

Phoretic copulation in the velvet ant *Sphaerophthalma pensylvanica* (Lepeletier) (Hymenoptera, Mutillidae): A novel behavior for Sphaerophthalminae with a synthesis of mating strategies in Mutillidae

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Abstract

Phoretic copulation, a form of phoresy in which a male physically transports a female by flight and/or foot from their initial site of contact before mating, is newly recorded in the Nearctic velvet ant *Sphaerophthalma pensylvanica* (Lepeletier, 1845) (Hymenoptera: Mutillidae). Further, this is the first record of the behavior in the species-rich subfamily Sphaerophthalminae. A description of the *S. pensylvanica* mating observation and photographs are provided. All published observations of copulation events in Mutillidae are critically reviewed in the context of mating strategy, and new terminology is proposed for the mating strategies currently known to occur in the family.

Keywords

Ethology, phoresy, sexual dimorphism

Introduction

Velvet ants (Hymenoptera: Mutillidae) are ectoparasitoids of immature holometabolous insects in the orders Hymenoptera, Coleoptera, Diptera, Lepidoptera, and possibly egg predators of Blattodea (Brothers 1989; Brothers et al. 2000). Despite

this wide spectrum of hosts, most host records for mutillids are from solitary bees and apoid wasps (Hymenoptera: Apoidea) (Krombein 1979; Brothers 1989; Brothers et al. 2000; Luz et al. 2016). Extreme sexual dimorphism is the general rule for the family and the sexes have little in common morphologically; males are usually macropterous and the females are always apterous. Sex associations have historically been a major challenge for researchers due to this dimorphism, and the collection of mating pairs in the field, while relatively rare, has been a reliable method for association (Mickel 1937; Nonveiller 1980; Manley and Pitts 2007). Two overarching mating strategies have been observed in Mutillidae: phoretic copulation and in situ copulation.

Phoresy is defined as an interaction between two or more animals in which one individual carries the other(s) for purpose of travel. The individual (or individuals) being carried is termed the phoront(s). Phoresy is particularly common with mites and pseudoscorpions wherein one or a number of individuals will simultaneously travel on a larger arthropod such as a beetle. The carrier animal rarely intentionally carries the phoront except in cases where the phoront is conspecific (or the carrier mistakes the phoront to be conspecific, a common occurrence in Thynnidae (Brown 2000)). Phoretic copulation in Hymenoptera is a form of phoresy in which a larger male physically transports a smaller conspecific female phoront by flight and/or foot from their initial site of contact before mating; the pair may settle on a substrate to mate, or mating may take place during flight (Evans 1969; Brothers 1989). The female is carried by the male primarily by either grasping her around the pronotal neck with his mandibles or by their terminalic union. Phoretic copulation has been observed in three distantly-related families of aculeate Hymenoptera with apterous females: Bethyridae, Mutillidae, and Thynnidae (Evans 1969; Clausen 1976; Brothers 1989; Gordh 1990; Osten 1999; Azevedo et al. 2016). Vivallo (2020) recently reviewed phoretic copulation in aculeate Hymenoptera as a whole with primary emphasis on Thynnidae and the biomechanical aspects of the behavior in that family. For Mutillidae, phoretic copulation has been reported in the following subfamilies and tribes: Dasylabrinae (Dasylabrini), Mutillinae (Ctenotillini, Ephutini, Smicromyrmini, and Trogaspidiini), Myrmosinae (Myrmosini), and Rhopalomutillinae (Table 1). The alternative strategy to phoretic copulation is in situ copulation, where the male does not transport the female from the initial site of contact to mate. These mating strategies in Mutillidae have, thus far, appeared to be representative of taxa at the subfamily and tribe levels. The subfamily Dasylabrinae is the exception wherein both phoretic copulation and in situ copulation have been observed (Table 1).

Sphaerophthalma pensylvanica (Lepeletier, 1845) is a widespread mutillid that occurs throughout the eastern half of the United States, extending as far west as Texas north to Kansas (Krombein 1979). It is one of the most well-studied mutillid species with respect to the parasitoid aspects of its biology (Krombein 1967; Matthews 1997; Pitts and Matthews 2000; Pitts et al. 2010a). Remarkably, there is no published information on its mating behavior. In this contribution, an observation

of phoretic copulation in *S. pensylvanica* is documented and described. Additionally, the published observations of mating strategies in Mutillidae are comprehensively reviewed in order to place this mating observation into the wider behavioral context of the family. This is the first known occurrence of phoretic copulation in Sphaerophthalminae, which is the second largest subfamily of Mutillidae comprising nearly 1,500 described species (Lelej 2005).

Results

The following observation by J. Roberts of the heretofore undocumented mating behavior of *Sphaerophthalma pensylvanica* occurred on August 3, 2018 in Morgan County, Alabama, along the border of the Highland Rim and Cumberland Plateau regions (Figs 1–4). During a walk through a semi-open deciduous wooded area in late afternoon, what was at first presumed to be a solitary male *S. pensylvanica*, was observed flying from the immediate leaf littered ground to the base branches of a short cedar tree, approximately 9–10 inches (23–25 cm) above the ground. It was when the male attempted to land on these lower twigs/leaves that it was then observed that he dropped a female that he had apparently carried from the leaf litter. The female tumbled a few inches directly below the male and landed on some of the lower twigs/leaves. In an unexpected move, the male immediately descended in a quick flight-assisted scurry to retrieve the female and gripped her firmly behind the head with his mandibles. He once again briefly took flight and carried her higher up into the same small cedar tree to a height approximately 24 inches (61 cm) above the ground. A somewhat blurry, but discernible photo was captured of the moment the male began his descent to retrieve the female after he dropped her (Fig. 1).

Once alighted on the upper twigs/leaves and quickly becoming stabilized, with the male's mandibular grip firm on the pronotal neck of the female, they began copulation at which point it appeared the female began to extrude her stinger which facilitated the coupling of genitalia (Fig. 3). The entire copulative duration was just under two minutes, during which time (and immediately prior to) the male's legs were very active in rhythmic flicking motions, tapping the female on both the metasoma as well as around the gena and pronotum, while alternately tapping the top of her head with the scape of his antennae in the same rhythmic fashion, in between leg tapping. During this process the female did not remain purely passive, but kept a grip on the plant material with her mandibles, fore legs, and mid legs (Figs 3, 4). Toward the end of copulation the female used her hind legs to stroke the mid and hind legs of the male, the purpose uncertain but speculatively could be a tactile communication to the male or simply an attempt to regain footing. Once copulation was complete, the male released the female within moments and promptly flew away, while she quickly climbed downward and eventually scurried back into the leaf litter. There was no post-copula interaction observed between the pair.

Discussion

Mating strategies in Mutillidae

This new observation of phoretic copulation in *S. pensylvanica* is recognized as an opportunity to critically review the published information regarding mating strategies in Mutillidae and to develop new terminology that accurately describes them. Data on the mating strategies for 62 mutillid species are comprehensively reviewed in Table 1. References that merely note a pair being collected in copula, or copulating in captivity, were excluded. These observations are numerous in the literature and usually provide no additional information other than the sex association itself. In compiling these data, it became apparent how little is known overall on the mating behavior of the family, especially behavior documented in natural settings. Observations of mating events in captivity have been deemed problematic, as males will attempt to mate with non-conspecific and even non-congeneric females (Ferguson 1962; Manley 1977; Manley and Pitts 2007). Copulation behavior and mating time observed in the laboratory may not be congruent with behavior that would normally occur in the field. The observations cited in Table 1 as being conducted in captivity should be kept with this in mind. The higher classification of Mutillidae in this contribution follows Brothers and Lelej (2017), except *Dolichomutilla* Ashmead, 1899 is considered a member of Mutillini rather than Trogaspidiini, and the two apparent genus-groups that comprise the Mutillini subtribe Ephutina (the *Ephuta* genus-group and the *Odontomutilla* genus-group) are considered full tribes within Mutillinae (Ephutini and Odontomutillini, respectively). These partial modifications in classification are used here in anticipation of a molecular phylogeny of Mutillidae using Ultra-Conserved Elements (Waldren et al. in prep.).

As mentioned previously, there have been two types of mating strategies recognized in mutillids: phoretic copulation and in situ copulation. Two subtypes of phoretic copulation were recognized by Brothers (1989). One was termed “true phoretic copulation” wherein the male initially uses his legs to pick up a female and once terminalic union occurs, phoresy is strictly effected by the genitalia and surrounding metasomal structures; mating occurs during flight or while nectaring. Within Mutillidae, this first subtype is known to occur in the myrmosine tribe Myrmosini and the subfamily Rhopalomutillinae (Table 1). “True phoretic copulation” also occurs in some subfamilies of Bethyridae and Thynnidae (Evans 1969; Osten 1999; Azevedo et al. 2016). The other subtype is known to commonly occur in the subfamily Mutillinae (excluding Mutillini and Odontomutillini) and now in Sphaerophthalminae (*S. pensylvanica*) (Table 1), wherein the female is primarily supported by the male’s mandibular clasp around her pronotal neck, and secondarily by his legs and terminalic union. The pair travels from the initial site of contact by male flight and/or foot and eventually settle on a substrate to finish mating (Nonveiller 1980; Brothers 1989; Brothers and Finnamore 1993). However, this second subtype is technically also “true phoretic copulation,” as the female is carried by the male with his mandibles throughout the mating event, even while the pair are resting on a substrate in copula

Table 1. Review of published mating strategy data for Mutillidae.

Taxon	Mating strategy	Size dimorphism	Time in copula	Conditions	Reference	Additional notes
Dasylabrinae: Apteromutillini						
–	–	–	–	–	–	–
Dasylabrinae: Dasylabrini						
<i>Chrestomutilla glossinae</i> (Turner, 1915)	MPC	–	–	in the field and in captivity	Lamborn (1916)	–
<i>Tricholabiodes lividus</i> (André, 1909)	ISC	♂ > ♀	–	in captivity	Bayliss and Brothers (1996)	–
<i>Tricholabiodes thisbe</i> (Péringuey, 1898)	ISC	♂ = ♀	“10–15 seconds”	in captivity	Bayliss and Brothers (1996)	–
Mutillinae: Ctenotillini						
<i>Ctenotilla caeca</i> (Radoszkowski, 1879)†	PC	♂ > ♀	–	in the field	Nonveiller (1963)	–
Mutillinae: Ephutini						
<i>Ephuta floridana</i> Schuster, 1951	PC	♂ > ♀	–	in the field	Deyrup and Manley (1986)	–
<i>Ephuta sabaliana</i> Schuster, 1951	PC	♂ > ♀	–	in the field	Deyrup and Manley (1986)	–
<i>Ephuta slossonae slossonae</i> (Fox, 1899)	MPC	–	–	in the field	Krombein and Norden (1996)	–
Mutillinae: Mutillini						
<i>Dolichomutilla sycorax</i> (Smith, 1855)	ISC	♂ = ♀	“60–100 seconds”	in captivity	Bayliss and Brothers (2001)	–
<i>Mutilla europaea</i> Linnaeus, 1758	ISC	–	a few minutes	in captivity	Drewsen (1847)	–
<i>Mutilla europaea</i> Linnaeus, 1758	ISC?	–	–	in captivity	Hoffer (1886)	–
<i>Mutilla europaea</i> Linnaeus, 1758	ISC?	–	–	in captivity	Su et al. (2019)	–
Mutillinae: Odontomutillini						
–	–	–	–	–	–	–
Mutillinae: Smicromyrmini						
<i>Nemka viduata</i> (Pallas, 1773)	MPC	–	45 minutes (field)	in the field and in captivity	Alicata et al. (1975)	–
<i>Nemka viduata</i> (Pallas, 1773)	PC	–	–	in the field	Matteini Palmerini (1992)	–
<i>Nemka viduata</i> (Pallas, 1773)	MPC	sizes variable	“more than 2 hours”; 45 minutes	in the field and in captivity	Matteini Palmerini (2013)	–
<i>Nemka viduata</i> (Pallas, 1773)	PC	♂ > ♀	–	in the field	Nonveiller (1963)	–
<i>Nemka viduata</i> (Pallas, 1773)	PC	sizes variable	–	in the field and in captivity	Polidori et al. (2013)	mating balls
<i>Nemka viduata</i> (Pallas, 1773)	MPC	sizes variable	“2 h–2 h 15 min” (captivity); “2 h 20 min”; “3 h 7 min”; “2 h 13 min”; “2 h 10 min” (field)	in the field and in captivity	Tormos et al. (2010)	–
<i>Physetopoda balensis</i> (Fabricius, 1787)‡	MPC	♂ > ♀	25 minutes	mating pair collected in the field and observed in captivity	Bertkau (1884)	–
<i>Proমেচিলা decora</i> (Smith, 1879)	MPC	–	“1 hour 22 minutes”	mating pair collected in the field and observed in captivity	Pagden (1934)	–

Taxon	Mating strategy	Size dimorphism	Time in copula	Conditions	Reference	Additional notes
<i>Smicromyrme benefactrix</i> (Turner, 1916)	ISC/PC	–	–	in the field and in captivity	Lamborn (1916)	males attempted female carriage with his mandibles around her pedicel
<i>Smicromyrme jovanovici</i> Nonveiller, 1963§	ISC	♂ = ♀	–	in the field	Nonveiller (1963)	–
<i>Smicromyrme rufipes</i> (Fabricius, 1787)	MPC	–	56 minutes (field); 1 hour 3 minutes (field); 1 hour 10 minutes (captivity)	in the field and in captivity	Crèvecoeur (1930)	–
<i>Sulcotilla</i> sp.	MPC	–	–	museum specimens	Brothers (1975)	–
Mutillinae: Trogaspidiini						
<i>Karlissaidia sexmaculata</i> (Swederus, 1787)	MPC	–	“hours”	in the field	Rothney (1903)	–
<i>Karlissaidia</i> sp. nr <i>sexmaculata</i> (Swederus, 1787)	PC	–	–	museum specimens	O’Toole (1975)	–
<i>Timulla cordillera</i> Mickel, 1938	MPC	–	“approx. 16 hours”	in captivity	Cambra et al. (2018)	–
<i>Timulla dubitata</i> (Smith, 1855)	MPC	♂ > ♀	–	mating pair collected in the field and observed in captivity	Sheldon (1970)	–
<i>Timulla floridensis</i> (Blake, 1879)	PC	♂ > ♀	–	in the field	Deyrup and Manley (1986)	–
<i>Timulla nisa</i> Mickel, 1938	MPC	♂ = ♀	–	in captivity	Cambra and Quintero (1993)	information gleaned from photographs
<i>Timulla oajaca</i> (Blake, 1871)	PC	♂ > ♀	–	mating pair collected in the field	Linsley (1960)	female was supported by male’s legs and genitalic union
<i>Timulla oajaca</i> (Blake, 1871)	PC	–	–	in the field	Hennessey and West (2018)	–
<i>Timulla rufogastra</i> (Lepeletier, 1845)	MPC	♂ > ♀	–	in the field	Bartholomay et al. (2017)	mixed-species mating aggregation
<i>Timulla runata</i> Mickel, 1938	MPC	–	“about 20 hours”	in captivity	Cambra et al. (2018)	–
<i>Timulla suspensa</i> (Gerstaecker, 1874)	MPC	♂ > ♀	–	museum specimens	Bartholomay et al. (2017)	–
<i>Timulla suspensa</i> (Gerstaecker, 1874)	PC	–	–	in the field	Hennessey and West (2018)	–
<i>Timulla vagans</i> (Fabricius, 1798)]	–	–	–	in the field	Fattig (1936)	mating ball
<i>Timulla vagans</i> (Fabricius, 1798)	–	–	“several minutes”	in the field	Shappirio (1947b)	–
<i>Timulla vagans</i> (Fabricius, 1798)	MPC	♂ > ♀	–	museum specimens	Sheldon (1970)	information gleaned from illustration
<i>Trogaspidia (Acutitropidia) aurata</i> (Bischoff, 1920)	MPC	♂ > ♀	–	in the field	Nonveiller (1980)	information gleaned from photograph

Taxon	Mating strategy	Size dimorphism	Time in copula	Conditions	Reference	Additional notes
<i>Trogaspidia</i> (<i>Acutitropidia</i>) <i>bugalana</i> (Bischoff, 1920)	MPC	♂ > ♀	–	museum specimens	Brothers (1989)	information gleaned from photograph
<i>Trogaspidia</i> <i>fedtschenkoi</i> (Radoszkowski, 1877)	MPC	♂ > ♀	–	museum specimens	Skorikov (1935)	information gleaned from illustration
<i>Wallacidia melmora</i> (Cameron, 1905)	MPC	–	–	museum specimens	O'Toole (1975)	–
<i>Wallacidia oculata</i> (Fabricius, 1804)	PC	–	–	museum specimens	O'Toole (1975)	venter to venter position
<i>Wallacidia oculata</i> (Fabricius, 1804)	MPC	–	–	in the field	O'Toole (1975)	–
<i>Wallacidia oculata</i> (Fabricius, 1804)	MPC	♂ > ♀	–	in the field	current study (Fig. 7)	–
Myrmillinae						
<i>Myrmilla calva</i> (Villers, 1789)♂	ISC	–	5 to 15 minutes	in captivity	Monastra (1989)	–
<i>Myrmilla erythrocephala</i> (Latreille, 1792)#	ISC	–	just over 20 minutes; roughly for 17 to 19 minutes	in captivity	Monastra (1989)	–
Myrmosinae: Kudakrumiini						
<i>Myrmosula parvula</i> (Fox, 1893)	ISC	–	"14 seconds"	in captivity	Brothers (1978)	–
Myrmosinae: Myrmosini						
<i>Myrmosa atra</i> Panzer, 1801	TPC	♂ > ♀	"9 minutes"; "47 minutes 26 seconds"	in the field	Saxton (2010)	venter to venter position
<i>Myrmosa bradleyi</i> Roberts, 1929	PC	–	–	mating pair collected in the field	Linsley (1960)	–
<i>Myrmosa unicolor</i> Say, 1824	TPC	♂ > ♀	–	mating pair collected in the field	Krombein (1956)	venter to venter position
<i>Myrmosa unicolor</i> Say, 1824	TPC	♂ > ♀	–	museum specimens	Cambra et al. (2018)	–
<i>Myrmosa unicolor</i> Say, 1824	TPC	♂ > ♀	–	in the field	current study (Fig. 6)	–
<i>Myrmosa</i> sp.	PC	–	–	mating pair collected in the field	Pate (1947)	–
Pseudophotopsidinae						
–	–	–	–	–	–	–
Rhopalomutillinae						
<i>Bischoffiella cristata</i> (Bingham, 1912)	TPC	♂ > ♀	–	museum specimens	Brothers (1989, 2015)	information gleaned from photograph
<i>Pherotilla oceanica</i> (Mickel, 1935)††	PC	–	–	in the field?	Pagden (1938)	–
<i>Pherotilla rufitincta</i> (Hammer, 1957)	TPC	♂ > ♀	–	museum specimens	Brothers (2015)	information gleaned from photograph
<i>Rhopalomutilla anguliceps</i> (André, 1897)	TPC	♂ > ♀	–	mating pair collected in the field	Brothers (1989)	mating aggregation
<i>Rhopalomutilla clavicornis</i> (André, 1901)	TPC	–	–	mating pair collected in the field	Bridwell (1917)	–
Sphaerophthalminae: Dasymutillini						
<i>Dasymutilla araneoides</i> (Smith, 1862)‡‡	–	–	–	in the field	Manley and Pitts (2007)	mating ball
<i>Dasymutilla araneoides</i> (Smith, 1862)	–	–	–	in the field	Quintero and Cambra (2001)	mating ball

[illegible]

Taxon	Mating strategy	Size dimorphism	Time in copula	Conditions	Reference	Additional notes
<i>Sphaerophthalma blakeii</i> (Fox, 1893)	ISC	—	“ten to twenty seconds”	in captivity	Ferguson (1962)	—
<i>Sphaerophthalma orestes</i> (Fox, 1899)##	ISC	♂ > ♀	“a few seconds”	in the field	Mickel (1938)	—
<i>Sphaerophthalma pensylvanica</i> (Lepeletier, 1845)	MPC	♂ > ♀	“just under 2 minutes”	in the field	current study (Figs 1–4)	—
Ticoplinae: Smicromyrmillini						
—	—	—	—	—	—	—
Ticoplinae: Ticoplini						
—	—	—	—	—	—	—

† as *Ctenotilla pectinifera* (André, 1893)

‡ as *Mutilla ephippium* Fabricius, 1793

§ *nomen nudum*

| as *Mutilla (Timulla) briaxus* Blake, 1871

¶ as *Myrmilla calva distincta* (Lepeletier, 1845)

as *Myrmilla erythrocephala bison* (Costa, 1887)

†† as *Rhopalomutilla javana* Pagden, 1938

‡‡ as *Dasymutilla deyrollesi* Mickel, 1937

§§ as *Dasymutilla pyrrhus* (Fox, 1899)

|| as *Dasymutilla clytemnestra* (Fox, 1899)

¶¶ as *Dasymutilla formicalia* Rohwer, 1912

as *Photopsis salmani* Mickel, 1938

(Nonveiller 1980; Cambra and Quintero 1993; Bartholomay et al. 2017; Cambra et al. 2018; current study). Active transport by flight while in copula is not required for the mating event to be considered “true phoretic copulation.”

In order to accurately characterize these patterns of behavior, new terminology is proposed with respect to Mutillidae to broadly define the two types of mating strategies currently known to occur in the family. **1) Phoretic Copulation (PC)** is a form of phoresy in which a male intentionally carries a female phoront for the majority of their mating event. There are two subtypes of phoretic copulation: **1a) Terminalic Phoretic Copulation (TPC)** is phoresy primarily effected by terminalic union (i.e. the genitalia and surrounding structures) between a male and a female phoront for the majority of their mating event (secondarily with his legs) (Fig. 6). **1b) Mandibular Phoretic Copulation (MPC)** is phoresy primarily effected by a male’s mandibular clasp around a female phoront’s pronotal neck for the majority of their mating event (secondarily with his legs and terminalic union) (Figs 2–4, 7). **2) In Situ Copulation (ISC)** is a non-phoretic mating event that occurs at or near the site of initial contact between a male and a female (Fig. 5).

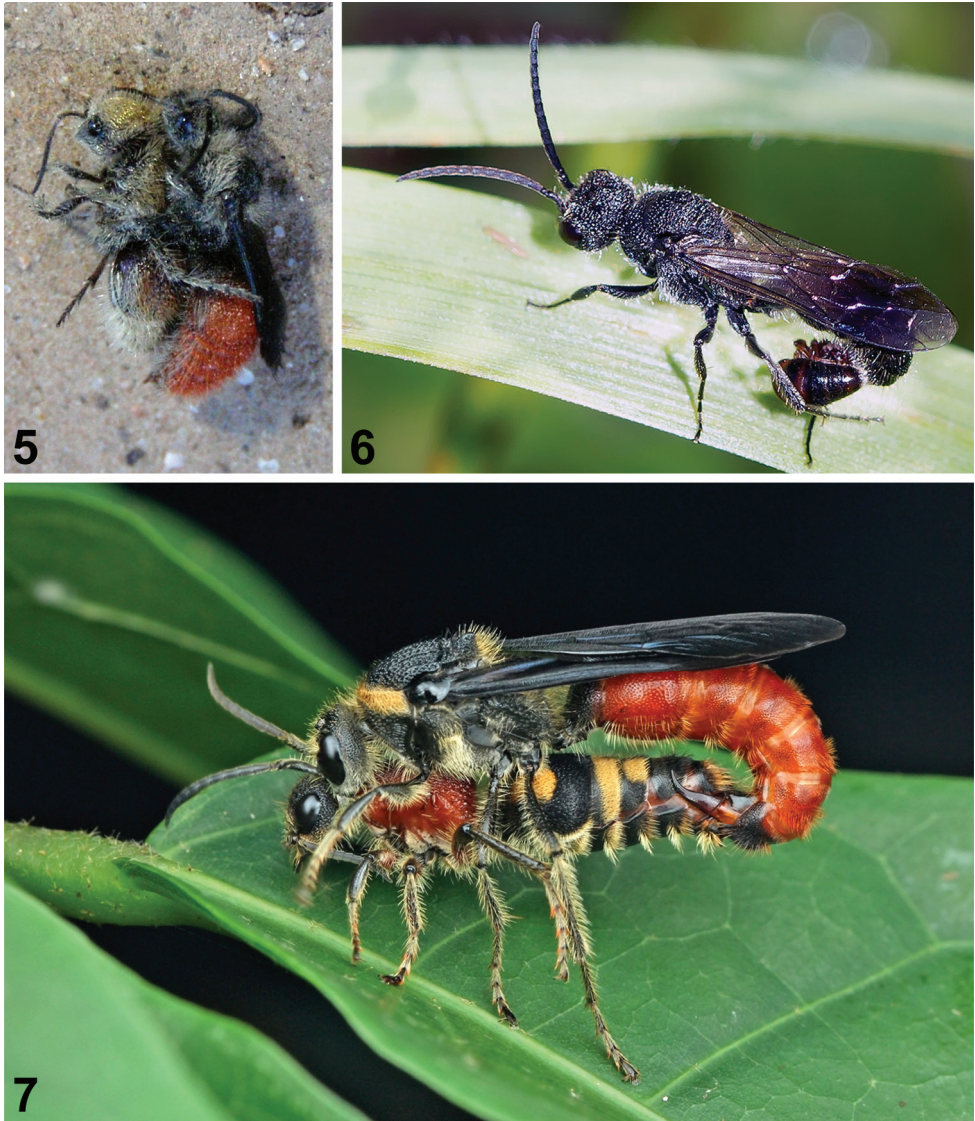
In ISC, there are some observations of males clinging to the dorsum of females during part of the mating event and even clasping their mandibles around the female’s pronotal neck (Cottrell 1936; Ferguson 1962; Bayliss and Brothers 1996, 2001); these events are not considered phoretic copulation as intentional carriage by the male does not occur. This behavior in the context of ISC may play a role in courtship, recognition of conspecificity between the sexes, and/or the biomechanics of mating. Subtypes of ISC may potentially be defined at a later date once more data are available. Mating duration for species that practice PC is often considerably longer than species that practice ISC (Table 1); consequently, mating pairs are collected more often in PC-



Figures 1–4. MPC-practicing pair of *Sphaerophthalma pennsylvanica* (Lepelletier, 1845) in Alabama, USA; photographs by Jason D. Roberts.

practicing taxa (Mickel 1937; Nonveiller 1980). The observation described herein for *S. pennsylvanica* is considered MPC.

A potential third subtype of phoretic copulation was described by O'Toole (1975) for the trogaspidiine species *Wallacidia oculata* (Fabricius, 1804) and congeners. As was described: “The posture of copulation in [*W.*] *oculata* is venter to venter, with the male uppermost. The female clings to the sides of the male mesosoma, with



Figures 5–7. Examples of each type of mating strategy in Mutillidae **5** ISC, *Dasymutilla foxi* (Cockerell, 1894) in Arizona, USA; photograph by Mark H. Brown **6** TPC, *Myrmosa unicolor* Say, 1824 in New York, USA; photograph by A. D. Levine **7** MPC, *Wallacidia oculata* (Fabricius, 1804) in Southern District, Hong Kong; photograph by ‘aabbabc.’

the tarsal claws gaining purchase on the coarse sculpture of the male.” This mating position is unusual, as most known mating observations in Mutillidae occur with the male venter to female dorsum (although sometimes with wide separation between the male and female’s bodies except for the terminalia). In contrast to this mating posture description, O’Toole (1975) also provided evidence that MPC occurs in *W. oculata* and the now full species *Wallacidia melmora* (Cameron, 1905): “I have seen

several pairs of [*W.*] *o. melmora* in museum collections in which the females are in the mandibular clasp of the males. J. Cardew (personal communication) found a male of [*W.*] *o. oculata* with a female in its mandibles, at Chang Mai, Thailand.” There are two additional published records that describe a venter to venter mating position in the TPC-practicing Myrmosini species *Myrmosa atra* Panzer, 1801 and *M. unicolor* Say, 1824. As detailed in Krombein (1956), both K. V. Krombein and H. K. Townes had independently observed mating pairs of *M. unicolor* in the field that were oriented venter to venter. Additionally, Saxton (2010) observed a mating pair of *M. atra* oriented venter to venter. Prior to the pair’s separation, the couple assumed an end to end mating position and Saxton (2010) determined that the male’s genitalia must have rotated 180° to a facultative strophandrous position (sensu Schulmeister 2001). Male genitalic rotation is also known to occur in the TPC-practicing Thynnidae that engage in male to female feeding (Evans 1969; Vivallo 2020). In contrast to these records, Cambra et al. (2018) included a photograph of a pair of *M. unicolor* that remained in copula after being collected in a Malaise trap which are in a male venter to female dorsum position. An online search for photographs of mating pairs of Myrmosini revealed that females’ bodies are rotated to various degrees with respect to the male. One of these photographs of a mating pair of *M. unicolor* is included here (Fig. 6) and shows a roughly 90° rotation of the female’s body.

For Myrmosini, variable female mating position and likely male genitalic rotation are supported by observations in the field by multiple researchers. For Trogaspidiini, information on venter to venter mating is limited to O’Toole (1975). It is unknown whether this mating posture was observed with live specimens or if it was inferred from museum specimens. If the description in O’Toole (1975) was based on preserved material, the venter to venter posture of the mating pair might be an artifact of how the collector mounted the specimens (and might be how the collector envisaged the posture of the mating pair during the act if they happened to terminate copulation and separate upon being captured). Further, a photograph of a mating pair of *W. oculata* is included in this study (Fig. 7) and they are practicing MPC. We ultimately regard the venter to venter mating position described in O’Toole (1975) as erroneous. All known mating descriptions suggest trogaspidiines practice MPC (Table 1) and the available evidence supports that *Wallacidia* species are no different.

The importance of intersexual size dimorphism for phoretic copulation

Sexual dimorphism in size, with the male being larger than the female, is an important criterion for phoretic copulation to effectively occur (Nonveiller 1963; Deyrup and Manley 1986; Brothers 1989; Tormos et al. 2010; Matteini Palmerini 2013). This size dimorphism is in contrast with other parasitoid Hymenoptera wherein females are commonly larger than males (Charnov et al. 1981; O’Neill 1985; Hurlbutt 1987; van den Assem et al. 1989). In some taxa that are known to normally practice MPC, some

male individuals are similar or smaller in body size to the female they are mating with and are physically unable to transport her by flight or even by foot; facultative ISC consequently occurs (Nonveiller 1963; Alicata et al. 1975; Deyrup and Manley 1986; Tormos et al. 2010; Matteini Palmerini 2013; Polidori et al. 2013). It is unknown if the reverse situation also occurs wherein a species that normally practices ISC due to similarity in male and female size might practice facultative MPC with unusually large males. In evidence against the latter situation, Cottrell (1936) observed that for *Dasymutilla bioculata* (Cresson, 1865), a sphaerophthalmine species that practices ISC, larger males were mechanically unable to copulate with smaller females. Females are often larger than males in this species, and mating was successful when smaller males mated with larger females. Additionally, male aptery and brachyptery, which are uncommon in Mutillidae (Cambra and Quintero 2007, 2017), would limit phoretic copulation by flight but not by foot; mating behavior for species with flightless males has yet to be observed, though. The cause of adult intra- and intersexual size differences within a mutillid species is primarily predicated upon host choice.

Mutillids are generally solitary ectoparasitoids that may parasitize more than one host species. It has long been known that the size of the host determines the size of the adult mutillid, which explains the common occurrence of adult size variation (Mickel 1924; Deyrup and Manley 1986; Brothers 1989; Hennessey 2002). If a female mutillid parasitizes more than one host species that vary in size in relation to one another, her offspring will consequently vary in size. In some mutillid taxa, one sex is on average larger than the other, and the underlying mechanics for sex allocation in mutillids remained unknown until relatively recently. Of critical relevance to the new discovery of phoretic copulation in *S. pensylvanica* is an investigation into sex allocation in this species by Pitts et al. (2010a). Their results supported facultative size-dependent sex allocation in which males typically develop from larger hosts and females develop from smaller hosts. Due to the sex-determination system of haplodiploidy in Hymenoptera, female *S. pensylvanica* are able to choose whether to oviposit a fertilized or unfertilized egg onto a specific host. Unfertilized eggs, which develop into males, are more often deposited on larger hosts, such as the organ pipe mud dauber *Trypoxylon politum* (Drury, 1773) (Hymenoptera: Crabronidae); female eggs are usually deposited on smaller *Trypoxylon* species and other taxa (Matthews 1997; Pitts et al. 2010a). Pitts et al. (2010a) concluded that female *S. pensylvanica* likely use host body length and/or nest diameter as criteria for which sex of egg—male or female—to oviposit on a host rather than the criterion of host mass. The difference in size between the male and female mating pair of *S. pensylvanica* documented herein is substantial (Figs 2–4), and the size dimorphism prerequisite for phoretic copulation is clearly met. Although a rare occurrence, female *S. pensylvanica* have been reared from *T. politum* and males reared from smaller *Trypoxylon* species (Pitts et al. 2010a). More mating observations are necessary for *S. pensylvanica* to see how mating is carried out, if at all, between these smaller males and larger females. Facultative size-dependent sex allocation is likely widespread among PC-practicing mutillids due to the importance of intersexual size dimorphism.

Phoretic copulation in Sphaerophthalminae

The genus *Sphaerophthalma* Blake, 1871 is a paraphyletic assemblage of 81 described species classified into 17 species-groups (Pitts et al. 2010b; Pitts and Sadler 2015). *Sphaerophthalma pensylvanica* (Lepeletier, 1845) is currently placed in the *S. pensylvanica* species-group along with *S. auripilis* (Blake, 1871), *S. boweri* Schuster, 1944, and *S. nocticarum* Pitts, 2005 (Pitts and Sadler 2015). Given that these other members of the species-group also show the same differences in body size between the sexes, it is likely that they practice MPC as well. Unfortunately, the females of most of the remaining *Sphaerophthalma* species, as well as the related large genera *Photomorphus* Viereck, 1903 and *Odontophotopsis* Viereck, 1903, are unknown. The known females are closer in size to the males and there seem to be no other likely candidates for MPC in *Sphaerophthalma* outside of the *S. pensylvanica* species-group or the related genera *Photomorphus* and *Odontophotopsis*.

There are a few unusual distributions in Sphaerophthalminae that might be due to dispersal via PC. Sphaerophthalmines primarily occur in the Nearctic, Neotropical, and Australasian regions, with two small genera occurring in the Palearctic (Europe, China, Japan, Republic of Korea) and Oriental (China, Taiwan) regions. These latter two genera, *Cystomutilla* André, 1896 and *Hemutilla* Lelej, Tu, & Chen, 2014 were recently reviewed by Tu et al. (2014). Molecular data has revealed that *Cystomutilla* is closely related to the nocturnal Nearctic Sphaerophthalminae (Waldren et al. in prep.). The practice of phoretic copulation, which has, in part, been hypothesized to aid the apterous females in traversing physical barriers such as water (Evans 1969), is not out of the realm of possibility in *Cystomutilla* and *Hemutilla* in light of the behavior being discovered in *S. pensylvanica*. Another genus in which PC may have played a role in dispersal is the primarily Australian genus *Ancistrotilla* Brothers, 2012. Several species are known to occur in New Caledonia and one in Vanuatu, an archipelago of volcanic origin (Brothers 2012; Lo Cascio 2015). The only species known so far from both sexes, *Ancistrotilla azurea* Brothers, 2012, which occurs in Vanuatu, meets the size prerequisite for phoretic copulation with males being larger than females. Additionally, the single known female was apparently collected in the same Malaise trap as fifteen males and could potentially have been carried into the trap by a male.

Conclusion

Based on prior knowledge, it was thought that mating strategies in Mutillidae were confined to the family-group levels of subfamily, tribe, or subtribe (Table 1). Members of the subfamily Sphaerophthalminae were previously known to only practice ISC. With the discovery of MPC in *S. pensylvanica*, it is revealed that membership to a higher taxon is not always reliable for predicting a species' mating strategy. Ironically, *S. pensylvanica* is the type species of *Sphaerophthalma* Blake, the genus from which the subfamily name Sphaerophthalminae is derived. As this is the only known mating observation for this species and species-group, more information is needed to determine the consistency of this behavior especially with respect to intersexual size

variation. Additional fieldwork is also necessary to get a better idea of how prevalent PC is in Sphaerophthalminae. Respecting the historical challenge of discovering mating mutillid pairs in the field, male morphology combined with consistent interspecific size differences in a species could be used as preliminary lines of evidence for the practice of phoretic copulation.

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