides against eye gnats and mosquitoes as affected by toxicant concentration. Mosq. News. 20: 362–367.

Mulla, M. S. 1961. Control of *Hippelates* gnats with soil treatments using organochlorine insecticides. J. Econ. Entomol. 54: 636–642.

Mulla, M. S. 1962a. The breeding niches of *Hippelates* gnats. Ann. Entomol. Soc. Am. 55: 389–393. doi:10.1093/aesa/55.4.389

Mulla, M. S. 1962b. Mass rearing of three species of *Hippelates* eye gnats (Diptera: Chloropidae). Ann. Entomol. Soc. Am. 55: 253–258.

Mulla, M. S. 1962c. Recovery of a cynipoid parasite from *Hippelates* pupae. Mosq. News. 3: 301–302.

Mulla, M. S. 1962d. Resistance in the eye gnat *Hippelates collusor* to soil insecticides. J. Econ. Entomol. 55: 130–133. doi:10.1093/jee/55.1.130

Mulla, M. S. 1963a. Chemical repellents for *Hippelates* eye gnats – a method and procedure for evaluation. J. Econ. Entomol. 56: 753–757. doi:10.1093/jee/56.6.753

Mulla, M. S. 1963b. An ecological basis for the suppression of *Hippelates* eye gnats. J. Econ. Entomol. 56: 768–770. doi:10.1093/jee/56.6.768

Mulla, M. S. 1964. Seasonal population trends of *Hippelates* gnats (Diptera: Chloropidae) in southern California. Ann. Entomol. Soc. Am. 57: 12–19. doi:10.1093/aesa/57.1.12

Mulla, M. S., and M. M. Barnes. 1957. On laboratory colonization of the eye gnat, *Hippelates collusor* Townsend. J. Econ. Entomol. 50: 813–816. doi:10.1093/jee/50.6.813

Mulla, M. S., and R. B. March. 1959. Flight range, dispersal patterns, and population density of the eye gnat, *Hippelates collusor*. Ann. Entomol. Soc. Am. 52: 641–646. doi:10.1093/aesa/52.6.641

Mulla, M. S., and H. Axelrod. 1974. Attractants for synanthropic flies: Attractant-toxicant formulations, their potency against a *Hippelates* eye gnat. J. Econ. Entomol. 67: 13–16. doi:10.1093/jee/67.1.13

Mulla, M. S., and U. Chansang. 2007. Pestiferous nature, resting sites, aggregation, and host-seeking behavior of the eye fly *Siphunculina funicola* (Diptera: Chloropidae) in Thailand. J. Vector Ecol. 32: 292–301. doi:10.3376/1081-1710(2007)32[292:PNRSAA]2.0.CO;2

Mulla, M. S., M. M. Barnes, and M. J. Garber. 1960a. Soil treatments with insecticides for control of the eye gnats, *Hippelates collusor* and *H. hermsi*. J. Econ. Entomol. 53: 362–365. doi:10.1093/jee/53.3.362

Mulla, M. S., R. W. Dorner, G. P. Georghiou, and M. J. Garber. 1960b. Olfactometer and procedure for testing baits and chemical attractants against *Hippelates* eye gnats. Ann. Entomol. Soc. Am. 53: 529–537. doi:10.1093/aesa/53.4.529

Mulla, M. S., H. Axelrod, and I. Toshiaki. 1973. Attractants for synanthropic flies: 3. Evaluation, development and formulation of attractive baits against *Hippelates collusor*. J. Econ. Entomol. 66: 1089–1094. doi:10.1093/jee/66.5.1089

Mulla, M. S., H. Axelrod, and M. J. Wargo. 1990. Chemical attractant formulations against the eye gnat *Hippelates collusor* (Diptera: Chloropidae). Bull. Soc. Vector Ecol. 15: 156–165.

Mussulman, J. 2011. Eye gnat. Discovering Lewis and Clark. https://www.lewis-clark.org/article/3137. Accessed 22 February 2022.

Nartshuk, E. P. 2014. Grass-fly larvae (Diptera, Chloropidae): diversity, habitats, and feed specializations. Entomol. Rev. 94: 514–525. doi:10.1134/S001387381404006X

Neal, T. M., and W. H. Whitcomb. 1972. Odonata in the Florida soybean agroecosystem. Fla. Entomol. 55: 107–114.

Needham, J. G. 1948. Ecological notes on the insect population of the flower heads of *Bidens pilosa*. Ecol. Monogr. 18: 431–446.

Nigh, E. L., C. Sumner, and T. Svodoba. 1997. An evaluation of biological agents for control of citrus nematode and *Liohippelates* eye gnat, pp. 82–90. *In* Citrus research report. College of Agriculture, University of Arizona, Tucson, AZ.

Parman, D. C. 1932. A box type trap to aid in the control of eye gnats and blowflies. U.S. Department of Agriculture, Washington, DC.

Payne, W. J., Jr, J. R. Cole, Jr, E. L. Snoddy, and H. R. Seibold. 1977. The eye gnat *Hippelates pusio* as a vector of bacterial conjunctivitis using rabbits as animal models. J. Med. Entomol. 13: 599–603.

Roberts, R. H. 1968. A feeding association between *Hippelates* (Diptera: Chloropidae) and Tabanidae on cattle: its possible role in transmission of anaplasmosis. Mosq. News. 28: 236–237.

Roberts, R. H., W. A. Pund, H. F. McCrory, J. W. Scales, and J. C. Collins. 1969. Culicidae and Tabanidae as potential vectors of anaplasmosis in Mississippi. Ann. Entomol. Soc. Am. 62: 863–868.

Rogoff, W. M. 1978a. Eye gnats (Family Chloropidae), pp. 52–59. *In* R. A. Bram (ed.), Surveillance and collection of arthropods of veterinary importance. Animal and Plant Health Inspection Service in Cooperation with Agricultural Research Service, U.S. Department of Agriculture, Washington, DC.

Rogoff, W. M. 1978b. Methods for collecting eye gnats (Diptera: Chloropidae). U.S. Department of Agriculture, Science and Education Administration, Berkeley, CA.

Russell, R., C. D. Otranto, and R. L. Wall. 2013. Eye flies (Diptera: Chloropidae and Drosophilidae), pp. 111–115. *In* R. C. Russell, C. D. Otranto, **and** R. L. Wall (eds.), The encyclopedia of medical and veterinary entomology. CABI, Boston, MA.

Sabrosky, C. W. 1941. The *Hippelates* flies or eye gnats: preliminary notes. Can. Entomol. 73: 23–27. doi:10.4039/Ent7323-2

Sabrosky, C. W. 1987. Chloropidae, pp. 1049–1068. *In* J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, **and** D. M. Wood (eds.), Manual of nearctic Diptera, vol. 2. Biosystematics Research Centre, Ottawa, ON.

Sanders, D. A. 1940. *Musca domestica* and *Hippelates* flies-vectors of bovine mastitis. Science. 92: 286.

Scherer, L. E. 1964. Studies of the emergence rhythm of the eye gnat *Hippelates pusio* Loew (Diptera: Chloropidae). Fla. Entomol. 47: 227–233.

Schwarz, E. A. 1895. The *Hippelates* plague in Florida. Insect Life. 7: 374–379.

Schwartz, P. H., Jr. 1964. Aspirator for rapid sexing and transfer of eye gnats, *Hippelates pusio*. J. Econ. Entomol. 57: 784–786.

Schwartz, P. H., Jr. 1965. Some observations of the reproduction of the eye gnat, *Hippelates pusio*. J. Med. Ent. 2: 141–144.

Schwartz, P. H., Jr, and R. B. Turner. 1965. A dietary study of the adult eye gnat *Hippelates pusio* (Diptera: Chloropidae). Ann. Entomol. Soc. Am. 59: 277–280.

Simmonds, F. J. 1958. The effect of lizards on the biological control of scale insects in Bermuda. Bull. Entomol. Res. 49: 601–612.

Snoddy, E. L. 1968. Simuliidae, Ceratopogonidae, and Chloropidae as prey of *Oxybelus emarginatum*. Ann. Entomol. Soc. Am. 61: 1029–1030.

Snoddy, E. L. 1974. Some aspects of trap color and designs for *Hippelates pusio* (Diptera: Chloropidae). J. Med. Ent. 11: 499–500.

Snoddy, E. L., J. R. Cole, and W. J. Payne, Jr. 1974. Studies on the bacterial flora of *Hippelates pusio* (Diptera: Chloropidae). J. Med. Entomol. 11: 226.

Stegmaier, C. E. 1966. A leaf-mining *Hippelates* in south Florida (Diptera: Chloropidae). Fla. Entomol. 49: 19–21.

Townsend, C. H. T. 1895. On the Diptera of Baja California, including some species from adjacent regions. Proc. Calif. Acad. Sci. 4: 593–620.

United States Department of Agriculture (July 2019). 2019. Factsheet vesicular stomatitis.

Wiesenborn, W. D. 2016. Conspecific pollen on insects visiting female flowers on the oak parasite *Phoradendron coryae* (*Viscaceae*). West. N. Am. Naturalist 76: 265–274.

Williams, D. F., and L. C. Kuitert. 1974. Dispersion and population densities of the eye gnat *Hippelates pusio*. Fla. Entomol. 57: 361–368.

Williams, D. F., C. S. Lofgren, and R. K. Vander Meer. 1990. Fly pupae as attractant carriers for toxic baits for red imported fire ants (Hymenoptera: Formicidae). J. Econ. Entomol. 83: 67–73.

Zuparko, R. L. 2015. Annotated checklist of California Encyrtidae (Hymenoptera). Zootaxa. 4017: 001–126.