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

George C. Waldren¹, Jason D. Roberts², James P. Pitts¹

¹ Utah State University, Department of Biology, Logan, Utah, 84322, USA ² Somerville, Alabama, 35670, USA

Corresponding author: George C. Waldren (gcwaldren@gmail.com)

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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 *Sphaeropthalma pensylvanica* (Lepeletier, 1845) (Hymenoptera: Mutillidae). Further, this is the first record of the behavior in the species-rich subfamily Sphaeropthalminae. 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: Bethylidae, 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).

*Sphaeropthalma 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 Sphaeropthalminae, 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 *Sphaeropthalma 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 Bethylidae and Thynnidae (Evans 1969; Osten 1999; Azevedo et al. 2016). The other subtype is known to commonly occur in the subfamily Mutilillinae (excluding Mutillini and Odontomutillini) and now in Sphaeropthalminae (*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: Apteronmutillini** | | | | | | |
| | | | | | | |
| **Dasylabrinae: Dasylabridi** | | | | | | |
| Cremestomutilla glauca (Turner, 1915) | MPC | – | – | in the field and in captivity | Lamborn (1916) | – |
| Tricholabiodes lividus (André, 1909) | ISC | ♂ > ♀ | – | in captivity | Bayliss and Brothers (1996) | – |
| Tricholabiodes thistle (Péringuey, 1898) | ISC | ♂ = ♀ | “10–15 seconds” | in captivity | Bayliss and Brothers (1996) | – |
| **Mutillinae: Ctenotillini** | | | | | | |
| Ctenovilla cecae (Radoszkowski, 1879)† | PC | ♂ > ♀ | – | in the field | Nonveiller (1963) | – |
| **Mutillinae: Ephutini** | | | | | | |
| Ephuta floridana Schuster, 1951 | PC | ♂ > ♀ | – | in the field | Deyrup and Manley (1986) | – |
| Ephuta sabuliana Schuster, 1951 | PC | ♂ > ♀ | – | in the field | Deyrup and Manley (1986) | – |
| Ephuta slavonica slavonica (Fox, 1899) | MPC | – | – | in the field | Krombein and Norden (1996) | – |
| **Mutillinae: Mutillini** | | | | | | |
| Dolichomutilla sycorax (Smith, 1855) | ISC | ♂ = ♀ | “60–100 seconds” | in captivity | Bayliss and Brothers (2001) | – |
| Mutilla europaea Linnaeus, 1758 | ISC? | ♂ = ♀ | – | in captivity | Drewsen (1847) | – |
| Mutilla europaea Linnaeus, 1758 | ISC? | ♂ = ♀ | – | in captivity | Hofler (1886) | – |
| Mutilla europaea Linnaeus, 1758 | ISC? | ♂ = ♀ | “more than 2 hours”; 45 minutes | in the field and in captivity | Matteini Palmerini (1992) | – |
| **Mutillinae: Odontomutillini** | | | | | | |
| Nemka viduata (Pallas, 1773) | MPC | ♂ > ♀ | 45 minutes (field) | in the field and in captivity | Alicata et al. (1975) | – |
| Nemka viduata (Pallas, 1773) | PC | ♂ = ♀ | – | in the field | Matteini Palmerini (1992) | – |
| Nemka viduata (Pallas, 1773) | MPC | sizes variable | “more than 2 hours”; 45 minutes | in the field and in captivity | Matteini Palmerini (2013) | – |
| Nemka viduata (Pallas, 1773) | PC | ♂ > ♀ | – | in the field | Nonveiller (1963) | – |
| Nemka viduata (Pallas, 1773) | PC | sizes variable | – | in the field and in captivity | Polidori et al. (2013) | mating balls |
| Nemka viduata (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) | – |
| **Mutillinae: Smicromyrmini** | | | | | | |
| Physetopoda halensis (Fabricius, 1787)† | MPC | ♂ > ♀ | 25 minutes | mating pair collected in the field and observed in captivity | Bertkau (1884) | – |
| Promecilla decorra (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                                                                 |
|-------------------------------------------|-----------------|-----------------|----------------|-------------------------------------|--------------------------|----------------------------------------------------------------------------------|
| Smicromyrmex benefactrix (Turner, 1916)    | ISC/PC          | –               | –              | in the field and in captivity       | Lamborn (1916)           | males attempted female carriage with his mandibles around her pedicel            |
| Smicromyrmex jovanovici Nonveiller, 1963§ | ISC             | ♂ = ♀           | –              | in the field                         | Nonveiller (1963)        |                                                                                  |
| Smicromyrmex rufipes (Fabricius, 1787)    | MPC             | –               | 56 minutes (field); 1 hour 3 minutes (field); 1 hour 10 minutes (captivity) | in the field and in captivity | Crévecoeur (1930)        |                                                                                  |
| Sulcotilla sp.                             | MPC             | –               | –              | museum specimens                     | Brothers (1975)          |                                                                                  |
| Mutillinae: Trogaspidiini                  |                 |                 |                |                                     |                          |                                                                                  |
| Karlissadia sexmaculata (Swederus, 1787)  | MPC             | –               | “hours”        | in the field                         | Rothney (1903)           |                                                                                  |
| Karlissadia sp. nr sexmaculata (Swederus, 1787) | PC             | –               | –              | museum specimens                     | O’Toole (1975)           |                                                                                  |
| Timulla cordillera Mickel, 1938           | MPC             | –               | “approx. 16 hours” | in captivity                        | Cambra et al. (2018)     |                                                                                  |
| Timulla dubitata (Smith, 1855)            | MPC             | ♂ > ♀          | –              | mating pair collected in the field and observed in captivity | Sheldon (1970)           |                                                                                  |
| Timulla floridenisi (Blake, 1879)         | PC              | ♂ > ♀          | –              | in the field                         | Deyrup and Manley (1986) |                                                                                  |
| Timulla nisa Mickel, 1938                 | MPC             | ♂ = ♀          | –              | in captivity                         | Cambra and Quintero (1993) | information gleaned from photographs                                           |
| Timulla oajaca (Blake, 1871)              | PC              | ♂ > ♀          | –              | mating pair collected in the field   | Linsley (1960)           | female was supported by male’s legs and genitalic union                           |
| Timulla oajaca (Blake, 1871)              | PC              | –              | –              | in the field                         | Hennessey and West (2018) |                                                                                  |
| Timulla oajaca (Blake, 1871)              | PC              | –              | –              | in the field                         | Hennessey and West (2018) |                                                                                  |
| Timulla rufogastra (Lepeletier, 1845)     | MPC             | ♂ > ♀          | –              | in the field                         | Bartholomay et al. (2017) | mixed-species mating aggregation                                                 |
| Timulla runata Mickel, 1938               | MPC             | –               | “about 20 hours” | in captivity                        | Cambra et al. (2018)     |                                                                                  |
| Timulla suspensa (Gerstaecker, 1874)      | MPC             | ♂ > ♀          | –              | museum specimens                     | Bartholomay et al. (2017) |                                                                                  |
| Timulla suspensa (Gerstaecker, 1874)      | PC              | –              | –              | in the field                         | Hennessey and West (2018) |                                                                                  |
| Timulla vagans (Fabricius, 1798)          | –               | –              | –              | in the field                         | Fattig (1936)            | mating ball                                                                      |
| Timulla vagans (Fabricius, 1798)          | –               | –              | “several minutes” | in the field                         | Shappirio (1947b)        |                                                                                  |
| Timulla vagans (Fabricius, 1798)          | MPC             | ♂ > ♀          | –              | museum specimens                     | Sheldon (1970)           | information gleaned from illustration                                           |
| Trogaspidia (Acutitropidia) aurata (Bischoff, 1920) | MPC             | ♂ > ♀          | –              | in the field                         | Nonveiller (1980)        | information gleaned from photograph                                              |
| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Trogaspidia (Acutitropidia) bugalana (Bischoff, 1920) | MPC | ♂ > ♀ | – | museum specimens | Brothers (1989) | information gleaned from photograph |
| Trogaspidia fedorchemki (Radoszkowski, 1877) | MPC | ♂ > ♀ | – | museum specimens | Skorikov (1935) | information gleaned from illustration |
| Wallacidia melinosa (Cameron, 1905) | MPC | – | – | museum specimens | O’Toole (1975) | – |
| Wallacidia oculata (Fabricius, 1804) | PC | – | – | museum specimens | O’Toole (1975) | venter to venter position |
| Wallacidia oculata (Fabricius, 1804) | MPC | ♂ > ♀ | – | in the field | O’Toole (1975) | – |

**Myrmillinae**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Trogaspidia (Acutitropidia) bugalana (Bischoff, 1920) | MPC | ♂ > ♀ | – | museum specimens | Brothers (1989) | information gleaned from photograph |
| Trogaspidia fedorchemki (Radoszkowski, 1877) | MPC | ♂ > ♀ | – | museum specimens | Skorikov (1935) | information gleaned from illustration |

**Myrmillosinae: Kudakrumiini**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Myrmilla calva (Villers, 1789) | ISC | – | 5 to 15 minutes | in captivity | Menstra (1989) | – |
| Myrmilla erythrocephala (Latreille, 1792) | ISC | – | just over 20 minutes; roughly for 17 to 19 minutes | in captivity | Menstra (1989) | – |

**Myrmillosinae: Myrmosini**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Myrmosia atra Parzer, 1801 | TPC | ♂ > ♀ | “9 minutes”: “47 minutes 26 seconds” | in the field | Saxton (2010) | venter to venter position |
| Myrmosia bradleyi Roberts, 1929 | PC | – | – | mating pair collected in the field | Linsley (1960) | – |
| Myrmosia unicolor Say, 1824 | TPC | ♂ > ♀ | – | mating pair collected in the field | Krombein (1956) | venter to venter position |
| Myrmosia unicolor Say, 1824 | TPC | ♂ > ♀ | – | museum specimens | Cambra et al. (2018) | – |
| Myrmosia unicolor Say, 1824 | TPC | ♂ > ♀ | – | in the field | current study (Fig. 6) | – |
| Myrmosia sp. | PC | – | – | mating pair collected in the field | Pate (1947) | – |

**Pseudophotopsidinae**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Bischoffella cristata (Bingham, 1912) | TPC | ♂ > ♀ | – | museum specimens | Brothers (1989, 2015) | information gleaned from photograph |
| Pherotilla oceana (Mickel, 1935) | PC | ♂ > ♀ | – | in the field? | Pagden (1938) | – |
| Pherotilla rufitincta (Hammer, 1957) | TPC | ♂ > ♀ | – | museum specimens | Brothers (2015) | information gleaned from photograph |
| Rhopalomutilla anguliceps (André, 1897) | TPC | ♂ > ♀ | – | mating pair collected in the field | Brothers (1989) | mating aggregation |
| Rhopalomutilla clavicornis (André, 1901) | TPC | ♂ > ♀ | – | mating pair collected in the field | Bridwell (1917) | – |

**Sphaeropthalminae: Dasymutillini**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|-----------------|-----------------|----------------|------------|-----------|-----------------|
| Dasymutilla arenivoides (Smith, 1862) | – | – | – | in the field | Manley and Pitts (2007) | mating ball |
| Dasymutilla arenivoides (Smith, 1862) | – | – | – | in the field | Quintero and Cambra (2001) | mating ball |
| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|----------------|----------------|----------------|------------|-----------|-----------------|
| Dasymutilla bioculata (Cresson, 1865) | ISC | ♂ < ♀ | “about twenty seconds” | in captivity | Cottrell (1936) | – |
| Dasymutilla bioculata (Cresson, 1865)§§ | ISC | – | “less than five seconds” | in the field | Manley and Deyrup (1989) | – |
| Dasymutilla coccineohirta (Blake, 1871) | ISC | – | “a few seconds” | in captivity while in the field | Hurd (1951) | – |
| Dasymutilla coccineohirta (Blake, 1871)|| ISC | – | “2 seconds” | in the field | Manley (1977) | – |
| Dasymutilla erythrina (Say, 1836)¶¶ | ISC | – | “five seconds” | in the field | Linsley et al. (1955) | – |
| Dasymutilla fusi (Cockerell, 1894) | ISC | ♂ = ♀ | – | in the field | current study (Fig. 5) | – |
| Dasymutilla fusi (Cockerell, 1894) | ISC | ♂ = ♀ | – | in the field | | – |
| Dasymutilla nigriper (Fabricius, 1878) | – | – | “less than 10 seconds” | – | Shappirio (1947b) | – |
| Dasymutilla nigriper (Fabricius, 1878) | – | – | “a very short period” | – | Shappirio (1947b) | – |
| Dasymutilla occidentalis (Linnaeus, 1758) | ISC | – | “2 to 5 seconds” | in the field | Tomberlin (1997) | – |
| Dasymutilla quadriguttata (Say, 1823) | ISC | – | “approximately three seconds” | in captivity while in the field | Remington (1944) | – |
| Dasymutilla sp. | – | – | “about 30 seconds” | – | Shappirio (1947b) | – |

**Sphaerophalminae: Pseudomethocini: Euspinoliina**

| Taxon | Mating strategy | Size dimorphism | Time in copula | Conditions | Reference | Additional notes |
|-------|----------------|----------------|----------------|------------|-----------|-----------------|
| Calomutilla panamensis Cambra, Brothers, & Quintero, 2020 | ISC | – | “35 seconds” | in captivity | Contreras 1993; Cambra et al. (2020) | – |
| Lophomutilla corna Casal, 1968 | ISC | – | “a minimum of 1 minute 48 seconds and the maximum recorded time was 2 minutes 25 seconds; mean copulation time was 2 minutes” | in captivity | Bergamaschi et al. (2010) | – |
| Lynbiatilla panama Cambra in: Bergamaschi et al. 2012 | ISC | – | “83 seconds and 70 seconds” | in captivity | Bergamaschi et al. (2012) | – |
| Pseudomethoca frigida (Smith, 1855) | ISC | – | “about 15 seconds” | in captivity | Brothers (1972) | – |
| Pseudomethoca frigida (Smith, 1855) | – | – | “about fifteen seconds” | in the field | Shappirio (1947a,b) | – |
| Pseudomethoca propinqua (Cresson, 1865) | – | – | “mating was frequent but brief” | in the field | Jellison (1982) | mating balls |
| Pseudomethoca punilla (Burmeister, 1854) | ISC | – | “less than one minute, with the maximum time recorded of 58 seconds” | in captivity | Bergamaschi et al. (2011) | – |
| Pseudomethoca similina (Smith, 1855) | – | – | “about fifteen seconds” | in the field | Shappirio (1947a,b) | – |

**Sphaerophalminae: Sphaerophalmini**
Phoretic copulation in Sphaeropthalma pensylvanica

| Taxon                        | Mating strategy | Size dimorphism | Time in copula                  | Conditions          | Reference          | Additional notes |
|-----------------------------|-----------------|-----------------|---------------------------------|---------------------|--------------------|------------------|
| Sphaeropthalma blakei       | ISC             | –               | “ten to twenty seconds”          | in captivity        | Ferguson (1962)    | –                |
| Sphaeropthalma orestei      | ISC             | ♂ > ♀           | “a few seconds”                  | in the field        | Mickel (1938)      | –                |
| Sphaeropthalma pensylvanica | MPC             | ♂ > ♀           | “just under 2 minutes”           | in the field        | current study (Figs 1–4) | –                |

Ticopinae: Smicromyrmillini

Ticopinae: Ticopini

† as Ctenotilla pectinifera (André, 1893)
‡ as Mutilla ephippium Fabricius, 1793
§ nomen nudum
| as Mutilla (Timulla) briaccus Blake, 1871
¶ as Myrmina calva distincta (Lepeletier, 1845)
# as Myrmina erythrocephala bison (Costa, 1887)
†† as Rhopalomutilla javana Pagken, 1938
‡‡ as Dasymutilla deyroldi 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-
practicing taxa (Mickel 1937; Nonveiller 1980). The observation described herein for *S. pensylvanica* 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
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 \textit{W.} \textit{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 \textit{W.} \textit{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 \textit{Myrmosa atra} Panzer, 1801 and \textit{M. unicolor} Say, 1824. As detailed in Krombein (1956), both K. V. Krombein and H. K. Townes had independently observed mating pairs of \textit{M. unicolor} in the field that were oriented venter to venter. Additionally, Saxton (2010) observed a mating pair of \textit{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 \textit{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 \textit{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 \textit{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 trogaspidines practice MPC (Table 1) and the available evidence supports that \textit{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 Sphaerophalminae

The genus *Sphaerophalma* Blake, 1871 is a paraphyletic assemblage of 81 described species classified into 17 species-groups (Pitts et al. 2010b; Pitts and Sadler 2015). *Sphaerophalma pensylvanica* (Lepeletier, 1845) is currently placed in the *S. pensylvanica* species-group along with *S. auripilis* (Blake, 1871), *S. bowieri* Schuster, 1944, and *S. nocticaro* 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 *Sphaerophalma* 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 *Sphaerophalma* outside of the *S. pensylvanica* species-group or the related genera *Photomorphus* and *Odontophotopsis*.

There are a few unusual distributions in Sphaerophalminae that might be due to dispersal via PC. Sphaerophalmines primarily occur in the Nearctic, Neotropical, and Australasian regions, with two small genera occurring in the Palaearctic (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 Sphaerophalminae (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 Sphaerophalminae 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 *Sphaerophalma* Blake, the genus from which the subfamily name Sphaerophalminae 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.
Phoretic copulation in Sphaerophalma pensylvanica

variation. Additional fieldwork is also necessary to get a better idea of how prevalent PC is in Sphaerophalmae. 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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References

Alicata P, Caruso D, Costa G, Motta S (1975 ["1974"] ) Richerche eco-etologiche sulla fauna delle dune costiere di Porto Palo (Siracusa). I. Smicromyrme viduata (Pall.) (Hymenoptera, Mutillidae): Ritmi di attivita migrazioni e accoppiamento. Animalia 1(1/3): 89–108.

Azevedo CO, Colombo WD, Alencar IDCC, de Brito CD, Waichert C (2016) Couples in phoretic copulation, a tool for male-female association in highly dimorphic insects of the wasp genus Dissomphalus Ashmead (Hymenoptera: Bethylidae). Zoologia 33(6): e20160076. https://doi.org/10.1590/s1984-4689zool-20160076

Bartholomay PR, Waldren GC, de Oliveira ML (2017) Observation of a mixed-sex, mixed-species aggregation of velvet ants, genus Timulla Ashmead, 1899 (Hymenoptera: Mutillidae) in the Brazilian Amazon, Roraima, with a new synonymy. Zootaxa 4362(1): 135–140. https://doi.org/10.11646/zootaxa.4362.1.8

Bayliss PS, Brothers DJ (1996) Biology of Tricholabides Radoszkowski in southern Africa, with a new synonymy and review of recent biological literature (Hymenoptera: Mutillidae). Journal of Hymenoptera Research 5: 249–258.

Bayliss PS, Brothers DJ (2001) Behaviour and host relationships of Dolichomutilla sycorax (Smith) (Hymenoptera: Mutillidae, Sphecidae). Journal of Hymenoptera Research 10(1): 1–9. https://biodiversitylibrary.org/page/2858630

Bergamaschi ACB, Cambra RA, Brothers DJ, Melo GAR (2012) Lynchiatilla Casal, 1963 (Hymenoptera: Mutillidae): A new species from Brazil associated with Paroxystoglossa spiloptera Moure (Hymenoptera: Apidae: Halictinae), and notes on other species. Zootaxa 3548: 55–64. https://doi.org/10.11646/zootaxa.3548.1.3

Bergamaschi ACB, Cambra RA, Melo GAR (2010) Male description and host record for Lophomutilla corupa Casal, 1968 (Hymenoptera: Mutillidae), with behavioural notes on mating behaviour and host nest attacks. Journal of Natural History 44(43–44): 2597–2607. https://doi.org/10.1080/00222933.2010.499574
Bergamaschi ACB, Cambra RA, Melo GAR (2011) New combinations, sex association, behavioural notes and potential host record for two Neotropical species of Pseudomethoca Ashmead, 1896 (Hymenoptera: Mutillidae). Zootaxa 3062: 55–63. https://doi.org/10.11646/zootaxa3062.1.6

Bertkau P (1884) Die begattung von Mutilla ephippium. Biologisches Centralblatt 3: 722–724. https://biodiversitylibrary.org/page/5324348

Bridwell JC (1917) Untitled [Exhibition of Rhopalomutilla clavicornis]. Proceedings of the Hawaiian Entomological Society 3(4): 1–260. https://biodiversitylibrary.org/page/25416358

Brothers DJ (1972) Biology and immature stages of Pseudomethoca f. frigida, with notes on other species (Hymenoptera: Mutillidae). The University of Kansas Science Bulletin 50(1): 1–38. https://biodiversitylibrary.org/page/3278313

Brothers DJ (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. The University of Kansas Science Bulletin 50(11): 483–648. https://biodiversitylibrary.org/page/4386602

Brothers DJ (1978) Biology and immature stages of Myrmosula parvula (Hymenoptera: Mutillidae). Journal of the Kansas Entomological Society 51(4): 698–710. https://www.jstor.org/stable/25083861

Brothers DJ (1989) Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). In: Bruton MN (Ed.) Alternative life-history styles of animals. Kluwer Academic Publishers (Dordrecht): 279–291. https://doi.org/10.1007/978-94-009-2605-9_14

Brothers DJ (2012) The new genus Ancistrotilla n. gen., with new species from Vanuatu and New Caledonia (Hymenoptera, Mutillidae). Zoosystema 34(2): 223–251. https://doi.org/10.5252/z2012n2a2

Brothers DJ (2015) Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): I, generic review with descriptions of three new genera. Journal of Hymenoptera Research 46: 1–24. https://doi.org/10.3897/JHR.46.5733

Brothers DJ, Finnamore AT (1993) Superfamily Vespoidea. In: Goulet H, Huber JT (Eds) Hymenoptera of the world: An identification guide to families. Agriculture Canada Publication (Ottawa): 161–278. https://cfs.nrcan.gc.ca/publications?id=35617

Brothers DJ, Lelej AS (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. Journal of Hymenoptera Research 60: 1–97. https://doi.org/10.3897/jhr.60.20091

Brothers DJ, Tschuch G, Burger F (2000) Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. Insectes Sociaux 47: 201–211. https://doi.org/10.1007/PL00001704

Brown GR (2000) Some problems with Australian tiphiid wasps, with special reference to coupling mechanisms. In: Austin AD, Dowton M (Eds) Hymenoptera: Evolution, biodiversity and biological control. CSIRO Publishing (Collingwood, Victoria, Australia): 210–217.

Cambra RA, Brothers DJ, Quintero D (2020) Review of Calomutilla Mickel, 1952, a new species, and comparison with Pertylella Mickel, 1952 (Hymenoptera: Mutillidae). Zootaxa 4789(2): 466–480. https://doi.org/10.11646/zootaxa.4789.2.6

Cambra RA, Quintero D (1993) Studies on Timulla Ashmead (Hymenoptera: Mutillidae): New distribution records and synonymies, and descriptions of previously unknown al-
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lotypes. The Pan-Pacific Entomologist 69(4): 299–313. https://biodiversitylibrary.org/page/56147381

Cambra RA, Quintero D (2007) *Chilemutilla*, a new genus of Mutillidae (Hymenoptera) from Chile, and the description of the first wingless mutillid male from South America. Transactions of the American Entomological Society 133(1–2): 167–180. https://doi.org/10.3157/0002-8320(2007)133[167:CANGOM]2.0.CO;2

Cambra RA, Quintero D (2017) *Sphaeropthalma pinedai* sp. nov.: Primer registro de un mutílido braquíptero para América del Sur (Hymenoptera: Mutillidae). Boletín Científico del Centro de Museos de la Universidad de Caldas 21(2): 220–230.

Cambra RA, Quintero D, Waldren GC, Bartholomay PR, Williams KA (2018) Taxonomic revision of the genus *Timulla* Ashmead, 1899 of Panama (Hymenoptera: Mutillidae). Tecnociencia 20(2): 23–57.

Charnov EL, Los-den Hartogh RL, Jones WT, van den Assem J (1981) Sex ratio evolution in a variable environment. Nature 289(1/8): 27–33. https://doi.org/10.1038/289027a0

Clausen CP (1976) Phoresy among entomophagous insects. Annual Review of Entomology 21: 343–367. https://doi.org/10.1146/annurev.en.21.010176.002015

Contreras R (1993) Captura y cría de los machos desconocidos de cinco géneros de mutílidas de Panamá (Hymenoptera: Mutillidae) mediante técnicas experimentales. Tesis de Licenciatura, Universidad de Panamá, Panamá, 63 pp.

Cottrell RG (1936) The biology of *Dasymutilla bioculata* (Cresson). MS Thesis, University of Minnesota, St. Paul, 42 pp.

Crèvecoeur A (1930) Recherches biologiques sur *Smicromyrme (Mutilla) rufipes* F. (Hym., Mutillidae). Bulletin and Annales de la Société Entomologique de Belgique 70: 271–284.

Deyrup M, Manley DG (1986) Sex-biased size variation in velvet ants (Hymenoptera: Mutillidae). Florida Entomologist 69(2): 327–335. https://doi.org/10.2307/3494937

Drewsen C (1847) *Mutilla europaea* Linné. Stettiner Entomologische Zeitung 8: 210–211. https://biodiversitylibrary.org/page/33704591

Evans HE (1969) Phoretic copulation in Hymenoptera. Entomological News 80: 113–124. https://biodiversitylibrary.org/page/2740524

Fattig PW (1936) An unusual mating of velvet ants (Hymen.: Mutillidae). Entomological News 47: 51–52. https://biodiversitylibrary.org/page/2597089

Ferguson WE (1962) Biological characteristics of the mutillid subgenus *Photopsis* Blake and their systematic values (Hymenoptera). University of California Publications in Entomology 27(1): 1–92.

Gordh G (1990) *Apenesia evansi* sp.n. (Hymenoptera: Bethylidae) from Australia with comments on phoretic copulation in bethylids. Journal of the Australian Entomological Society 29: 167–170. https://doi.org/10.1111/j.1440-6055.1990.tb00341.x

Hennessey RD (2002) Population-level characteristics of *Dasymutilla nigripes*, *D. vesta*, and *Timulla vagans* (Hymenoptera: Mutillidae). Florida Entomologist 85(1): 245–253. https://doi.org/10.1653/0015-4040(2002)085[0245:PLCODN]2.0.CO;2

Hennessey RD, West SA (2018) Reproductive strategies of diurnal mutillid wasps (Hymenoptera: Mutillidae). Contributions in Science 526: 181–188. http://zoo-web02.zoo.ox.ac.uk/group/west/pdf/Hennessey&West_2018.pdf
Hoffer E (1886) Zur biologie der Mutilla europaea L. Zoologische Jahrbücher. Zeitschrift für Anatomie und Biologie der Thiere 1: 679–686. https://biodiversitylibrary.org/page/9960310

Hurd Jr PD (1951) The California velvet ants of the genus Dasymutilla Ashmead (Hymenoptera: Mutillidae). Bulletin of the California Insect Survey 1(4): 89–118. [plate 10] https://essig.berkeley.edu/documents/cis/cis01_4.pdf

Hurlbutt B (1987) Sexual size dimorphism in parasitoid wasps. Biological Journal of the Linnean Society 30: 63–89. https://doi.org/10.1111/j.1095-8312.1987.tb00290.x

Jellison WL (1982) Concentrations of mutillid wasps (Hymenoptera: Mutillidae). Entomological News 93(1): 27–28. https://www.biodiversitylibrary.org/item/20655#page/271/mode/1up

Krombein KV (1956) Biological and taxonomic notes on the wasps of Lost River State Park, West Virginia, with additions to the faunal list (Hymenoptera, Aculeata). Proceedings of the Entomological Society of Washington 58(3): 153–161. https://biodiversitylibrary.org/page/16196792

Krombein KV (1967) Trap-Nesting Bees and Wasps: Life Histories, Nests, and Associates. Smithsonian Institution Press, Washington, 570 pp. https://doi.org/10.5962/bhl.title.46295

Krombein KV (1979) Family Mutillidae. In: Krombein KV, Hurd Jr PD, Smith DR, Burks BD (Eds) Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington, 1276–1314. https://biodiversitylibrary.org/page/4575397

Krombein KV, Norden BB (1996) Behavior of nesting Episyron conterminus posterus (Fox) and its cleptoparasite Ephuta s. slossonae (Fox) (Hymenoptera: Pompilidae, Mutillidae). Proceedings of the Entomological Society of Washington 98(2): 188–194. https://biodiversitylibrary.org/page/28254367

Lamborn WA (1916) Third report on Glossina investigations in Nyasaland. Bulletin of Entomological Research 7(1): 29–50. https://doi.org/10.1017/S0007485300017053

Lelej AS (2005) Catalogue of the Mutillidae (Hymenoptera) of the Oriental Region. Dalnauka, Vladivostok, 252 pp. https://archive.org/details/LelejA.S.CatalogueOfTheMutillidaehymenopteraOfTheOrientalRegion

Linsley EG (1960) A fragmentary observation on the mating behavior of Timulla (Hymenoptera: Mutillidae). The Pan-Pacific Entomologist 36(1): 1–36. https://biodiversitylibrary.org/page/53497042

Linsley EG, MacSwain JW, Smith RF (1955) Observations on the mating habits of Dasymutilla formicalia Rohwer (Hymenoptera: Mutillidae). The Canadian Entomologist 87: 411–413. https://doi.org/10.4039/Ent87411-9

Lo Cascio P (2015) Worldwide checklist of the island mutillid wasps (Hymenoptera Mutillidae). Biodiversity Journal 6(2): 529–592. http://www.biodiversityjournal.com/contents2015_2.html#monograph3

Luz DR, Waldren GC, Melo GAR (2016) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). Revista Brasileira de Entomologia 60(4): 302–307. https://doi.org/10.1016/j.rbe.2016.06.001

Manley DG (1977) Notes on the courtship and mating of Dasymutilla Ashmead (Hymenoptera: Mutillidae) in California. The Southwestern Naturalist 21(4): 552–554. https://www.jstor.org/stable/30054044
Manley DG, Deyrup MA (1989) Notes on the biology of Dasymutilla pyrrhus (Fox) (Hymenoptera: Mutillidae). Journal of Entomological Science 24(1): 53–56. https://doi.org/10.18474/0749-8004-24.1.53
Manley DG, Pitts JP (2007) Tropical and subtropical velvet ants of the genus Dasymutilla Ashmead (Hymenoptera: Mutillidae) with descriptions of 45 new species. Zootaxa 1487: 1–128. https://doi.org/10.11646/zootaxa.1487.1.1
Matteini Palmerini M (1992 ["1989"]) Mutillidae del Museo Civico di Storia Naturale di Verona (Hymenoptera). Bollettino del Museo Civico di Storia Naturale di Verona 16: 187–226. Matteini Palmerini M (2013) Remarks on the behaviour of the velvet ant Nemka viduata (Pallas, 1773) (Insecta Hymenoptera Mutillidae). Quaderno di Studi e Notizie di Storia Naturale della Romagna 37: 237–260. http://www.ssnr.it/37-18.pdf
Matthews RW (1997) Unusual sex allocation in a solitary parasitoid wasp, Sphaeropthalma pensylvanica (Hymenoptera: Mutillidae). The Great Lakes Entomologist 30: 51–54. https://scholar.valpo.edu/tgle/vol30/iss1/5
Mickel CE (1924) An analysis of a bimodal variation in size of the parasite Dasymutilla bio-culata Cresson (Hymen.: Mutillidae). Entomological News 35: 236–242. https://www.biodiversitylibrary.org/item/20269#page/292/mode/1up
Mickel CE (1937) The mutillid wasps of the genus Timulla which occur in North America north of Mexico. Entomologica Americana 37(1): 1–56. [37(2): 57–119.] https://www.biodiversitylibrary.org/item/205663#page/13/mode/1up
Mickel CE (1938) Photopsoid mutillids collected by Dr. K. A. Salman at Eagle Lake, California. The Pan-Pacific Entomologist 14(4): 178–185. https://biodiversitylibrary.org/page/53412159
Monasta A (1989) Nuovi dati sui Mutillidi et Mirmosidi italiani. 1. Mutillidae Myrmillinae Bisch. (Hymenoptera). Bollettino della Società Entomologica Italiana 121: 204–212.
Nonveiller G (1963) Quelle est la cause de la rareté des Mutillides? Résultats de l’étude de certains de leurs caractères biologiques et écologiques (Hymenoptera, Mutillidae). Memorie della Società Entomologica Italiana 42: 24–57.
Nonveiller G (1980) Recherches sur les Mutillides de l’Afrique (Hymenoptera, Mutillidae). X. Bref aperçu des résultats des recherches sur la faune des Mutillides du Cameroun, effectuées au cours de la période de 1962–1975. Memoires publiés par l’Institut pour la Protection des Plantes, Beograd 14: 11–68.
O’Neill KM (1985) Egg size, prey size, and sexual size dimorphism in digger wasps (Hymenoptera: Sphecidae). Canadian Journal of Zoology 63: 2187–2193. https://doi.org/10.1139/z85-323
Osten T (1999) The phoretic copulation of Thynninae in an ecological and evolutionary perspective. Linzer biologische Beiträge 31(2): 755–762. https://www.zobodat.at/publikation_articles.php?id=787
O’Toole C (1975) The systematics of Timulla oculata (Fabricius) (Hymenoptera, Mutillidae). Zoologica Scripta 4(5–6): 229–251. https://doi.org/10.1111/j.1463-6409.1975.tb00733.x
Pagden HT (1934) Biological notes on some Malayan aculeate Hymenoptera I. (Sphecoidea and Vespoidea). Journal of the Federated Malay States Museums 17: 458–466.
Pagden HT (1938) On a new species of Rhopalomutilla (Hym. Mutillidae) from Java. Journal of the Federated Malay States Museums 18(2): 213–217.
Pate VSL (1947) A conspectus of the Tiphiidae, with particular reference to the Nearctic forms (Hymenoptera, Aculeata). Journal of the New York Entomological Society 55(2): 115–145. [plates VI–VII] https://www.jstor.org/stable/25005210

Pitts JP, Matthews RW (2000) Description of the larva of *Sphaeropthalma pensylvanica* (Lepeletier) (Hymenoptera: Mutiliidae: Sphaeropthalminae). Journal of Entomological Science 35(3): 334–337. https://doi.org/10.18474/0749-8004-35.3.334

Pitts JP, Sadler EA (2015) Description of a new species and species-group of *Sphaeropthalma Blake* (Hymenoptera: Mutiliidae) with an updated classification of the genus. Zootaxa 3947(2): 282–288. https://doi.org/10.11646/zootaxa.3947.2.10

Pitts JP, Tanner DA, Waldren GC, Parker FD (2010a) Facultative size-dependent sex allocation in *Sphaeropthalma pensylvanica* Lepeletier (Hymenoptera: Mutiliidae) with further host records. Journal of the Kansas Entomological Society 83(1): 68–75. https://doi.org/10.2317/JKES0812.15.1

Pitts JP, Wilson JS, von Dohlen CD (2010b) Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutiliidae) driven by Neogene orogeny and Pleistocene glaciations. Molecular Phylogenetics and Evolution 56: 134–145. https://doi.org/10.1016/j.ympev.2010.03.033

Polidori C, Beneitez A, Asís JD, Tormos J (2013) Scramble competition by males of the velvet ant *Nemka viduata* (Hymenoptera: Mutiliidae). Behaviour 150: 23–37. https://doi.org/10.1163/1568539X-00003035

Quintero D, Cambra RA (2001) On the identity of *Scaptopoda* F. Lynch Arribalzaga, new taxonomic changes and new distribution records for Neotropical Mutiliidae (Hymenoptera), with notes on their biology. Transactions of the American Entomological Society 127(3): 291–304. https://www.jstor.org/stable/25078749

Remington CL (1944) The relationship of *Dasymutilla permista* Mickel to *Dasymutilla quadriguttata* (Say) and behavior notes on the species. Annals of the Entomological Society of America 37(2): 198–200. https://doi.org/10.1093/aesa/37.2.198

Rothney GAJ (1903) The aculeate Hymenoptera of Barrackpore, Bengal. Transactions of the Entomological Society of London 1903: 93–116. https://doi.org/10.1111/j.1365-2311.1903.tb01128.x

Saxton SM (2010) Mating behaviour of *Myrmosa atra* (Hymenoptera: Mutiliidae) with a consideration of the adaptive significance of long copulation duration. British Journal of Entomology and Natural History 23: 33–37.

Schulmeister S (2001) Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthetredinoidea s. str. (Insecta, Hymenoptera, ‘Symphyta’). Acta Zoologica 82: 331–349. https://doi.org/10.1046/j.1463-6395.2001.00094.x

Shappirio DG (1947a) Observations on wasps. The Scientific Monthly 64(4): 348–350. https://www.jstor.org/stable/19377

Shappirio DG (1947b) Observations on the biology of some mutiliid wasps (Hymenoptera, Mutiliidae). Bulletin of the Brooklyn Entomological Society 42(5): 162–163. https://biodiversitylibrary.org/page/50582603

Sheldon JK (1970) Sexual dimorphism in the head structure of Mutiliidae Hymenoptera: A possible behavioral explanation. Entomological News 81(3): 57–61. https://biodiversitylibrary.org/page/2740852
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Skorikov AS (1935) Zur Mutilliden-fauna Zentralasiens. Trudy Tadzhikskoi Bazy, Akademiya Nauk SSSR 5: 257–349.

Spangler HG, Manley DG (1978) Sounds associated with the mating behavior of a mutillid wasp. Annals of the Entomological Society of America 71(3): 389–392. https://doi.org/10.1093/asesa/71.3.389

Su W, Liang C, Ding G, Jiang Y, Huang J, Wu J (2019) First record of the velvet ant Mutilla europaea (Hymenoptera: Mutillidae) parasitizing the bumblebee Bombus breviceps (Hymenoptera: Apidae). Insects 10: 1–9. https://doi.org/10.3390/insects10040104

Tomberlin JK (1997) Mating behavior of Dasymutilla occidentalis (Hymenoptera: Mutillidae). Entomological News 108(4): 310–317. https://biodiversitylibrary.org/page/16343807

Tormos J, Asís JD, Polidori C, Benéitez A, Storino G (2010) The mating behaviour of the velvet ant, Nemka viduata (Hymenoptera: Mutillidae). Journal of Insect Behavior 23: 117–127. https://doi.org/10.1007/s10905-009-9200-5

Tu BB, Lelej AS, Chen XX (2014) Review of the genus Cystomutilla André, 1896 (Hymenoptera: Mutillidae: Sphaeropthalminae: Sphaeropthalmini), with description of the new genus Hemutilla gen. nov. and four new species from China. Zootaxa 3889(1): 71–91. https://doi.org/10.11646/zootaxa.3889.1.4

van den Assem J, van Iersel JJA, Los-den Hartog RL (1989) Is being large more important for female than for male parasitic wasps? Behaviour 108(1–2): 160–195. https://doi.org/10.1163/156853989X00114

Vivallo F (2020) Phoretic copulation in Aculeata (Insecta: Hymenoptera): A review. Zoological Journal of the Linnean Society, zlaa069. https://doi.org/10.1093/zoolinnean/zlaa069