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## Contests between male *Maratus vespertilio* (Simon 1901) (Araneae: Salticidae)

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### Abstract

Male *Maratus vespertilio* were observed in the field or placed near each other in a naturalistic setting and their interactions were observed with camera and video. Males displayed to other males at a distance (up to at least 30 cm), moved (*hopped*) toward them, and engaged in prolonged *hopping contests*, consisting of a series of *hops* or 'attacks' by each spider in turn, in close proximity. Displays between males at a distance, during their approach to each other, and during these 'attacks', all involved the alternation of a crouching stance with a sudden extension of legs III (and I, in proximity), elevation of the body on legs II and IV, followed by a forward rocking movement or *hop*. During each display the opisthosoma was elevated and lateral opisthosomal flaps bearing iridescent scales were held in an extended position. Male courtship display to a sighted female was quite different from these male-male interactions, involving rapid vibration of the raised fan at a distance, and a complex series of bilateral semaphores with extended legs III as the female was approached. This is the first report of the use of the opisthosomal fan by a *Maratus* in male-male contests.

### Introduction

We recently (Otto and Hill 2011a, 2011b) reported on the occurrence of the 'Bat Peacock Spider' *Maratus vespertilio* (Simon 1901) across southern Australia. Unlike all other known *Maratus*, males of this species are quite cryptic in colouration, with dull green iridescent scales occurring primarily on the lateral flaps of the opisthosoma. Outside of the contexts of courtship or male-male interaction, these flaps are folded around the sides of the opisthosoma. The use of the elevated opisthosoma with extended flaps as part of the courtship of other *Maratus* species has been known for some time, and has received much attention recently (Waldock 1993, Waldock 2007, Hill 2009, Otto and Hill 2010, Hill and Otto 2011, Girard *et al.* 2011). To date, however, there have been no reports or descriptions of the interactions of male *Maratus* with other males.

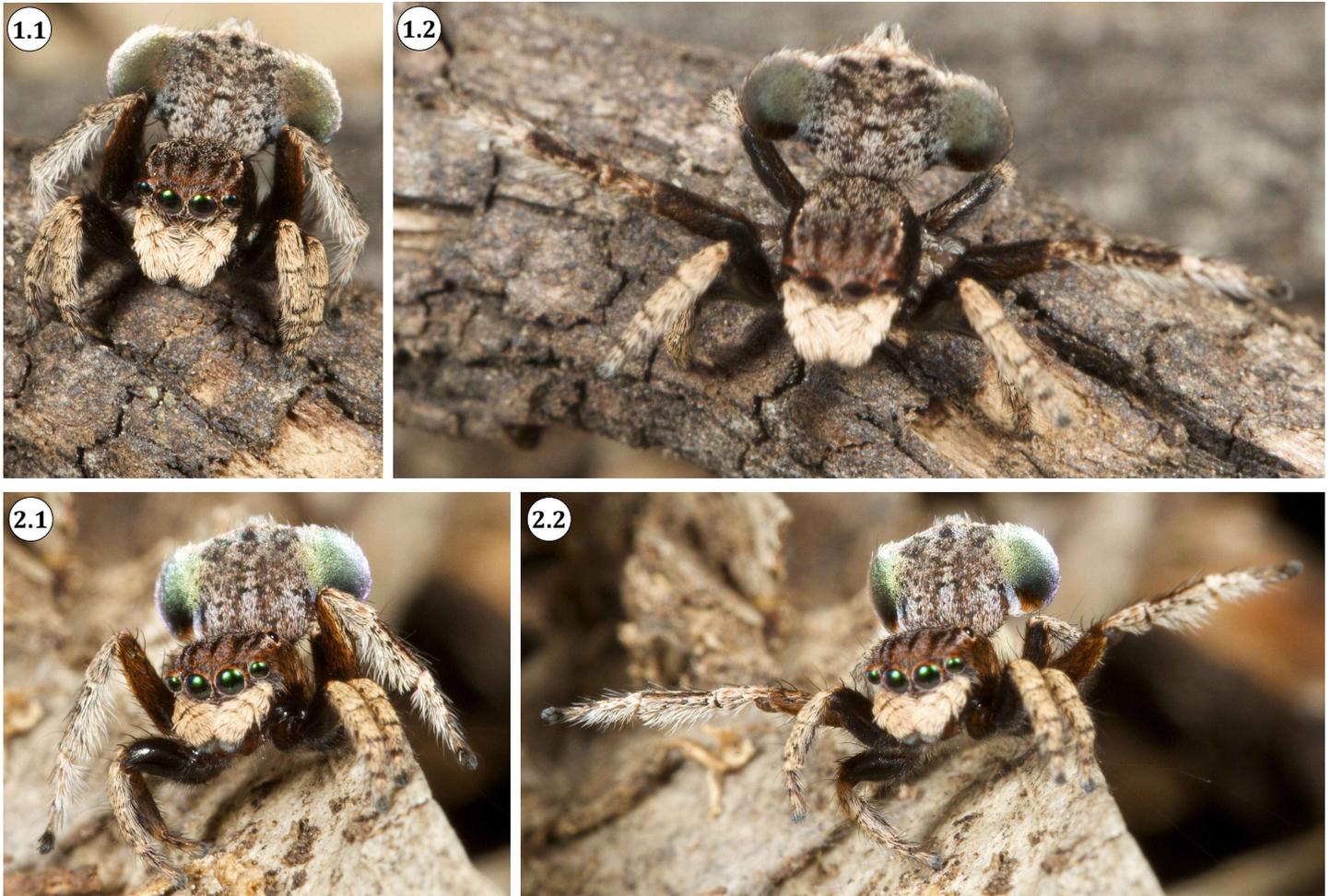
### Methods and subjects of this study

Male *Maratus vespertilio* engaged in combat with other males were first observed and filmed in their natural habitat in Whitton, New South Wales, and were later placed together in a naturalistic setting, based on materials (soil, litter, dung pads) collected from the Whitton site and placed on a 60 x 45 cm cork board (the *set*). Up to 25 males and 25 females were placed on this board simultaneously. Spiders were observed either indoors using ordinary desk lamps for illumination, or the set was transferred to a garden tent where natural light was the main source of illumination. An on-camera filming light was also used. Spiders were not constrained as they were filmed, but were returned to the set from time to time. Observations were made with or without the presence of females, a factor that did not appear to influence the male-male contests that were observed. Male encounters with females, and the resulting courtship displays, were also documented for purposes of comparison with male-male interaction. The video

recording rate was 25 frames/second, and positions associated with each  $1/25$  (or 0.04) second frame are depicted here in images and charts.

### Contests between males

*Display at a distance.* When a male sighted another male at a distance (up to at least 30 cm), it sometimes assumed a characteristic crouching stance with elevated opisthosoma, extended opisthosomal flaps and the pedipalps held together in front of the chelicerae (Figure 1, 1.1 and 2.1). During this display, a male would suddenly extend its legs III and rise on legs II and IV, then moved forward and down, quickly returning to the crouching stance (Figure 1, 1.2 and 2.2). Here we will refer to this sudden movement as a *hop*.



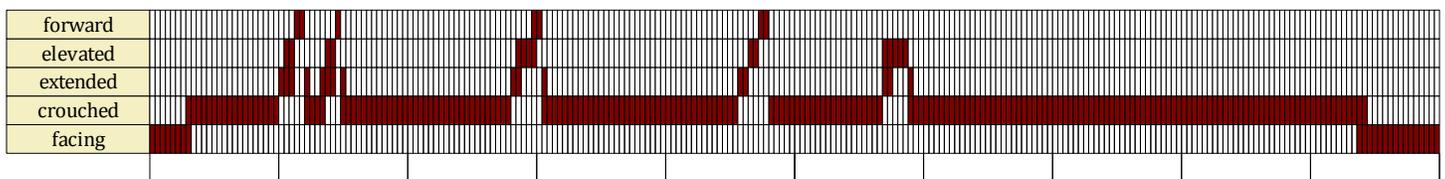
**Figure 1.** *Hopping display* by two different male *Maratus vespertilio*, after sighting another male (1.1–1.2, 2.1–2.2). Each characteristic *hop* began and ended in a crouching position (1.1, 2.1). During the *hop* each spider held legs III in a widely extended position, and reared up off the substrate on legs II and IV (1.2, 2.2). Note how the shiny, dark anterior femora contrast with the bright pedipalps of the crouching spider when viewed from the front.

Males did not always display to nearby males, and some males were much more likely to display than were others. It is possible that males respond to other males that appear to have an interest in taking over their local 'lookouts' or territories, but this is a subject that will requires more study.

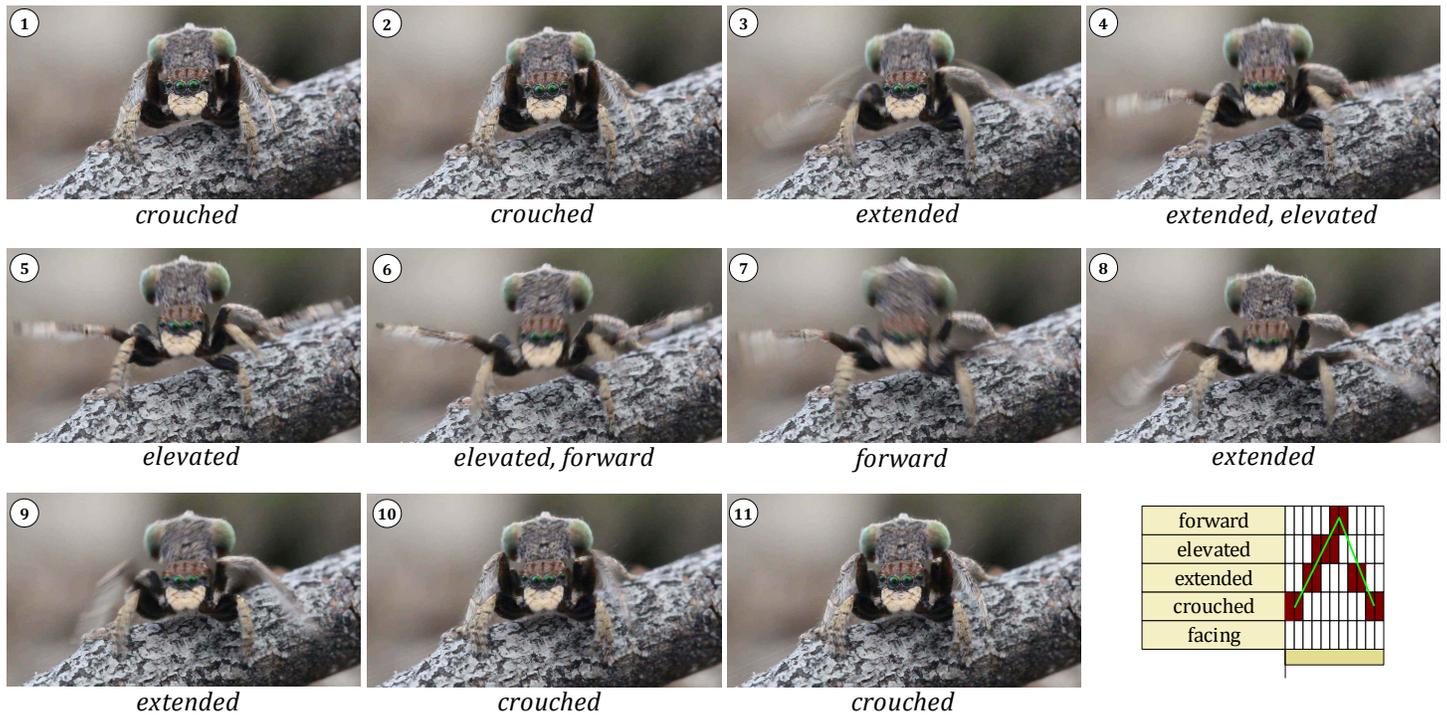
Examples of this hopping display are shown in Figures 2–9. At times, spiders would execute a series of 2–4 hops (*a hop group*) in the span of one second. Hop groups were usually separated by one or more seconds during which the crouching position, facing the oponent, was maintained. Sometimes spiders would hold this crouching position for a prolonged time (5–20 s or longer) without hopping.



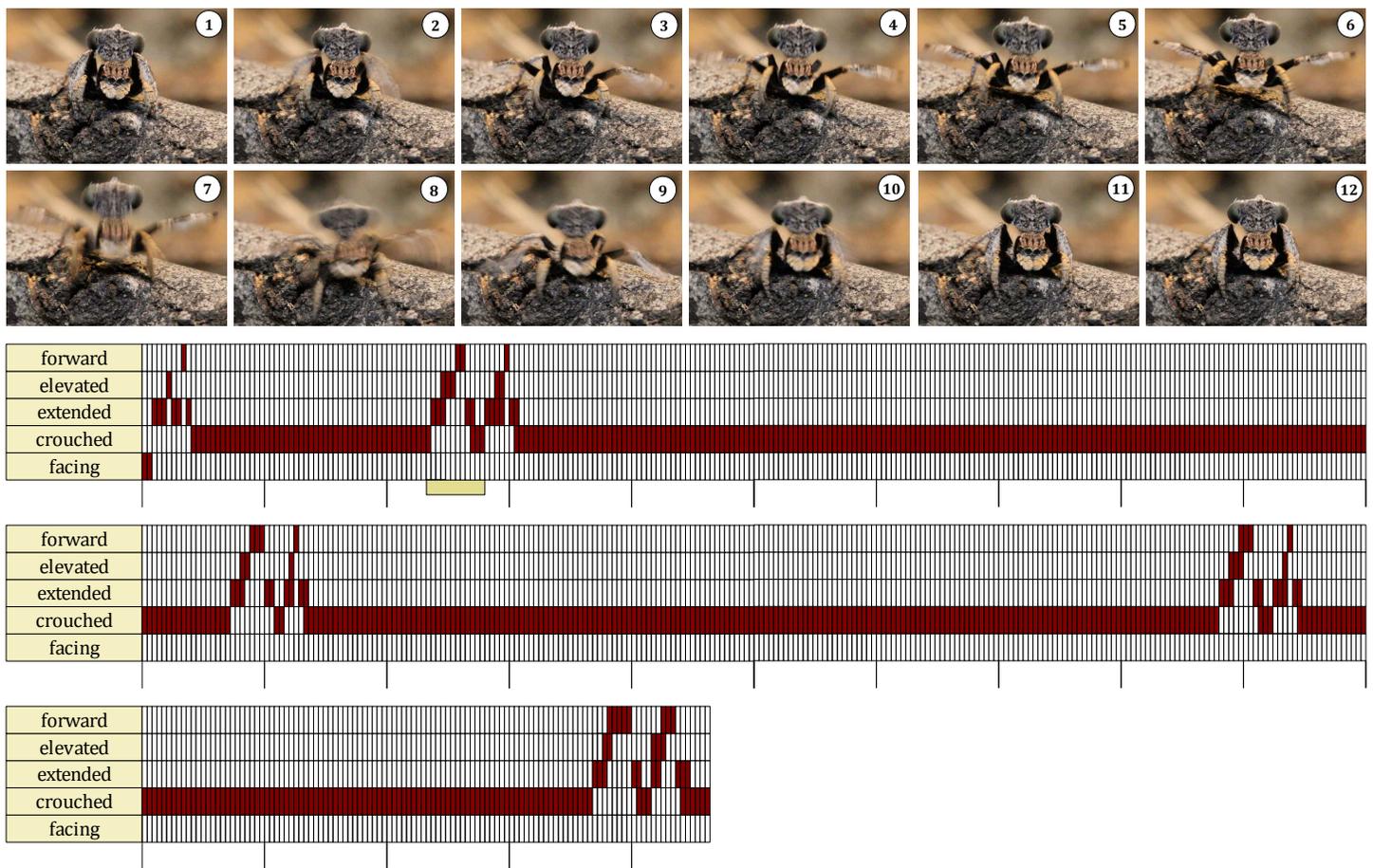
**Figure 2.** Sequence of frames (1–14) recorded at 0.04 s intervals, depicting a single hop by a male *Maratus vespertilio*. The position of the spider in each frame was scored according to whether the spider was *crouched*, had its legs *extended*, had its legs extended and the body was *elevated*, or was moving *forward* from the elevated position before returning to a crouching position, shown in the chart at lower left. In this chart, and in charts presented subsequently in this paper, each scored box represents a 0.04 s interval, and the bar below the chart indicates the position of the frames that are shown here. The duration of this entire hop sequence was about 1/2 s.



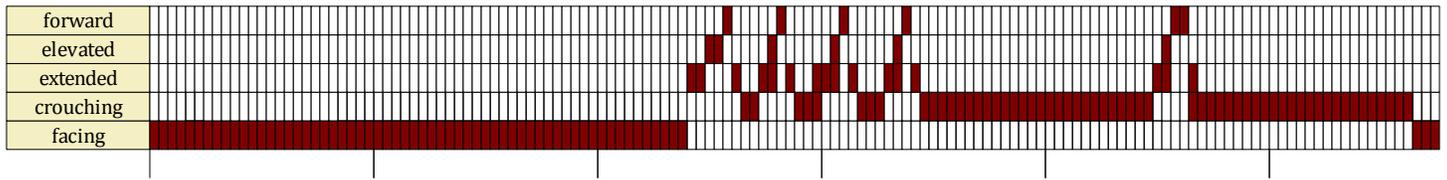
**Figure 3.** Chart depicting a 10 second sequence of display by a male to another male. Tick marks at the bottom of this, and subsequent charts, mark each second (25 consecutive frames) of the sequence. In this example, there were four *hop groups*, separated by intervals of about 2 seconds. Note that the first hop group included 2 hops, each about 0.2 s in duration, in rapid succession.



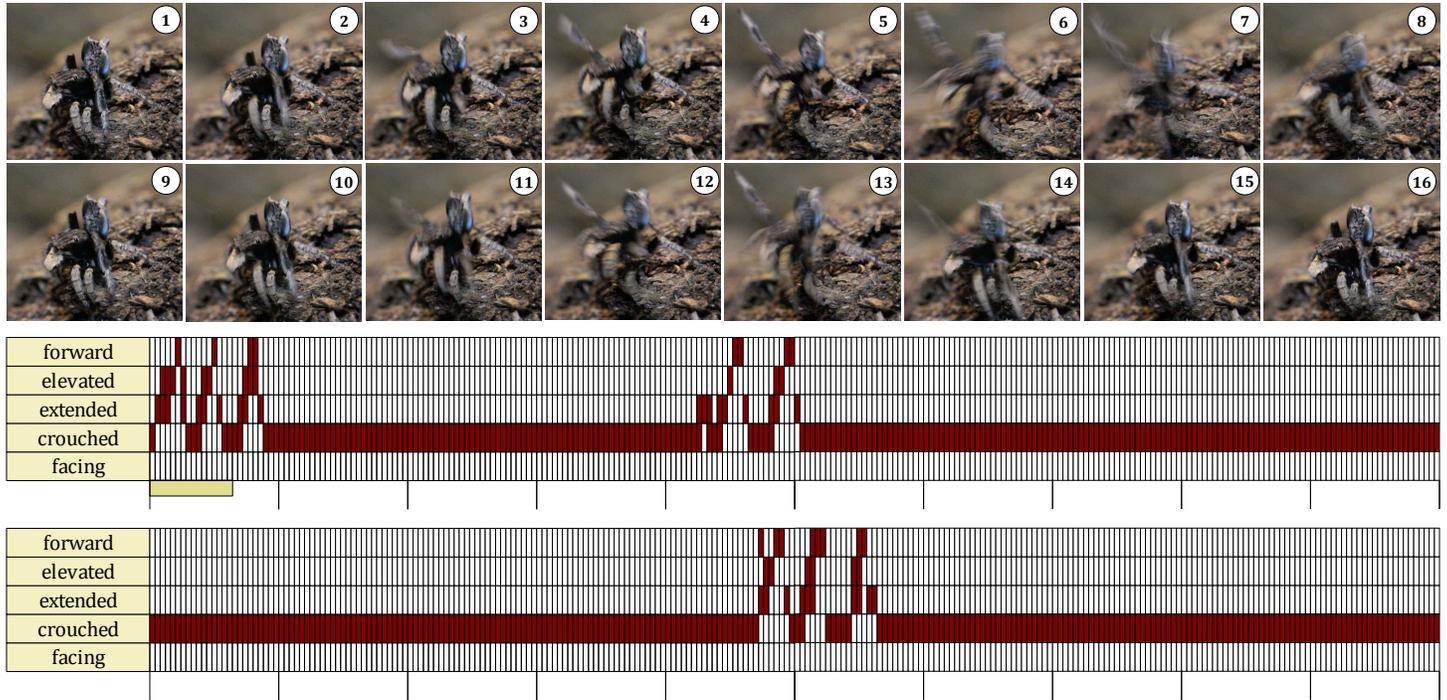
**Figure 4.** Sequence of frames (1–11) recorded at 0.04 s intervals, depicting a single hop by a male *Maratus vespertilio*, viewed from the front.



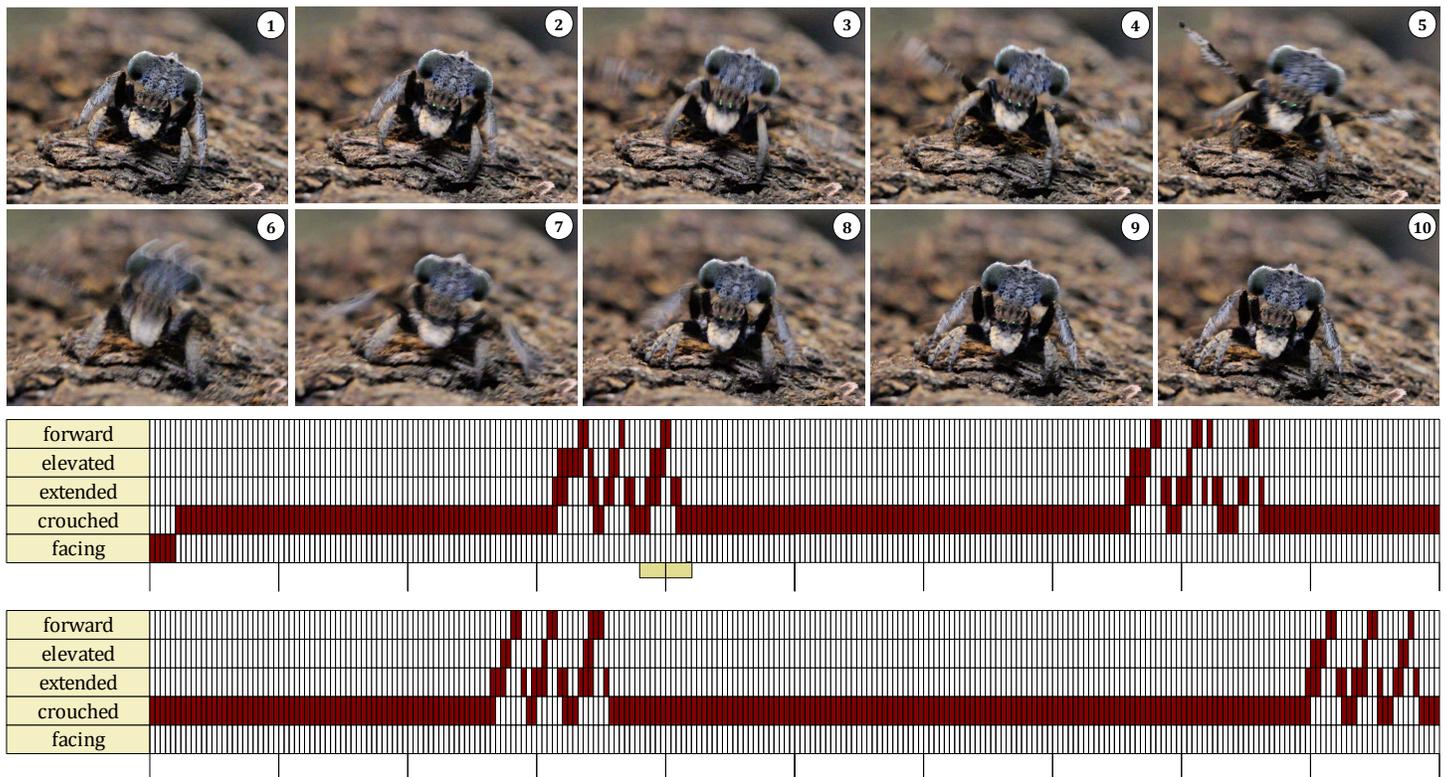
**Figure 5.** Longer (~25 s) sequence of display by a male *Maratus vespertilio* facing another male, viewed from the front. The position of the sequence of frames shown at top (1–12) is indicated by the solid bar in the chart, below. Some individuals consistently displayed with multiple hops in each group, as shown here. Between hop groups, spiders crouched and faced each other for longer periods of time.



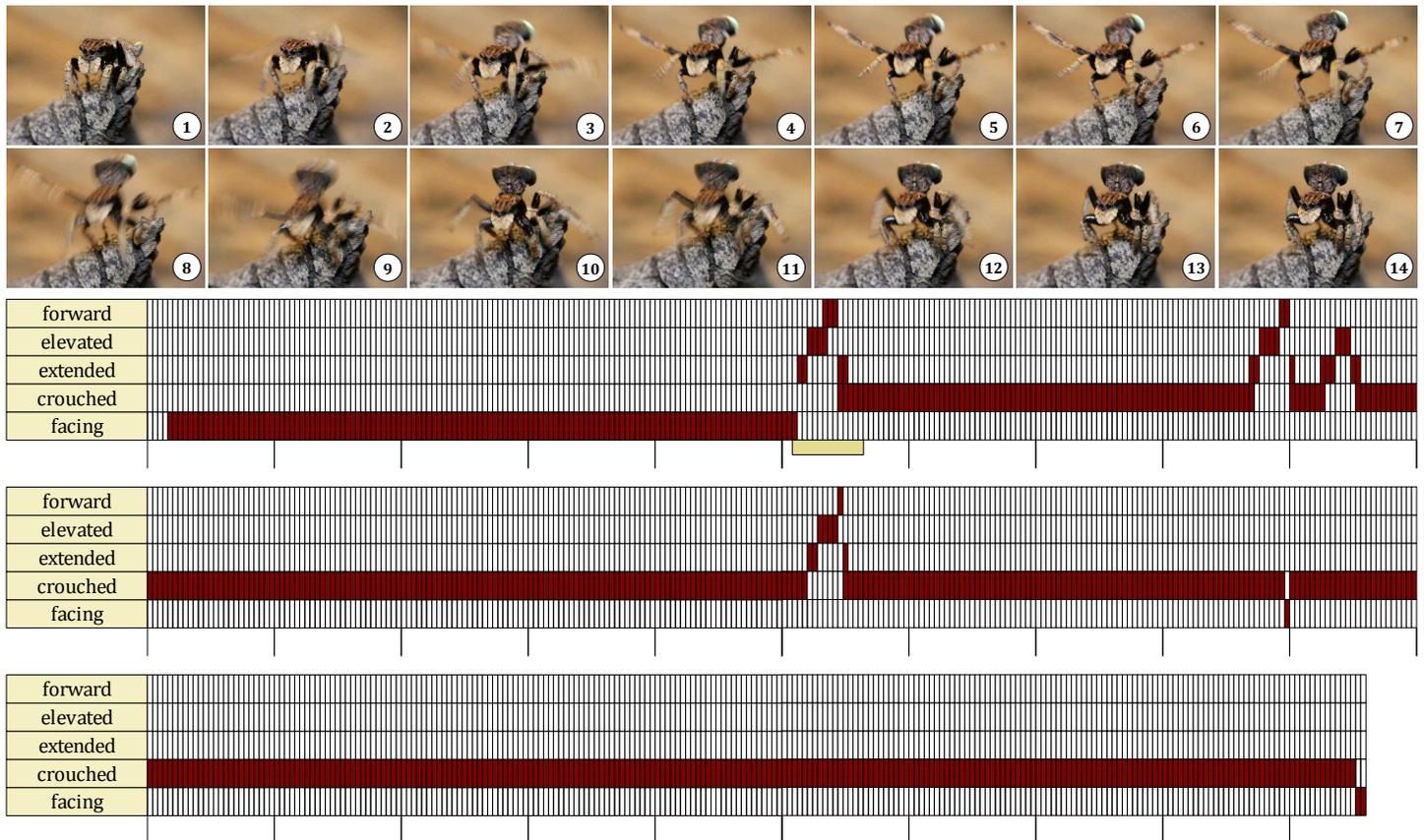
**Figure 6.** Chart depicting a sequence of display by a male to another male. Note the grouping of four hops in rapid succession in this example.



**Figure 7.** Sequence of display by a male to another male, with three hops in each hop group.

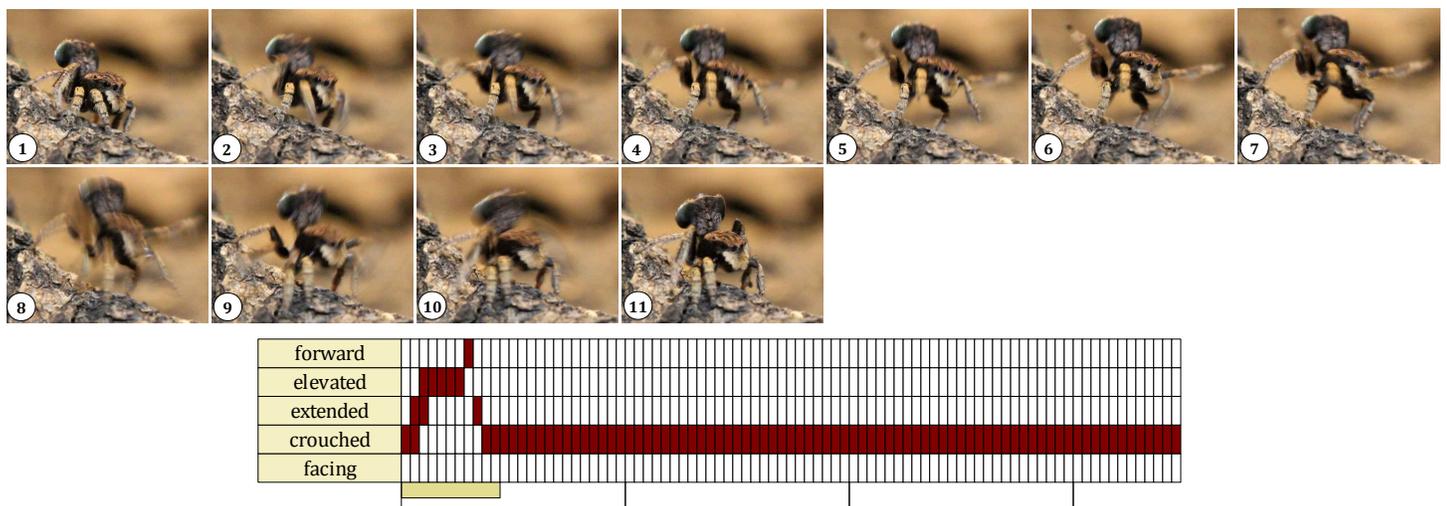


**Figure 8.** Another sequence of display by a male to another male, with three hops in each hop group.



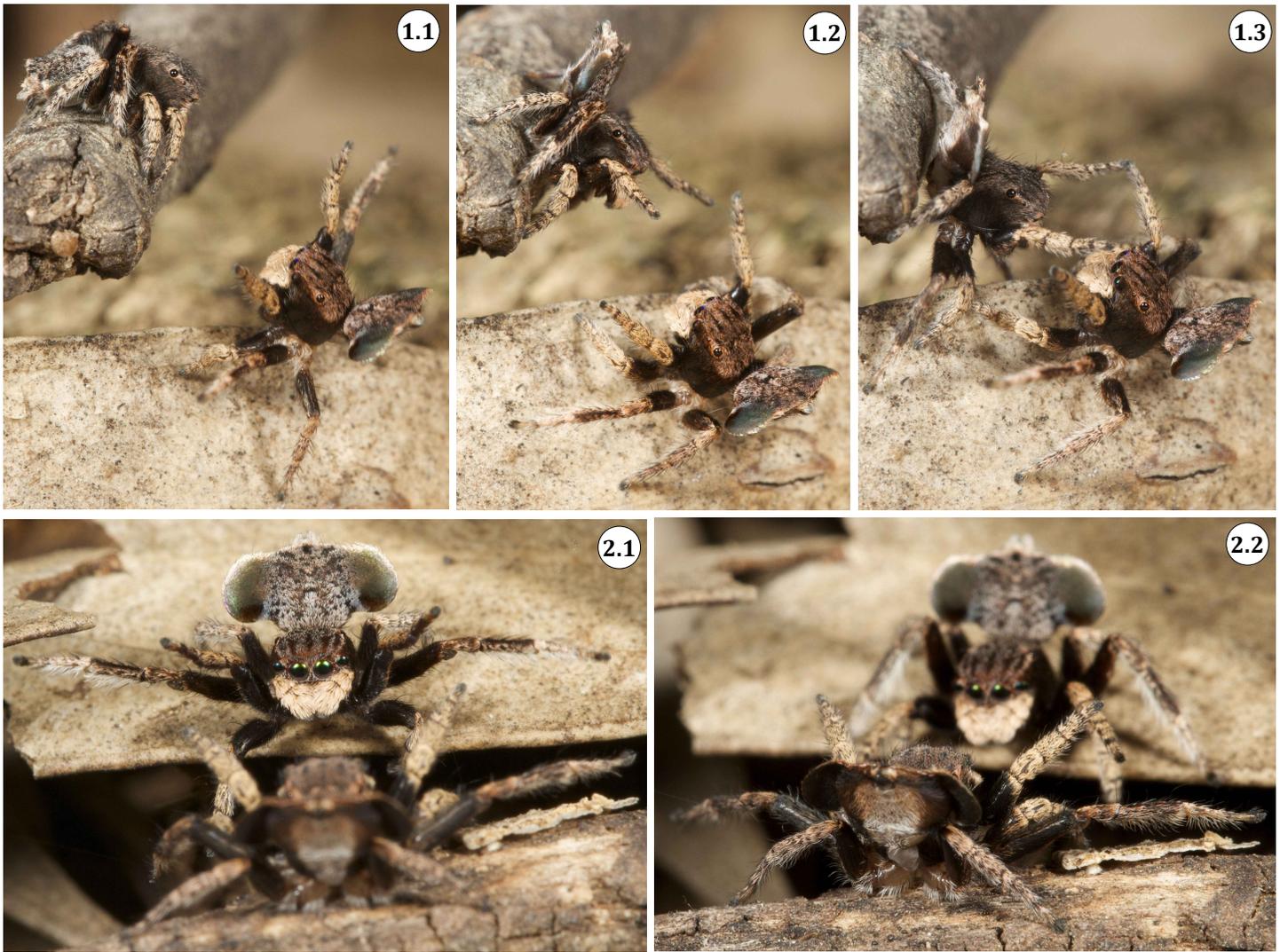
**Figure 9.** Sequence of display by a male to another male. In this example, the crouching position was maintained for about 14 seconds after the last hop. Note how in the selected sequence of frames (1–14), this spider moved forward during the hop, but maintained the attachment of legs IV to the substrate and returned to its original position.

*Forward movement.* Although spiders often returned to their starting position at the end of each hop, the forward movement phase of a hop often resulted in movement of the attachment site of legs IV and forward movement of the spider as a whole to a new crouching position nearer to its opponent. This movement was only slight in some example, but in other examples it included hopping on legs II and IV, or running, to cover a distance of as much as 6-10 body lengths. Thus the postures observed in the case of a hop in place are the same as those associated with hopping movement of the spider toward its opponent (Figure 10).



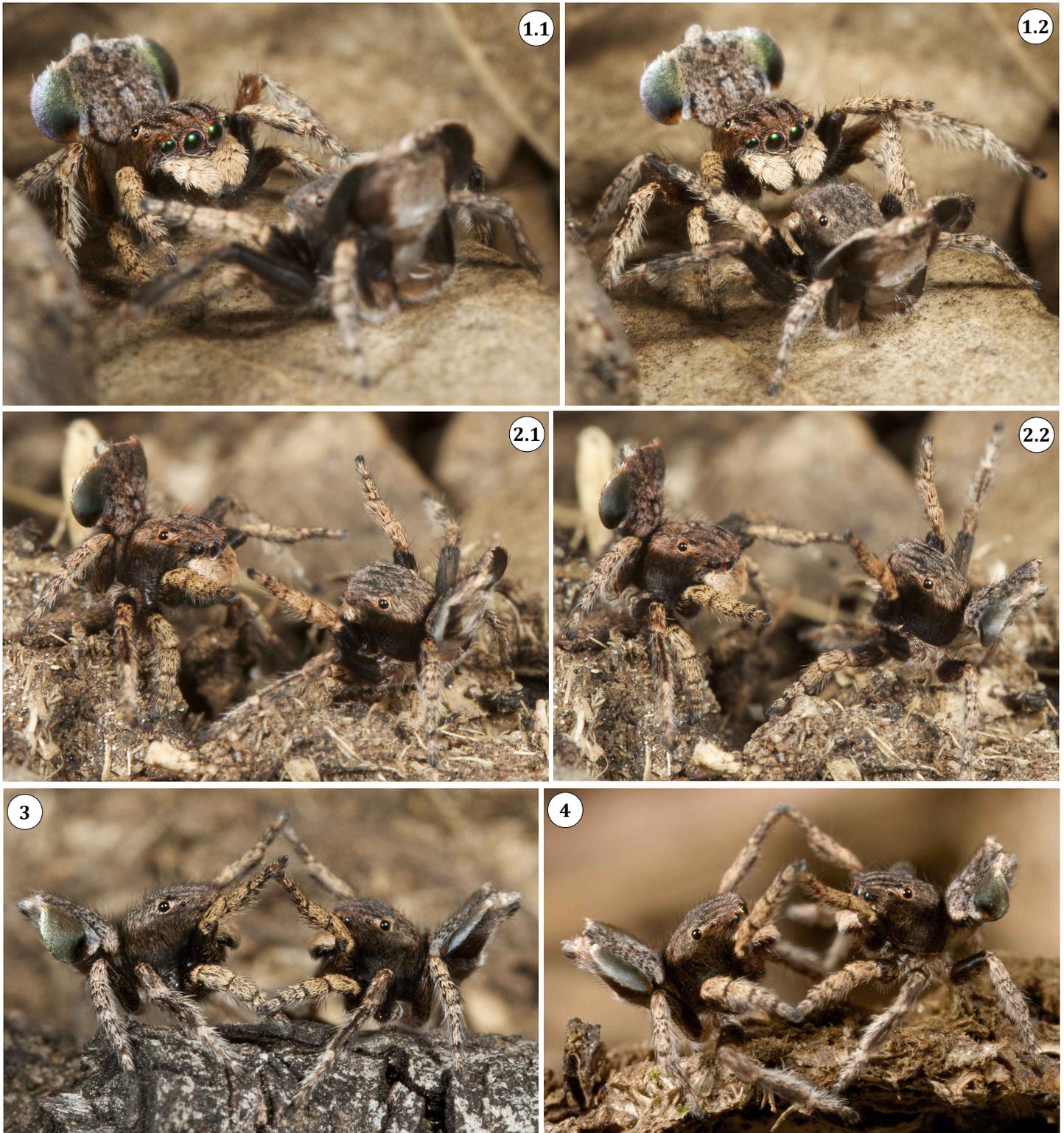
**Figure 10.** Hop by a male with slight movement toward the opposing male, followed by a longer crouching interval.





**Figure 12.** Images from two sequences of close approach by two hopping males. In sequence 1 (1.1–1.3), the male at upper left moved down to contact the other male with legs I. In sequence 2 (2.1–2.2), the hopping males held legs I in an elevated position, but were prevented from making direct contact by a gap in the substrate.

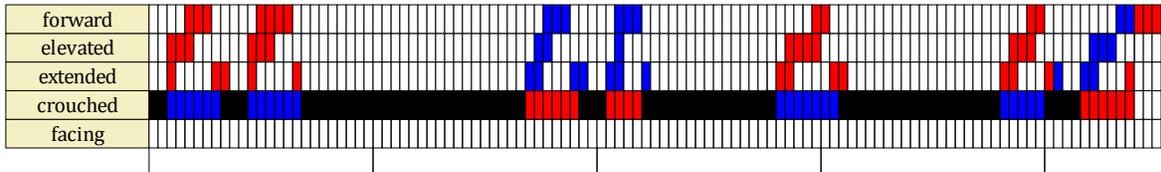
*Close combat.* After two males moved into a position in close proximity, facing each other, they would engage in *close combat*, generally taking turns in executing their hops or 'attacks' upon each other, sometimes for more than one minute (Figures 13–18). The longest recorded close combat sequence lasted for 184 seconds (00:03:04). In many respects these contests followed the pattern of the hopping display at a distance, but in proximity males would also hold legs I in an elevated position as part of their crouching stance (as in Figure 12, 2.1), prepared to meet each 'attack' of the opponent with outstretched legs I and II. In the course of each hop, a male would extend its legs III, elevate its body, and then move forward and down onto (or at least near, if not touching) its opponent. Often males would maintain contact with legs I or legs I and II for 1–3 seconds (Figures 13.3–13.4, 16–17) during crouching intervals between hops. Close combat usually ended after one male would stop taking its hopping turns, and would then jump away (Figure 19), or after both spiders embraced and grappled in what would appear to be the most dangerous phase of combat escalation (Figure 20), with no apparent rules to prevent injury to either spider. Nonetheless, all spiders that were observed emerged from these contests without any injuries.



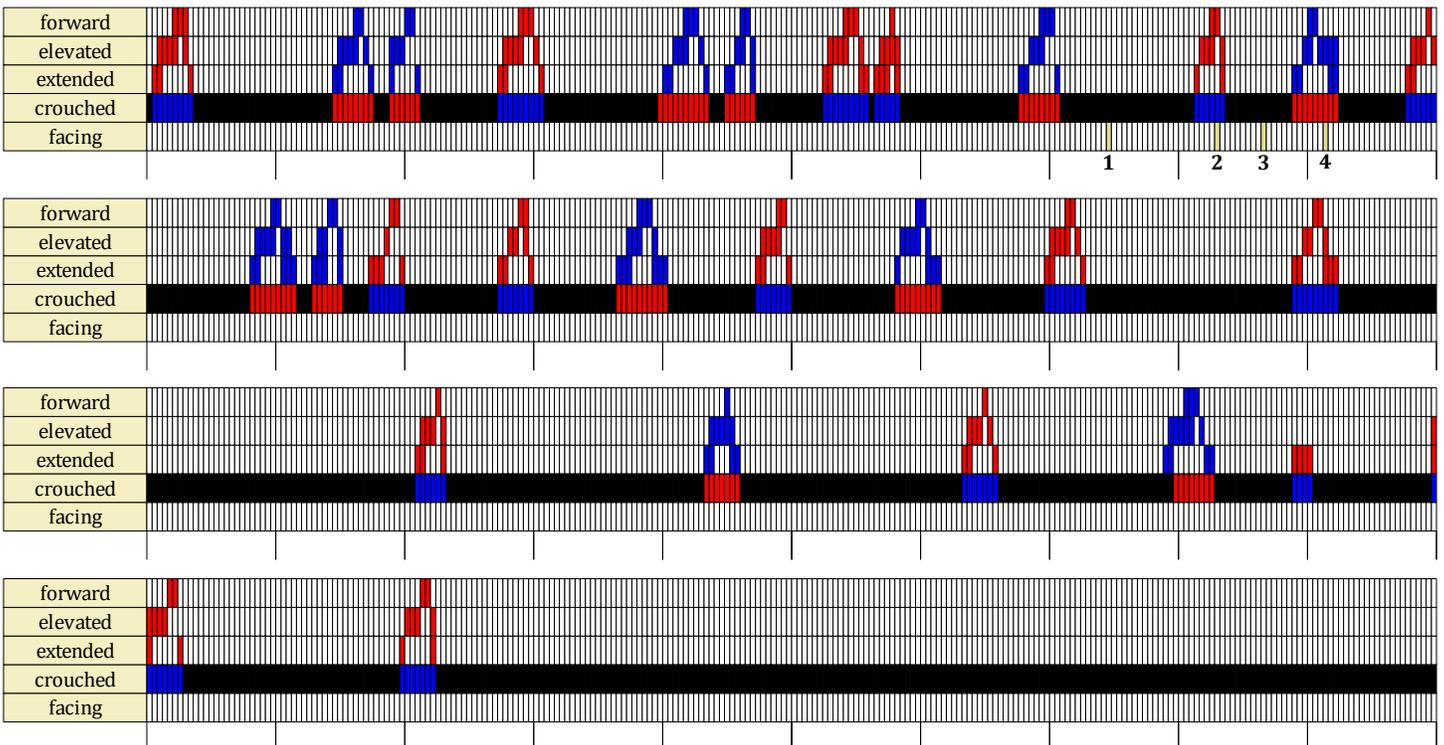
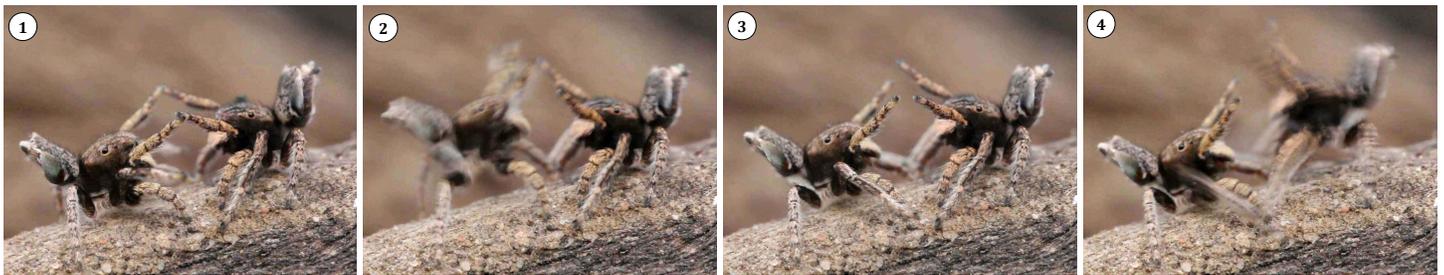
**Figure 13.** Images taken from four sequences of close combat between males. **1**, A hop by the male at lower right (1.1) was followed by a hop by the other male (1.2). **2**, (2.1–2.2) Two stages in a hopping 'attack' by the male at lower right. **3–4**, In these two engagements the males maintained contact with legs I and II between hops, and supported themselves with legs III and IV.



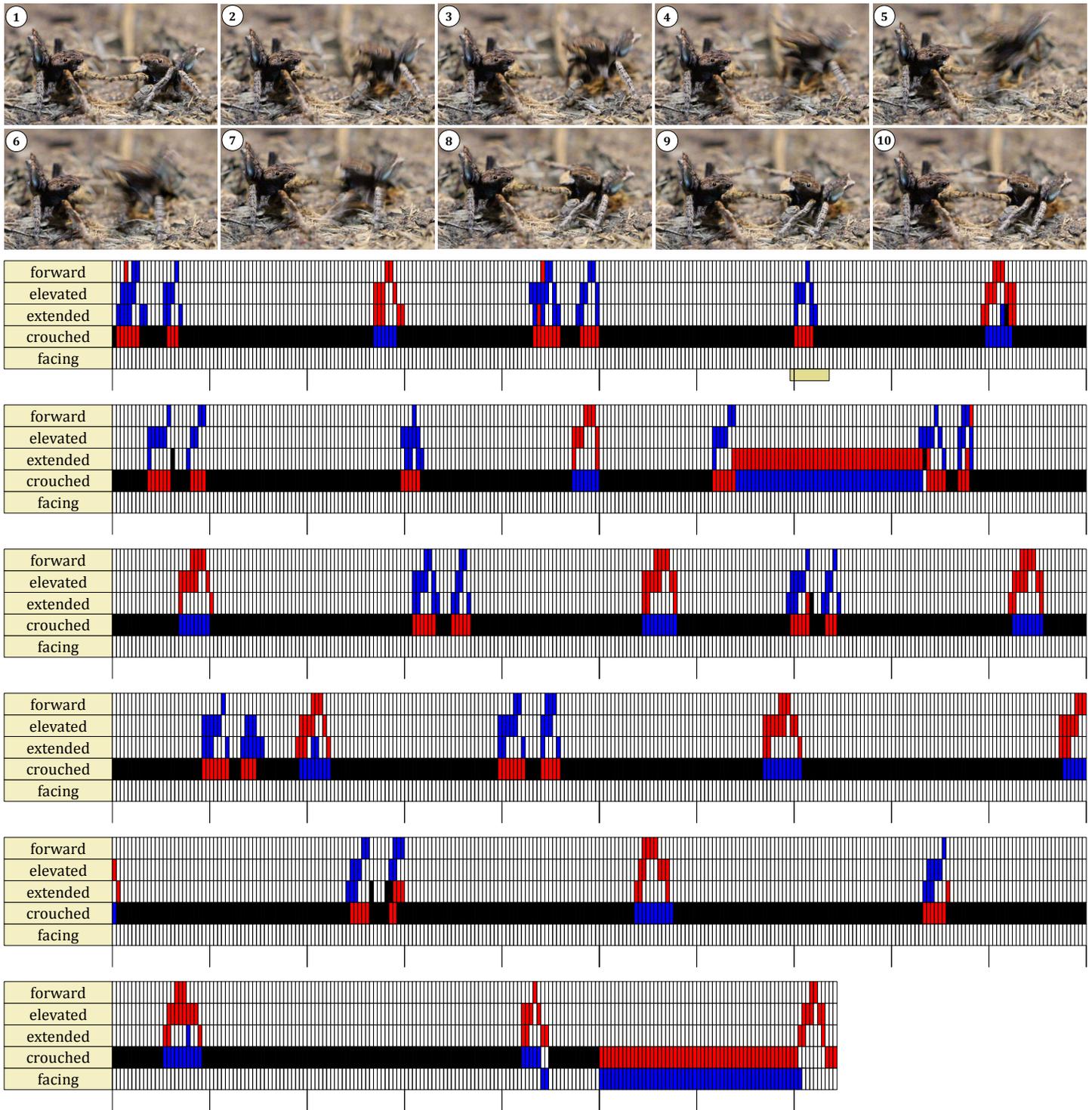
**Figure 14.** Sequential frames (interval not specified) taken from a close combat sequence between two males. **1**, Hop or 'attack' by the male at left. **2**, Hop by male at right. **3**, Hop by male at left. **4**, Both males maintaining a crouching stance with legs I extended.



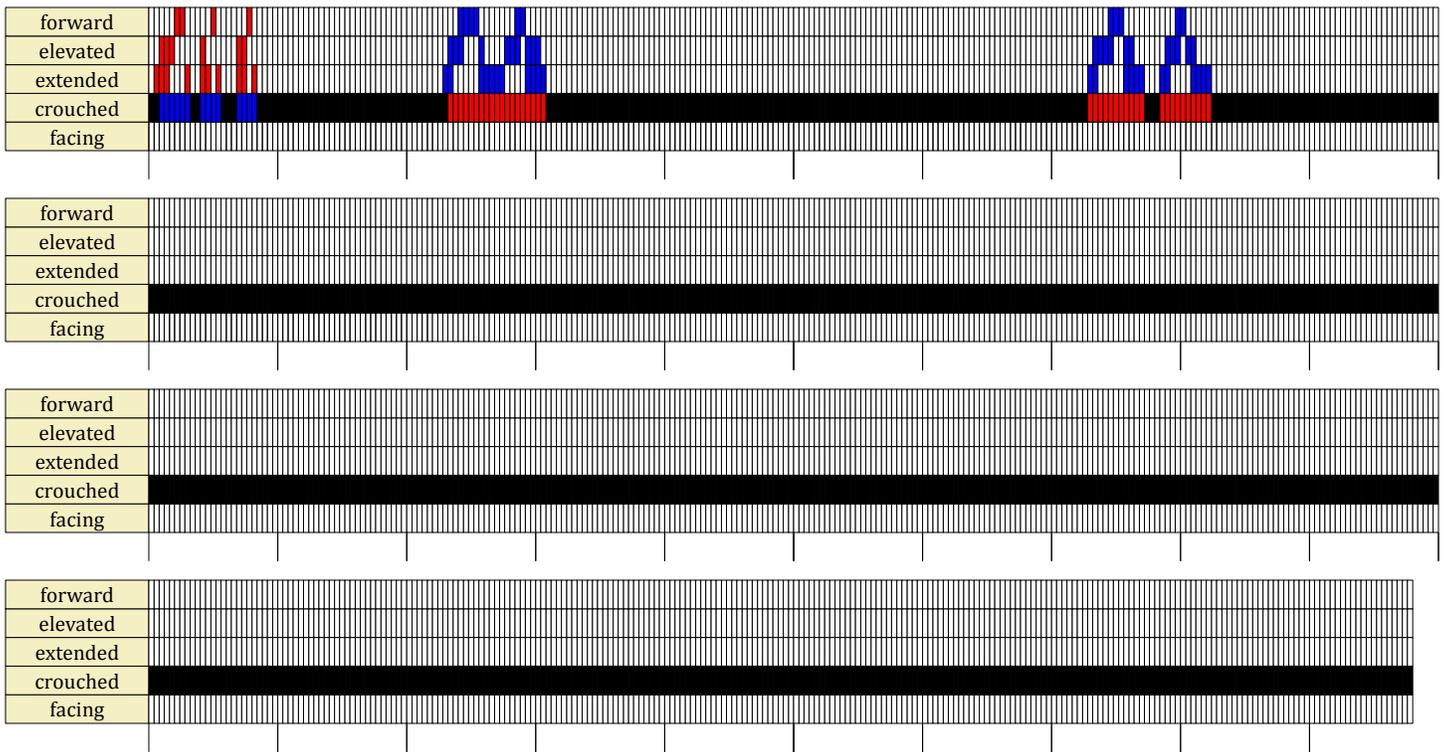
**Figure 15.** Chart of a close combat sequence between two males, showing alternating execution of hop groups.



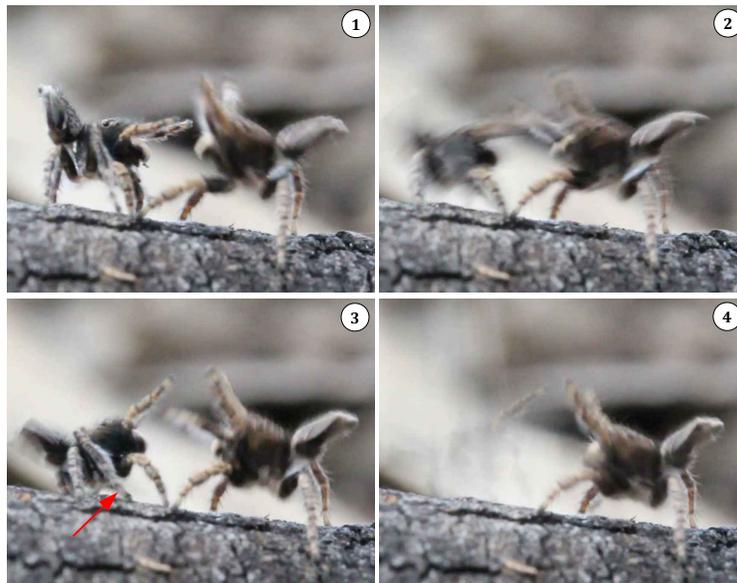
**Figure 16.** Close combat sequence between two males, showing alternating execution of hop groups, and reduction in frequency of hopping over time. The position of frames 1–4 is indicated with numbers in the chart. **1**, Crouching, in contact. **2**, Hop by male at left. **3**, Crouching. **4**, Hop by male at right.



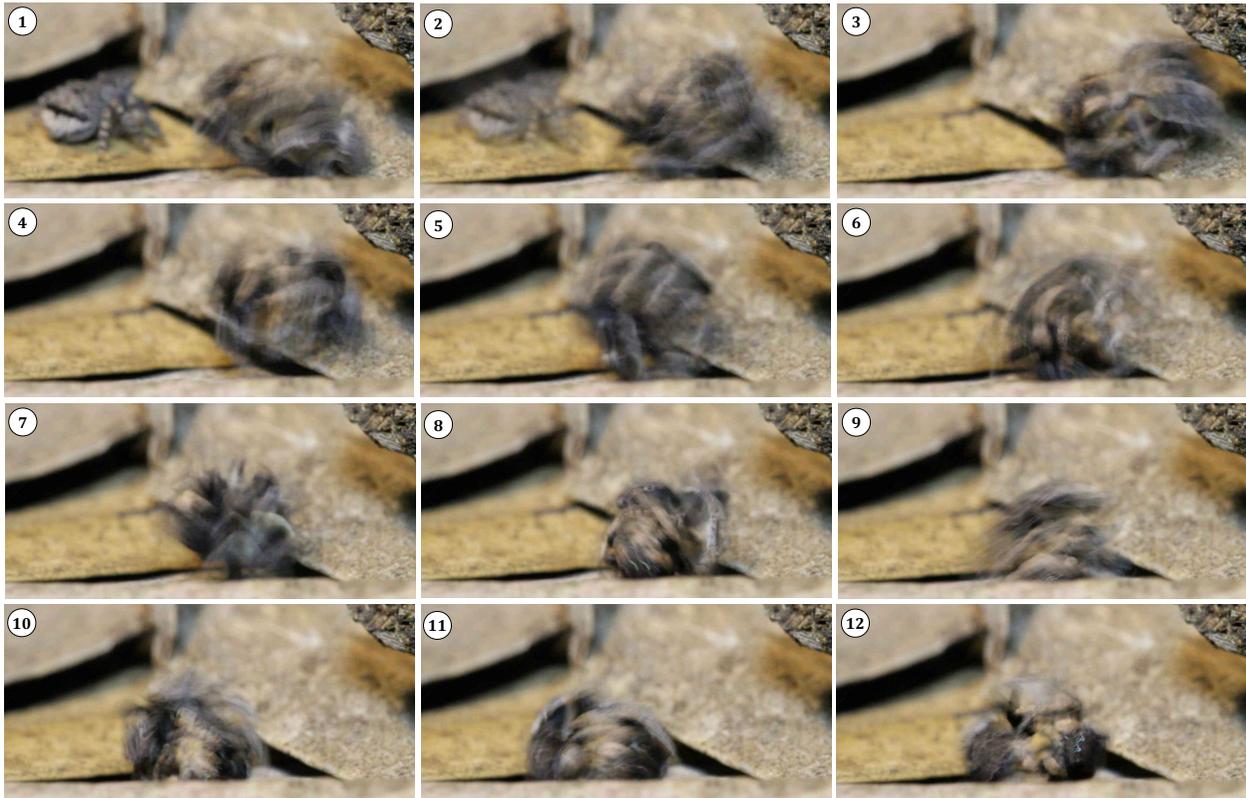
**Figure 17.** Close combat sequence between two males in contact with legs I when crouching. The series of frames at top (1–10) shows one hop by the male at right (position of frames in this series indicated by bar on the chart). Note the regular alternation between single hops by the spider on the left (indicated in red), and hop groups of two by the spider on the right (blue). Toward the end of this sequence, the spider at right stopped responding to the hops of the other spider, then stopped crouching (scored as *facing* at the bottom of the chart), and then moved away from this contest.



**Figure 18.** Chart of close combat sequence between two males with prolonged crouching.



**Figure 19.** Sudden end to a contest between two males, in 4 consecutive frames, each separated by 0.04 s. **1–2**, The male at right was moving forward from the top of its attack, to hit its crouching opponent. **3**, The male at left rotated legs III (arrow) to the rear in preparation for a jump. **4**, Vertical jump by the male at left, executed so quickly that only a blurred set of vertical lines can be seen.



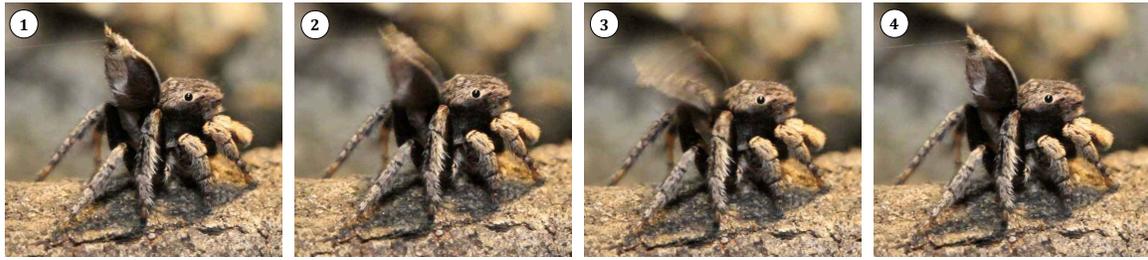
**Figure 20.** Part of a grappling sequence (1–12, 0.04 s interval between frames) between two males. A third spider (at left in frames 1–2) actually initiated this grappling by jumping one of the two males from the rear as it was engaged in a hopping contest with the other male, but this intruder was quickly cast off as the second male in the contest lunged forward. After grappling for  $\sim 1.2$  s, the pair resumed their formal hopping contest. Frame exposure time and capture rate (25/s) could not capture the details of this fast-paced but brief struggle.

### Courtship display by males

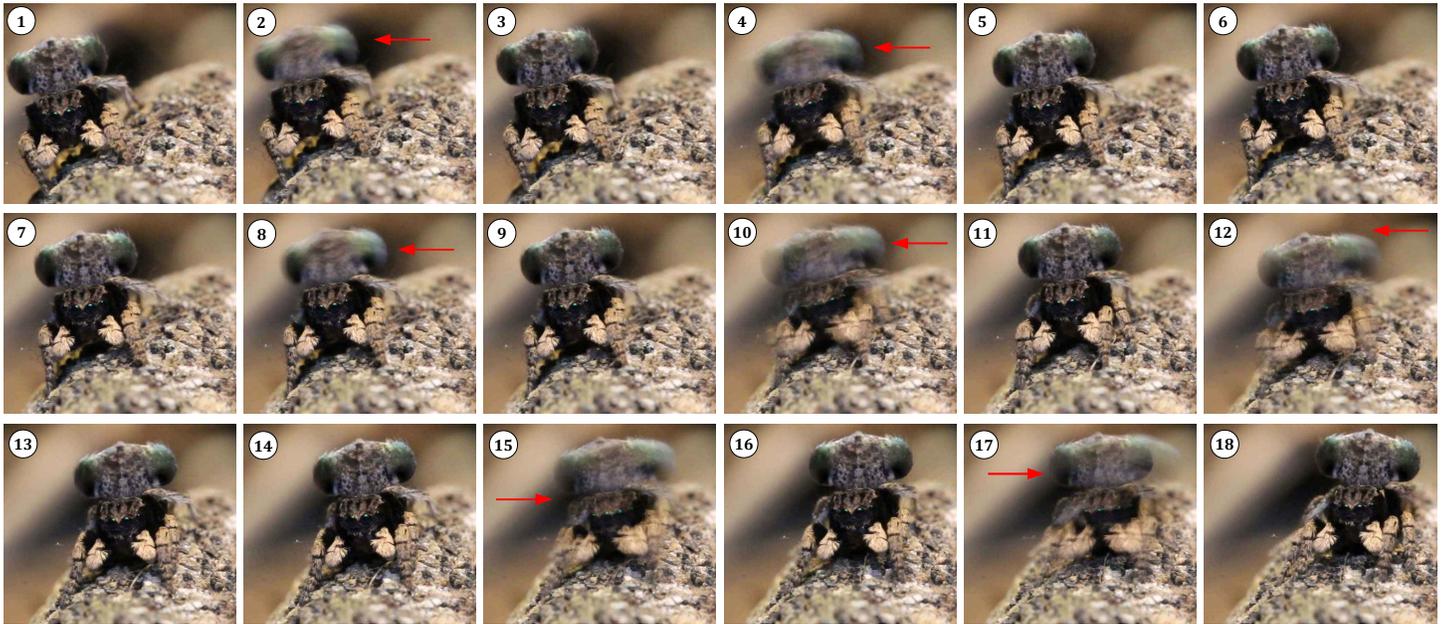
A brief description of male courtship display is presented here to highlight how this differs from male–male interaction. Initially courtship by a male also includes crouching with the opisthosoma elevated and the flaps extended, but when facing the female, the expanded opisthosoma is bobbed or vibrated at a variable rate (Figures 21–24), and legs III may be unilaterally (or, less often, bilaterally) extended and raised (not shown here) as in other *Maratus* species (Hill and Otto 2011). In this position the pedipalps are separated, held in a lateral position exposing the shiny yellow-brown anterior surface of the chelicerae to the view of the female. In the second phase of courtship (Figure 25), the male advances to meet the female with the opisthosoma lowered and flaps folded away, performing a series of bilateral semaphore displays with the extended legs III, including marked flexion at the the tibio-metatarsal joint.



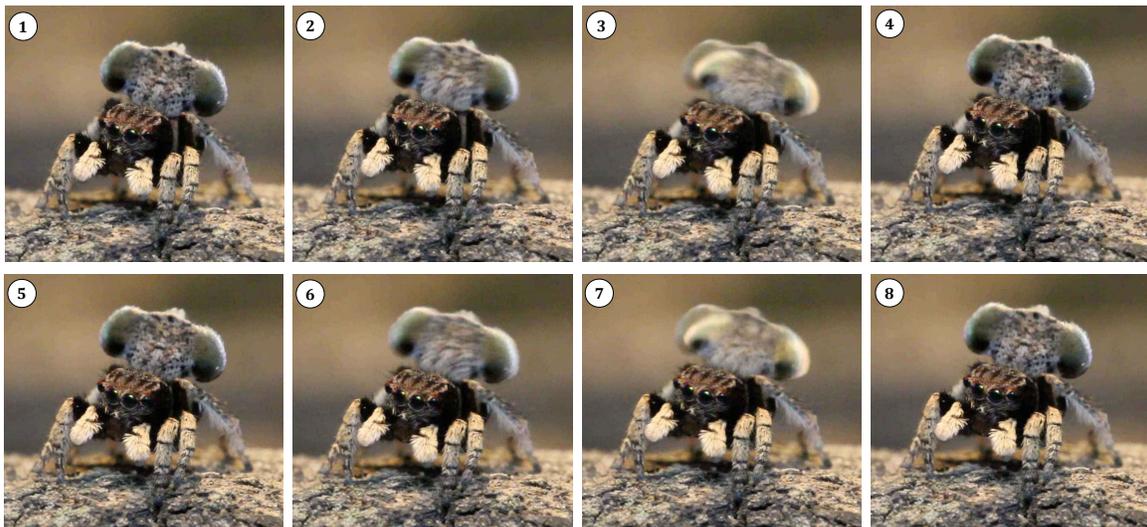
**Figure 21.** Sequence (1–5, 0.04 s interval between frames) depicting rapid bobbing or vibration of the opisthosoma (red arrows) of a male *Maratus vespertilio* facing a female. Note also the separation of the pedipalps. As all vibration took place within the span of a single frame, the number of cycles of vibration in each frame, and the frequency of vibration, could not be estimated. The frequency and speed of this activity varied greatly, and could be much slower than shown in this example.



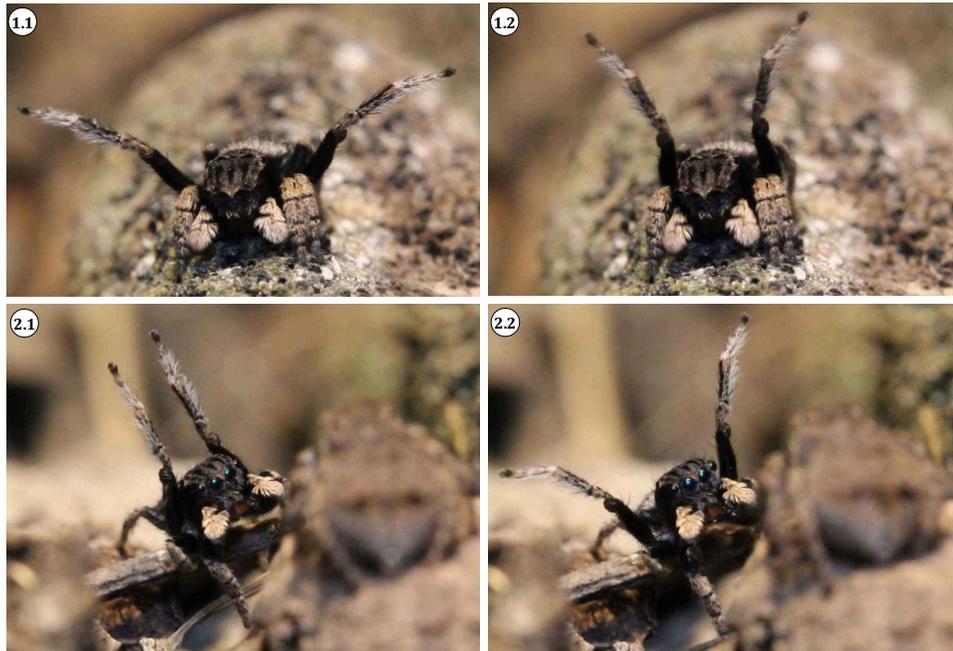
**Figure 22.** Sequence (1–4, 0.04 s interval between frames) depicting rapid bobbing or vibration of the opisthosoma (red arrows) of a male *Maratus vespertilio* facing a female. In this example, depression of the rapidly vibrating opisthosoma (3) was more marked.



**Figure 23.** Sequence (1–18, 0.04 s interval between frames) depicting rapid bobbing or vibration of the opisthosoma (red arrows) of a male *Maratus vespertilio* facing a female. Note once again the separation of the pedipalps. In this example, the fan was waved or vibrated as the spider side-stepped to its left. The side-to-side component of this vibration may be a result of the side-stepping. Within a span of about 2/3 second, this spider engaged in 7 bouts of rapid vibration of the opisthosoma.



**Figure 24.** Sequence (1–8, 0.04 s interval between frames) depicting rapid bobbing or vibration of the opisthosoma of a male *Maratus vespertilio* facing a female. This example illustrates the shimmering visual effect (frames 3, 7) of the fan as it was rotated backward.



**Figure 23.** Images from two sequences depicting the close approach of a courting male *Maratus vespertilio* to a female. As in the fan dance or display at a distance, the pedipalps were separated to reveal the yellow-brown anterior surface of the chelicerae to the female. Semaphore movement between positions was rapid and 'jerky' (or interrupted), including both extended (2.1) and flexed (2.2) metatarsi of legs III. As legs III were moved toward the female, extreme tibio-metatarsal flexion at angles greater than 90° was also observed. The use of these complex semaphore signals in close interaction with a female deserves further study.

## Discussion

However it has been called, male-male interaction, ritual combat, or *agonistic behaviour* has been reported and described in many salticids (Richman 1981, Li *et al.* 2002, Lim and Li 2004). One of the authors (D. E. Hill) has observed this behaviour in a diverse group of salticids, including *Lyssomanes*, *Phidippus*, *Platycryptus*, *Thiodina* and *Zygoballus*. In all of these genera, male-male contests include both display at a distance and close combat positions and behaviours, distinct from those associated with courtship. At the same time, many distinctive male features that figure in the courtship display of a particular species also play a role in the male-male interactions of that species. For example, the iridescent chelicerae, or the long and powerful legs I, of a *Phidippus* male may be displayed to both a male and to a female. Thus it should come as no surprise that the opisthosomal fan of a male *Maratus*, so important in courtship, can also play an important role in communication with other males. According to the *armament-ornament model* (Berglund *et al.* 1996, Tobias *et al.* 2011), male traits related to success during male-male contests can be subsequently used by females as an indicator of male quality. It is also generally recognized that this could work in the opposite direction, whereby male traits originating with female selection are later incorporated into male-male contests. In any case, both male-male contests and male-female interactions should be studied together, within a broader framework of intraspecific socialization.

We have not observed these contests when males of other *Maratus* species (*M. linnaei*, *M. mungaich*, *M. splendens*, *M. volans*, *M. species A*, *M. species B*, *M. species C*; Otto and Hill 2011b) were in close proximity to other males. In general, they would watch other males, but did not display to them or engage in combat. The single exception to this rule involved the semaphore (legs III extended) display of a male *M. species B* to another male of the same species (Otto and Hill 2011b, Figure 28, 2).

One possible explanation for the ritual combat of male *M. vespertilio* lies in the fact that these spiders live inland, in a harsher environment subject to occasional droughts. In this environment, survival may only be possible at small local sites, or patches. At the Whitton, New South Wales locality these spiders were abundant at only two of these patches, each associated with a cluster of small trees, where the ground was partially covered with green vegetation. In between these tree clusters, the ground was fairly bare, and no *Maratus* were found. But at each suitable site they were found in a much higher density than has been observed for any other *Maratus*. Given that they are so cryptic, don't hop around much and also have the tendency to dig themselves into the ground, the actual population was undoubtedly much higher than could be observed. Combat may have evolved in at least some populations of *M. vespertilio* as a response to high local population density.

Although higher population density, or a relative scarcity of females, does sometimes correlate with increased aggression between males as our intuition would suggest (Caldwell and Dingle 1975, 1977), this is not always the case. In some studies higher population density has been associated with *less* male-male aggression or *less* development of male armaments (Conner 1989, Pomfret and Knell 2008, Knell 2009), or *no change* in the level of male-male aggression (Casalini *et al.* 2010). Knell (2009) found that, taken collectively, recent studies support the hypothesis that *aggressive tactics should be found at intermediate population densities*. At a low population density, greater size and armament of males may not lead to greater mating success (Rittschof 2010), and at high population density the increased probability of injury and cost of combat may outweigh the reduced probability of mating success, favoring instead a strategy that is focused on finding females. Since they are predators, most spider population densities probably range from *low* (favoring less male-male aggression) to *intermediate* (favoring male-male aggression). Even within a species, there may be a density-dependent *switchpoint* between low-aggression and high aggression modes of behavior (Kokko and Rankin 2006).

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