

Stabilizing selection to maintain the two male forms of the jumping spider *Maevia inclemens* (Araneae: Salticidae: Marpissina)

David E. Hill¹

¹ 213 Wild Horse Creek Drive, Simpsonville SC 29680, USA, *email* platycriptus@yahoo.com

Abstract. The existence of two very different male forms of the jumping spider *Maevia inclemens* has been the subject of a series of studies in recent years. Because something close to a 1:1 ratio of these forms appears to be found in the many, widely-distributed populations of this common species, a robust stabilizing mechanism, similar to that associated with the 1:1 Fisherian sex ratio, is likely. Here I propose that the tendency of females to avoid a male form encountered in a previous mating is not only responsible for preservation of this 1:1 ratio of the two male forms (*grey* and *tufted*), but that this has also driven the divergence of those two forms. This is demonstrated with a simple mathematical model in which the least common of the two male forms is the most successful at mating. This is possible because in *M. inclemens*, unlike many other salticids, mating appears to be driven by the attack and capture of females by aggressive males, and a female may mate many times with different males. The possibility of an allopatric, sympatric, or combined allopatric/sympatric origin of the two divergent male forms is also discussed.

Key words. courtship, dimorphic jumping spider, dimorphism, divergent selection, Fisherian sex ratio, mating systems, *Paraphidippus aurantius*, serial polygamy

Maevia inclemens (Walckenaer 1937) is commonly known as the “dimorphic jumping spider” because of the unusual presence of two male forms in almost equal numbers in each population (Figures 1-3). For most of its history this spider was known as *Maevia vittata* (Hentz 1846), until Barnes (1955) followed the lead of Chamberlin & Ivie (1944) and used the name *M. inclemens*. Richman (1978) suggested that *M. inclemens* is more properly a *nomen dubium*, but this name is now entrenched in recent usage. *M. inclemens* is widely-distributed and locally common throughout the eastern United States and southern Canada, most often found in the woodland sub-story or on plants near the woodland margin.

Because the presence of two very different male forms (*grey*, Figure 2, and *tufted*, Figure 3) is so unusual, there have been many laboratory studies of the courtship behavior of *M. inclemens*. From these studies we can obtain many clues related to the origin and maintenance of two male forms in each population. The ratio of these genetically determined forms in a population is close to 1:1 (Painter 1913; Clark 1992; Clark & Biesiadecki 2002). In laboratory trials, the mating success of each form is the same (Clark & Uetz 1990; Clark 1994; Clark & Morjan 2001; Clark & Biesiadecki 2002; Lietzenmayer & Taylor 2018).

Previous hypotheses that have been advanced to explain this dimorphism have focused on laboratory observations related to differences between the *grey* and *tufted* forms. Clark & Uetz (1992) found that differences in movement by the courting male affected female selection. The tufted form appeared to have an advantage at a greater distance (Clark & Morjan 2001). Tufted males may be less visible to predators like *Phidippus audax* (Clark, Simmons & Bowker 2018), although the importance of that species as a predator on *M. inclemens* is not known. One hypothesis is that tufted males communicate condition or fitness, and *grey* (*striped*) males reduce female aggression (Lietzenmayer, Clark & Taylor 2019), although it is not clear how this would result in a stable 1:1 ratio of the two forms.

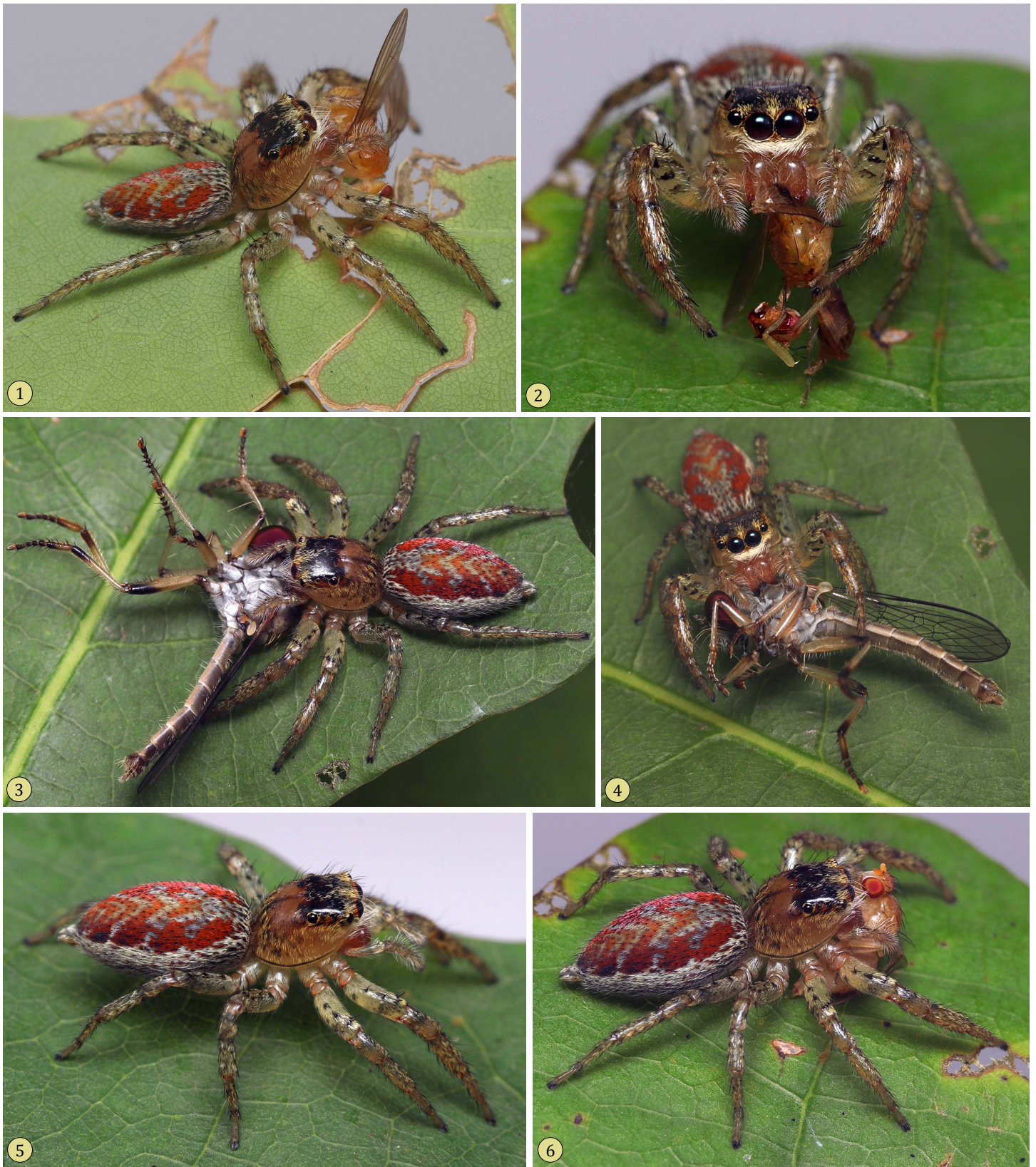


Figure 1. Adult female *Maevia inclemens*. 1-2, 6, Feeding on a small fly (Diptera: Brachycera). 3-4, Feeding on a small robber fly (Diptera: Asilidae). With the exception of Figure 5:8, only three *M. inclemens* individuals, two males and one female, all photographed on plants in the laboratory, are shown in this paper. All were collected in Massachusetts, June 2020.

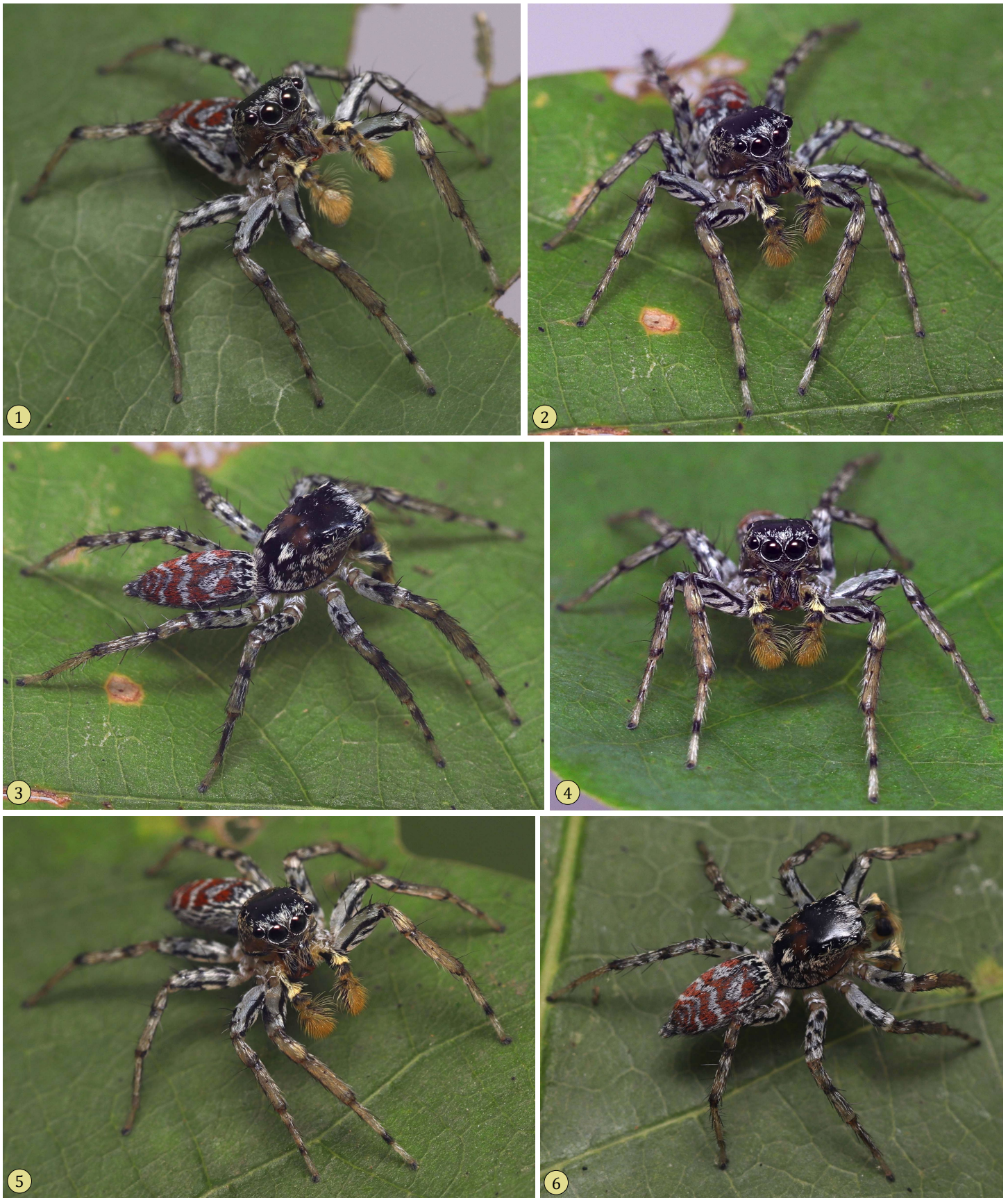


Figure 2. Adult male *Maevia inclemens*, grey (striped) form. Note the stripes on the prolateral surface of each femur.



Figure 3. Adult male *Maevia inclemens*, tufted (black) form. The tufts of the dorsal carapace may not be present in all males of this form. Note the lack of stripes on the uniformly-colored legs. **2**, Feeding on mosquito (Diptera: Culicidae).

Females appear to accept either of the two forms, but are less likely to accept intermediates (Clark & Uetz 1990, 1993). In support of this idea, Busso & Rabosky (2016) more recently described what they called *disruptive sexual selection*, finding that females preferred larger tufted males with a longer duration of courtship, and smaller grey males with a shorter duration of courtship. Females appeared to look for something different in each male form. However, all of these studies are based on the assumption that female receptivity (or acceptance of a male) can be gauged by their posture, or their movement toward a male (Clark & Uetz 1990, 1993). In most studies of salticids, female acceptance of a male is indicated by lack of movement of that female, including a cessation of turns to face the courting male (Figure 4; Hill 2014, 2018a, 2018b; Otto & Hill 2016). Thus movement of a female toward a courting male is by itself unusual, unless that female is stalking the male as prey.



Figure 4. Four sequential positions of a male (1-4) during the successful courtship of a female *Paraphidippus aurantius* (Lucas 1833) on a plant in the laboratory. Males were placed on plants with three recently molted females, all from Greenville County, South Carolina. In each case the female stopped moving soon after she sighted the male, and the male advanced to mate successfully when she did not turn to face him as he stepped from side to side. In this example the female stopped moving at a distance of about 10 cm from the approaching male. The subsequent mating included insertion of each pedipalp on the respective side of the epigynum, and occupied more than 20 minutes. *P. aurantius* males will cohabit with and defend penultimate females (Thurlow 2016), and their large chelicerae are associated with the ritual male-male combat (*agonistic behavior*) that may ensue. This represents a pattern seen in many other salticids (e.g., *Lyssomanes viridis*, Tedore & Johnsen 2012, 2013, 2015), in which male-male contests account for most sexual selection. At the other end of the spectrum of sexual selection lie the highly ornamented salticids of the genus *Maratus*, for which male-male contests are virtually unknown (save one species), and a female may examine the details of male ornamentation up-close before acceptance (Otto & Hill 2021). Most salticids appear to fall somewhere between these two extremes, relying to some extent on both male-male combat and active selection by females.

Here (Figures 5-10) I provide photographic documentation of the interactions of two male *Maevia inclemens*, one of each form, with a single female *M. inclemens*, all collected in June, 2020, in Massachusetts. All encounters shown here took place on plants in the laboratory under artificial lights, and thus may not represent the actual behavior of these spiders in nature.

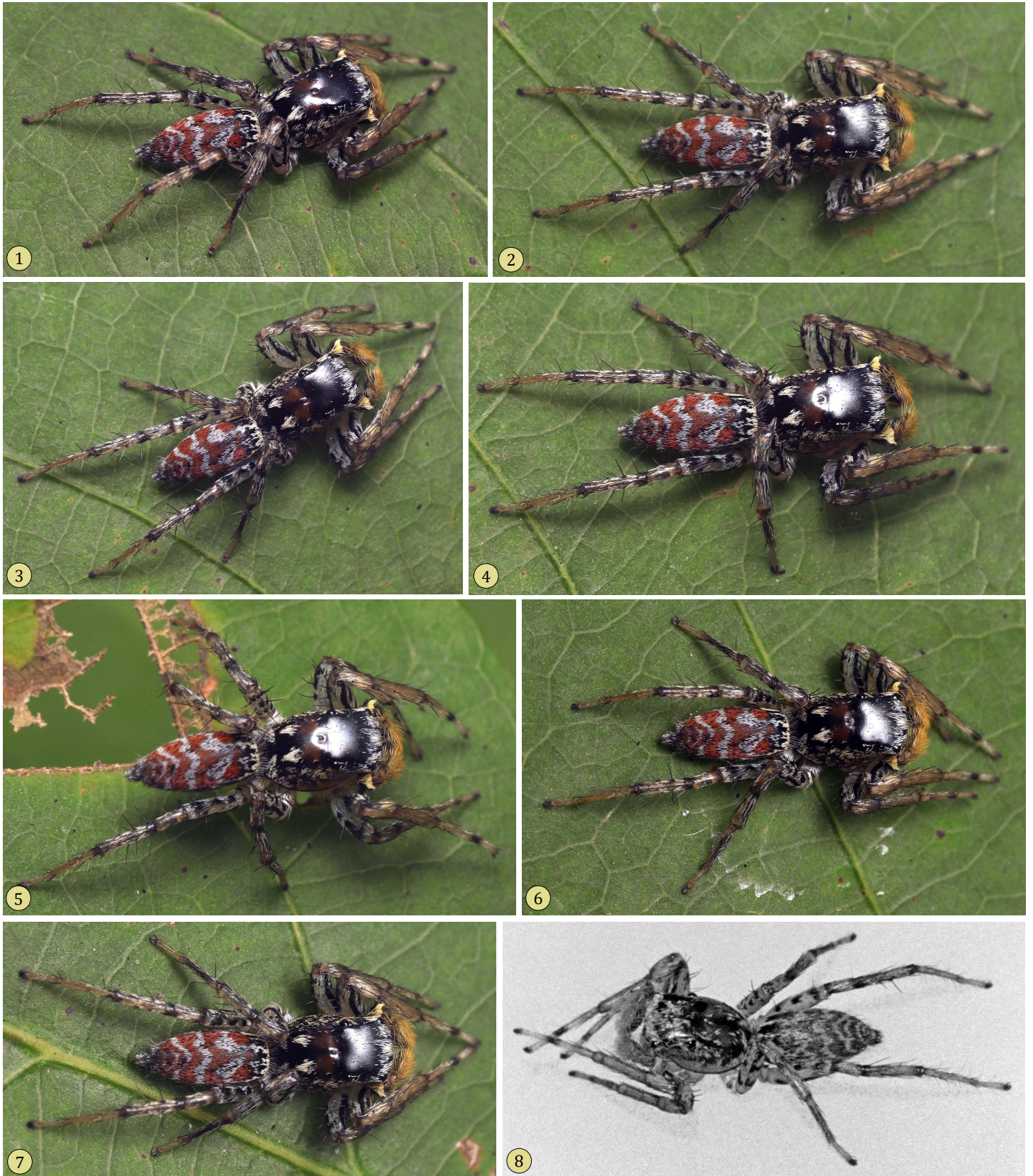


Figure 5. Display by grey males, *Maevia inclemens*. **1-7**, Successive (*low crawl*) positions of the grey male male from Massachusetts, advancing to successfully mate with the female. When close, this male jumped and captured the female (Figure 9:7). **8**, Display by a grey male from Sherburne County, Minnesota, recorded in 1982.

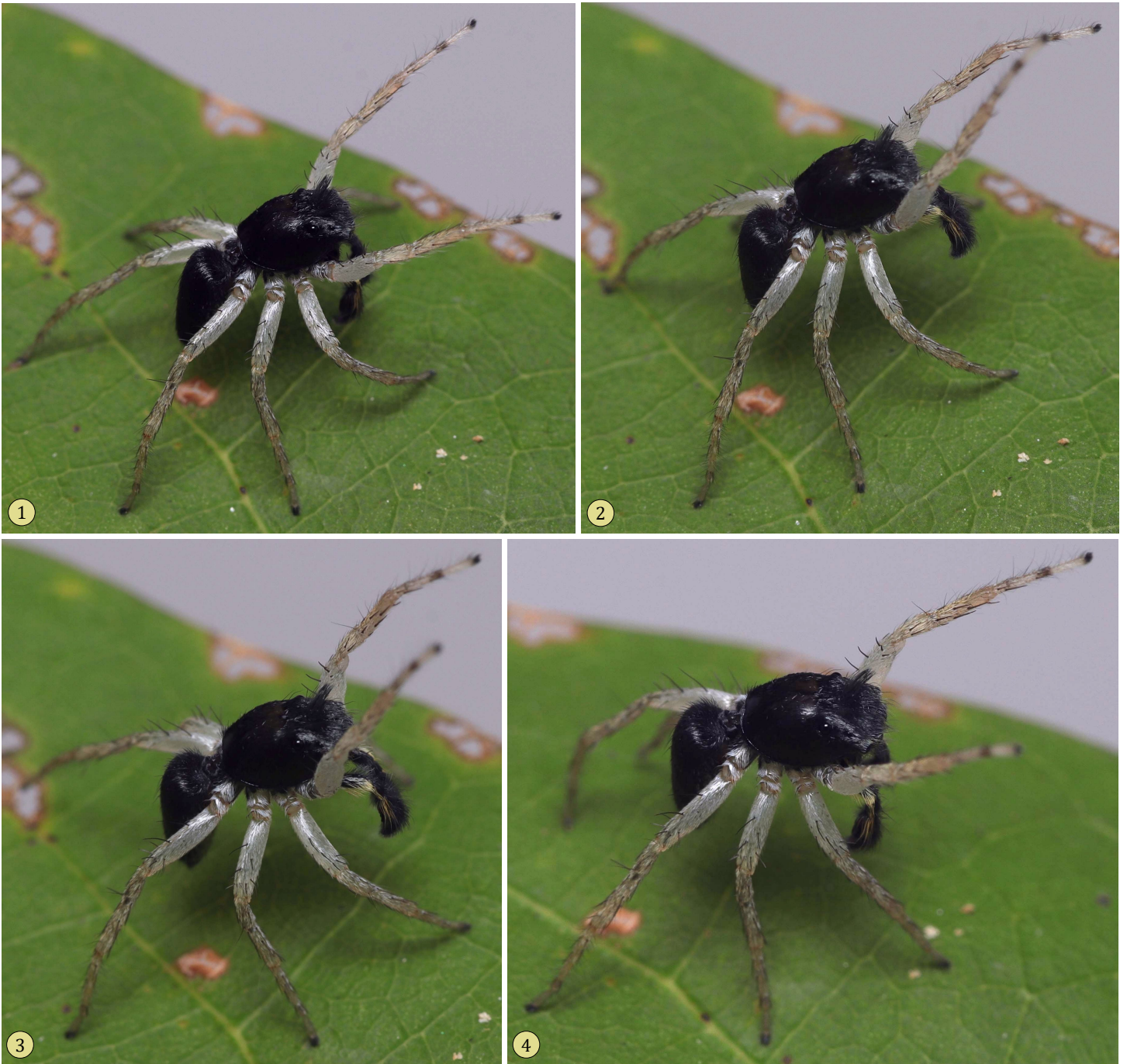


Figure 6. Sequential positions (1-4) of the tufted male *Maevia inclemens* as he advanced toward the female. Facing the female, this male maintained an elevated position with the opisthosoma turned down, stepping and waving both legs I and pedipalps. As with the grey male (Figure 5), this male also mated successfully with the female (Figure 9:3), jumping and capturing her after advancing to a near position.

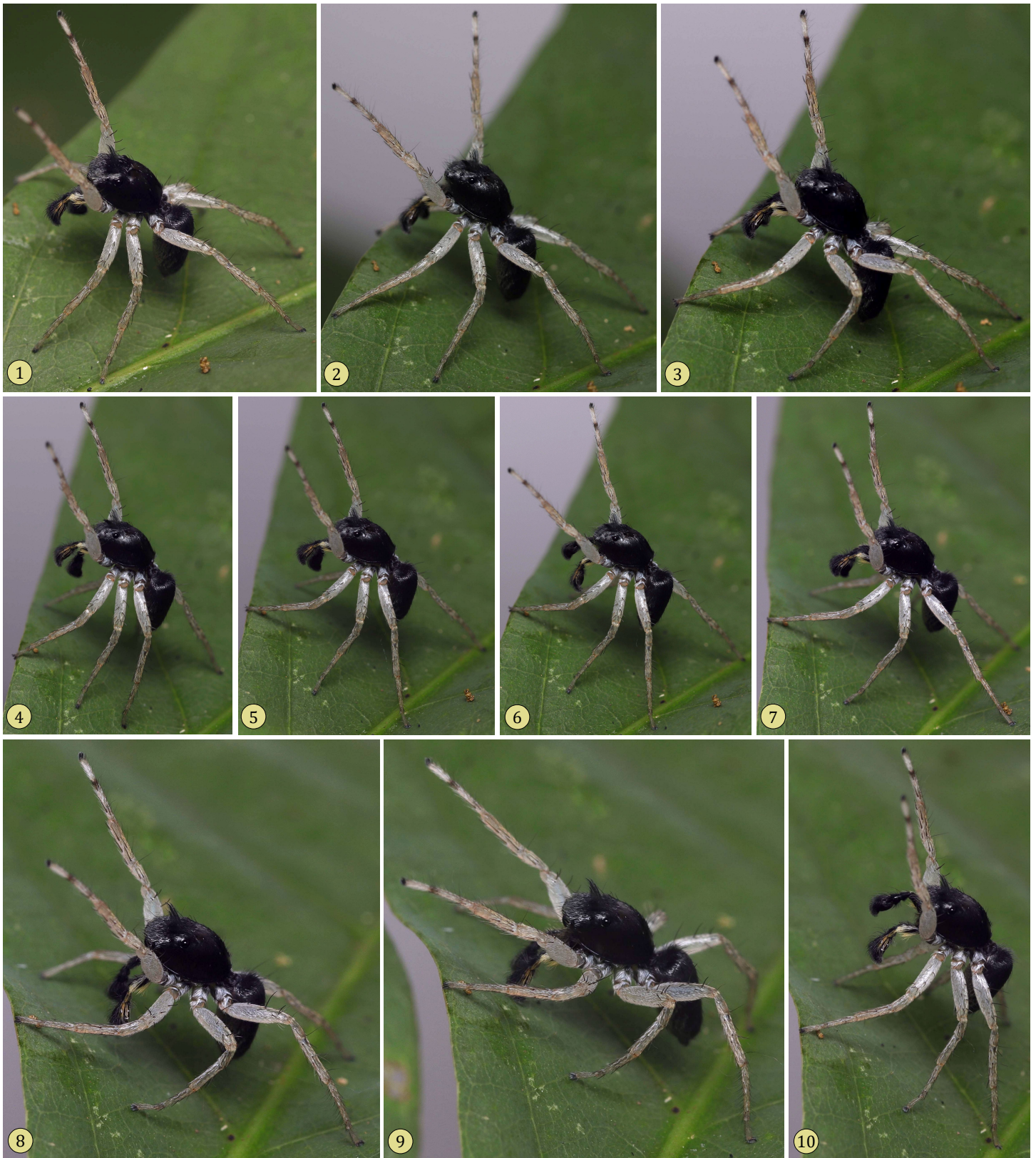


Figure 7. Sequential positions (1-10) of the tufted male *Maevia inclemens* as he advanced toward the female in a later mating attempt (after Figure 6).



Figure 8. Sequential positions (1-4) of the tufted male *Maevia inclemens* as he advanced toward the female in a still later mating attempt (after Figure 7). Here the view of the female is shown. **1-2**, Waving legs I. **3**, Fully extended for maximum height. **4**, Display from a lower position with raised legs I.

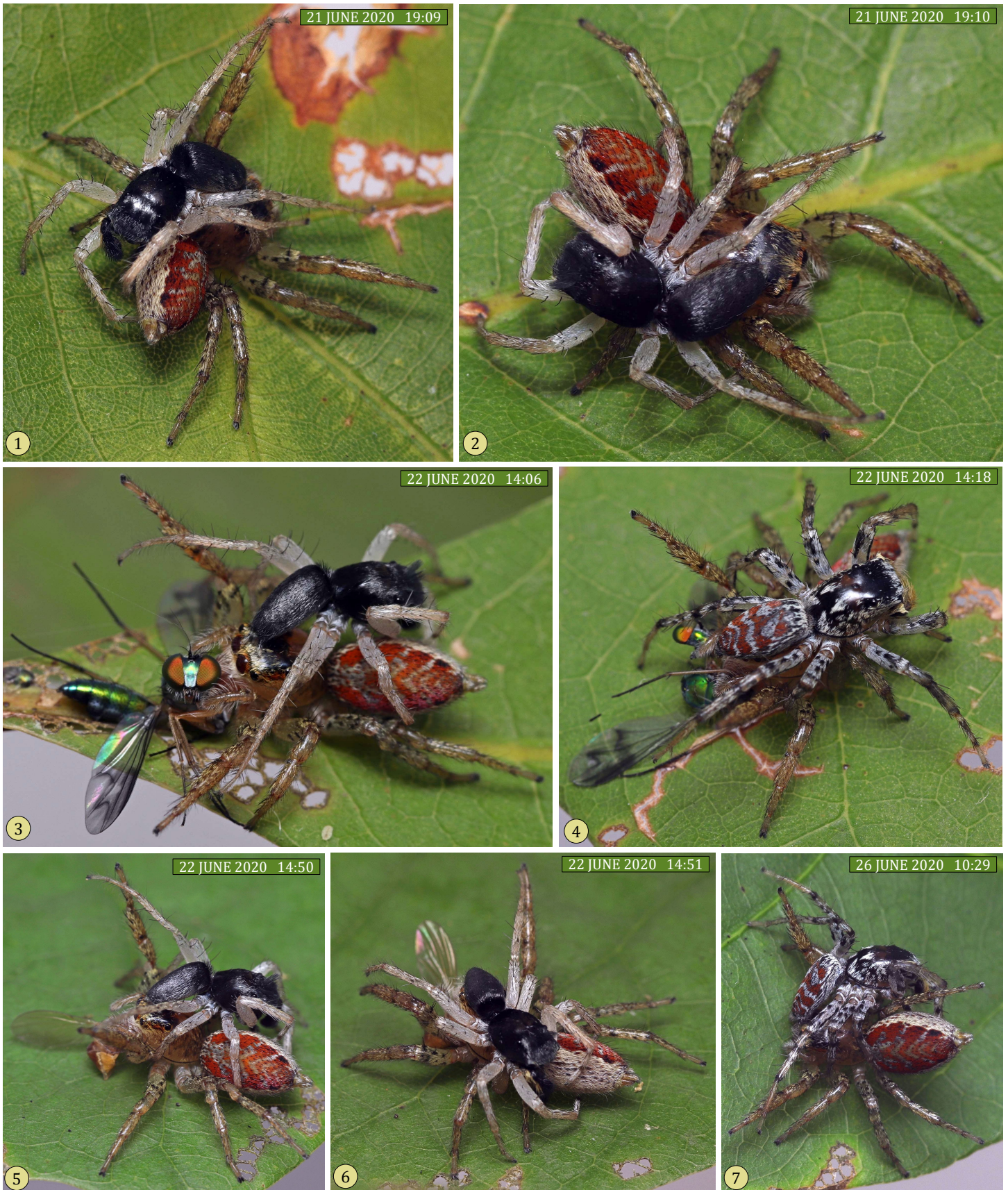


Figure 9. Five sequential matings (1-2, 3, 4, 5-6, 7) of the two male forms with the same female *Maevia inclemens* over the course of five days. **1-2**, This mating was interrupted as the male switched from one side to the other, but after an atypical low crawl display with legs I extended, the tufted male quickly recaptured the female and continued to mate on the other side. **5-6**, mating on the right and then left sides. Note the many erect spines on the legs of the mating male in each instance.

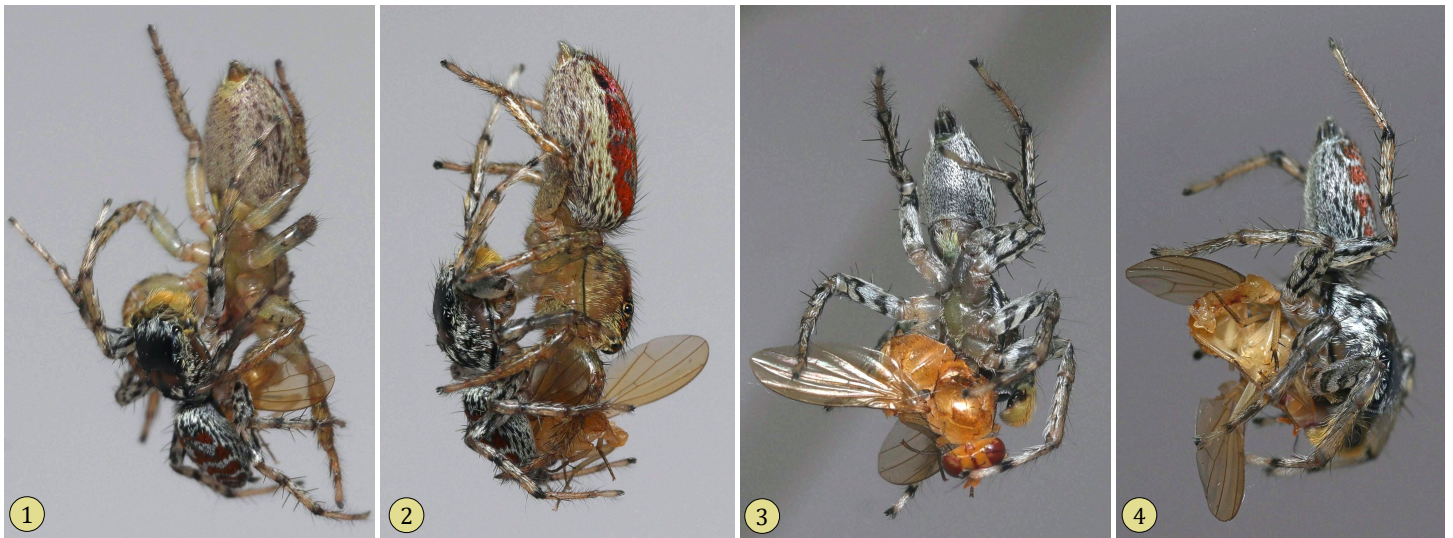


Figure 10. Attempted mating by the grey male *Maevia inclemens*. This sequence shows how the male jumped the female while she was suspended from her dragline, just after capturing a fly (1), and attempted to mate with her (2). The female promptly released her prey, and the male then fed on it for many minutes (3-4), still in a suspended position [23 JUNE 2020 14:09-14:13]. Three days later this male approached and mated successfully with the female for a second time (Figures 5:1-7, 9:7).



Figure 11. Sequential (1-2) views of encounter between the two male forms of *Maevia inclemens*. Apart from a brief defensive reaction by the grey male (2), no ritual combat ensued and the males did not appear to recognize that they were conspecific.

There are two important questions related to the existence of two equally successful male forms in *Maevia inclemens*:

- 1) How is the 1:1 ratio of these forms maintained in populations of these spiders?
- 2) How did this unusual situation arise?

To address the first question, all of the answers presently on the table (Clark & Uetz 1992; Clark & Morjan 2001; Busso & Rabosky 2016; Clark, Simmons & Bowker 2018; Lietzenmayer, Clark & Taylor 2019) suggest that each of the two forms may have a relative advantage in different situations. The *divergent sexual selection* described by Busso & Rabosky (2016) provides us with some insight, but none of these studies has provided a viable mathematical model that could explain the persistence and stability of this 1:1 ratio across many populations of this species.

Other possibilities include variation in environmental conditions, local community structure, or population density. Any of these could favor one male form over the other in some situations. Related hypotheses could be tested in the future. One might expect to find a correlation between any of these variables and the extent to which one of the male forms is favored in the mating population. The problem that I have with these hypotheses lies in the fact that the 1:1 ratio is so robust across multiple localities. This is highly unusual, and it seems to demand a much more robust selective regime, much like that proposed by the *Fisherian sex ratio theory* that explains the 1:1 ratio of males to females in most species (Fisher 1930). But these environmental hypotheses still merit study and testing.

The possibility that female *M. inclemens* may mate multiple times (or *polygamy*) has not been taken into account. Most descriptions of salticid mating systems assume that a *monogamous* female selects a single mate based on characteristics of his movement or appearance. In these systems, coevolution of female selection and male display can evolve directly from *mate recognition* to *evaluation of mate condition* and finally the the extreme features of *Fisherian runaway* selection (Fisher 1930; Pomiankoski & Iwasa 1993; Hall, Kirkpatrick & West 2000). As noted previously, male-male combat or agonistic behavior can be more important than female selection in many salticid species.

But is *Maevia inclemens* really monogamous? My anecdotal observations, those documented here as well as earlier observations in both Minnesota and New York state, suggest that this is not the case. As shown in Figure 9, a single female from Massachusetts mated with both male forms multiple times over a five day period. This situation would not be unique in the Salticidae. For example, *Hentzia mitrata* (Hentz 1846) males will chase females over some distance to mate briefly, and can mate many times with the same female (Hill 2011). The mating system of *M. inclemens* may lie completely outside of the spectrum between male guarding (with cohabitation and an emphasis on agonistic behavior) and extreme female selection (or Fisherian runaway). My own observations suggest that both male forms of *M. inclemens* advertise in an attempt to get close enough to a female, so that they can effectively *jump and capture* that female for mating. In this mating system, neither female selection nor male guarding would be of particular importance. My limited observations of male-male encounters in *M. inclemens* (Figure 11) has given me the impression that neither male form recognizes the other as a conspecific, and I have seen no indications of ritual agonistic behavior. However, I have not yet had the opportunity to study male-male encounters involving two males of the same form.

Thus my working hypothesis for the maintenance of a stable 1:1 ratio of the two male forms (*grey* and *tufted*) of *Maevia inclemens* is as follows:

- 1) A female will mate multiple times over a period of at least several days. This is based on capture of females by males that attract their attention in order to approach them.
- 2) Females tend to selectively avoid the male form that has previously captured them and/or mated with them, at least for several hours. This is a significant tendency, but not an absolute rule.
- 3) Each male in a population, whether *grey* or *tufted*, has about the same likelihood of mating an unmated (*naive*) female.
- 4) If one male form is more common, then there are proportionately more matings of unmated females by males of that form. Thus there are more mated females that have previously mated with the more common form.
- 5) Because of (2) and (4), a male of the less common form is more likely to mate in a subsequent encounter with a female.

The 1:1 equilibrium is thus driven by the fact that either male form, if less common, is more successful at mating with a previously mated female. This can be expressed in a simple mathematical model as follows:

- p_1 = fraction of first form males in population
- p_2 = fraction of second form males in population = $(1 - p_1)$
- s_1 = fraction or chance of finding previously mated female
- s_2 = fraction or chance of finding unmated female = $(1 - s_1)$
- c_1 = fraction or chance that an unmated female mates first form male
- c_2 = fraction or chance that an unmated female mates second form male
- c_3 = fraction or chance of mating a female that mated same form
- c_4 = fraction or chance of mating a female that mated different form
- m_1 = mating success per encounter of first form male
- m_2 = mating success per encounter of second form male

Assume that the male forms are equally successful with unmated females, $c_1 = c_2 = c$, then:

$$m_1 = s_2c + s_1(p_1c_3 + p_2c_4)$$

$$m_2 = s_2c + s_1(p_2c_3 + p_1c_4)$$

Then the mating advantage ($m_2 - m_1$) of the second form can be stated as:

$$(m_2 - m_1) = s_1(p_2c_3 + p_1c_4 - p_1c_3 - p_2c_4) = s_1(c_4 - c_3)(p_1 - p_2)$$

Thus the mating advantage for the second male form is the product of three factors, the relative chance of finding a previously mated female (s_1), the relative preference of a female for a different form ($c_4 - c_3$), and the relative number of males of the first form in the population ($p_1 - p_2$). The more common the male form, the less its mating success. As the breeding season progresses, the fraction of previously mated females in a population (s_1) will increase, further increasing the mating advantage of the less common male form. Because this works in both directions, it drives the ratio of the two forms to 1:1. In addition, as supported by the observations of Busso & Rabosky (2016) on *disruptive selection*, this hypothesis predicts *divergent selection* to make the two male forms as different as possible. The more different the less common male is from his counterpart, the less likely that he will be avoided in an encounter with a female.

But do female *Maevia inclemens* really learn the characteristics of males that have captured them, and tend to avoid these males in future encounters? This ability has precedent in the known behavior of many salticids, in which females, after mating, signal both recognition and rejection to males at the same time. In an earlier publication (Hill 2016) I demonstrated *learned avoidance* of toxic prey by jumping spiders of the genus *Phidippus*. The avoidance of toxic prey by these spiders lasted for hours, but also decayed rapidly by human standards. Avoidance by female *M. inclemens* may also be of limited duration, but nonetheless significant. In any case this hypothesis can be measured or tested directly in laboratory or field studies.

The second question, of how the dimorphic condition of male *Maevia inclemens* arose, may be more difficult to address. Clearly this is an uncommon, hence improbable, condition. This might have been initiated by the joining of two previously separate populations, each of which had evolved its own male form. In a hybridization zone between the two populations, the success of both male forms would be buffered by migration out of each respective population. This might last long enough to drive the evolution of females that were locked into the equilibrium and stability of the unusual mating system that we observe today. We can call this the *allopatric hypothesis* for the origin of dimorphic males.

We can also entertain a *sympatric hypothesis*, whereby chance mutations gave some males in a single population the ability to take advantage of female avoidance behavior. Once initiated, this process could have driven the divergence of two forms to the level that we see today.

In any case, sympatric evolution of each male form would have driven the divergence of the two forms after an allopatric origin.

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