

Visual display by male *Maratus pavonis* (Dunn 1947) and *Maratus splendens* (Rainbow 1896) (Araneae: Salticidae: Euophryinae)

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Summary

Male spiders from Sydney's Lane Cove National Park were found to be consistent with Rainbow's (1896) description of *Attus* (now *Maratus*) *splendens* from Sydney, particularly with respect to definitive steel-blue and bright scarlet bands (with curvature directed forward) of the antero-dorsal carapace. Specimens of *Maratus pavonis* (Dunn 1947) from Tasmania, Western Australia, the syntype of *M. pavonis* from Victoria in the Museum Victoria, and a series of specimens from the collection of the Museum of Comparative Zoology (Harvard), were not so coloured, with the antero-dorsal carapace covered with uniform brown to red-brown scales. Many of these *pavonis* had lateral opisthosomal flaps of varying size, and their size is not (contrary to Dunn 1947) considered to be a defining character for this species.

Visual displays of male *M. pavonis* and *M. splendens* were studied by the examination of sequential frames of a series of recent video clips taken during encounters with females. All observed behavioural components of advertisement or display (*pedipalp flicker*, *opisthosomal bobbing*, *single leg wave*, *fan dance*, *semaphore*, and *tapping*) were very similar for the two species, but differed in specific details. The single leg wave of *M. pavonis* was interrupted ("jerky") relative to the smooth wave of *M. splendens*. Rapid lateral (side-to-side) movement, or oscillation, of the elevated opisthosoma was continuous during the fan dance of *M. pavonis*, but did not continue during longer, motionless intervals between the more discrete movements of the fan dance in *M. splendens*. *M. pavonis* may rely more on movement, and *M. splendens* more on colouration, during courtship display.

Introduction

In a recent (Otto and Hill 2010) paper we reviewed the reported features of courtship display by a number of species of the endemic Australian genus *Maratus* Karsch 1878, and suggested that species-specific behavioural differences might be found within the genus. *Maratus* males are distinguished by the elevation and display of their dorsal opisthosoma (or *fan*), in the manner of a peacock parading in front of a peahen. One of us (Jürgen Otto) recently collected *Maratus* specimens in Sydney, as well as on the northern coast of Tasmania, that resembled *M. pavonis* (Dunn 1947) in a number of aspects, most importantly in the presence of a red "ring" on the opisthosoma. However, closer examination of specimens from both localities revealed a number of striking differences between the two, indicating that only the Tasmanian specimens belonged to the relatively common and widespread *M. pavonis*, while the Sydney spiders appeared consistent with Rainbow's (1896, Appendix 1) description of a species that has been referred to as either *M. splendens* or *M. rainbowi*. In the present paper we discuss which of the names that have been used for this spider should be adopted, and we describe, illustrate, and compare the male display behaviour in both species. Dunn's "co-type" (syntype) of *M. pavonis* in the Museum Victoria is illustrated in Appendix 2. In an effort to locate the specimen described by Rainbow, one of us (David Hill) examined and photographed historic specimens of *Maratus* and related spiders in the Museum of Comparative Zoology at Harvard (MCZ), including specimens from the Peckham collection, and these are illustrated in Appendix 3. Although many of these could be identified as *M. pavonis*, no specimens that fit Rainbow's description of *M. splendens* were found in collections. It appears that most spiders identified as *splendens* prior to Dunn's description of *pavonis* in 1947 would now be identified as *M. pavonis*.

Subjects and methods

Photographs and video clips of spiders included in this study are listed in Table 1.

Table 1. Spiders represented in this study. Individual spiders were not tracked, and all encounters except those involving *M. pavonis* from Mount Stuart were staged by bringing the male and female together. *M. splendens* voucher specimens will be deposited in the Australian Museum, Sydney.

Species (<i>Maratus</i>)	Locality	Description	Photographer
<i>M. pavonis</i>	Stanley, Tasmania (40.78 S, 145.28 E)	2 males in videos (25 fps) and still photographs, in encounters with 2 females of an undescribed species of <i>Maratus</i>	Jürgen C. Otto
<i>M. pavonis</i>	Mount Stuart, near Hobart, Tasmania	Videos (30 fps) and still photographs of multiple spiders observed at different times in a garden, with as many as 4 seen in one sitting	Kristi Ellingsen
<i>M. pavonis</i>	Herdsmen Lake near Perth, Western Australia	Photographs of 2 males and 1 female	Farhan Bokhari
<i>M. splendens</i>	Lane Cove National Park, Sydney, New South Wales (33.78 S, 151.14 E)	At least 7 different males in videos (25 fps) and still photographs, in encounters with females of either <i>M. splendens</i> or <i>M. volans</i>	Jürgen C. Otto

It should be noted that several key limitations exist in this kind of study. First, although the male behaviours described here were elicited by nearby females (in most cases of the same species), the physical circumstances encountered in more natural conditions, and the relationship of each female in particular to its surroundings (*e. g.*, whether in a home territory or not), would necessarily produce different results. In addition, related behaviour of females was not studied. Second, although some general results are suggested at the species level by this sampling, only a limited number of individuals could be observed and the range of variability, both geographic and individual, can be expected to be much higher in nature. The use of video frames supports a much more detailed temporal description of the movements associated with each display, but is still limited by frame rate in its ability to resolve certain features of movement, such as the frequency of vibrations (presumably acoustic) greater than about 15–20/s. More advanced instrumentation, including high speed video (*e. g.*, Elias *et al.* 2006b) could provide much greater resolution of these frequencies.

Measurements of leg angle, elevation, or orientation of the opisthosoma that are presented here should be viewed as *estimates only*, based on the use of compass and ruler in the examination of separate video frames and images. Given variation in the angle of view relative to the orientation of the spider in each case, this approach was necessary. At the same time, this did not detract from our ability to resolve the occurrence and timing of observed events, which was its primary purpose.

Comparison of *M. pavonis* and *M. splendens*

A comparison of field marks or features that can be used to distinguish male *M. pavonis* from *M. splendens* is presented in Figure 1 and Table 2. Apart from its relatively large and vivid fan, the transverse band of iridescent blue scales surrounded by bright scarlet-red scales on the carapace of *M. splendens* is most distinctive. As shown in Figure 1, the structural colour of this iridescent band is highly directional, varying from dark steel-blue to intense or amplified light blue, depending on the angle of observation. All male *M. splendens* from Sydney had a well-developed opisthosomal fan, but not as large as that figured by Rainbow (1896). The enormous flaps figured in Rainbow's description (Appendix 1, Figure 3) were almost certainly exaggerated, particularly when compared with the much smaller size of the circular red pattern in his Figures 3 and 3a. Dunn (1947) distinguished *M. pavonis* from *M. splendens* by the small size of the lateral margins (flaps) of the opisthosoma in the former, but examination of a number of photographs and specimens (see Appendix 3) indicate that this character varies greatly in *pavonis*.

Figure 1. Field marks useful in the identification of adult male *Maratus pavonis* and *M. splendens*. 1–3, two different *M. pavonis* males from Stanley (1–2) and Mount Stuart (3), Tasmania. 4–6, three different *M. splendens* males from Lane Cove National Park, Sydney. 7–8, two frames from a video clip of *M. splendens* performing a single leg wave, showing how the “steel-blue” band of the carapace (arrows) “flashes” with a change in angle of the carapace. The same change in appearance can be seen in a comparison of (5) with (6). Both Rainbow (1896) and Dunn (1947) associated the dark appearance of this band with the background colour of the carapace, and described the area to the rear as a red, crescent-shaped (*curved to the front*) band against this background. The steel-blue band is, however, covered with iridescent scales, which are responsible for both light and dark colours. This is better described as an anterior-facing crescentic band of iridescent blue scales between the PLE, traversing a field of uniform scarlet-red scales separated at the rear by a diamond-shaped, median patch of white scales. In (1) and (4), images are shown upside-down, and represent maximal flattening or extension of the dorsal opisthosoma during a *fan dance* by respective males. As shown in (4), the blue to blue-green lateral margins of *M. splendens* are at least as wide as the red “parens” that they surround. Photograph (3) © Kristi Ellingsen, used with permission.

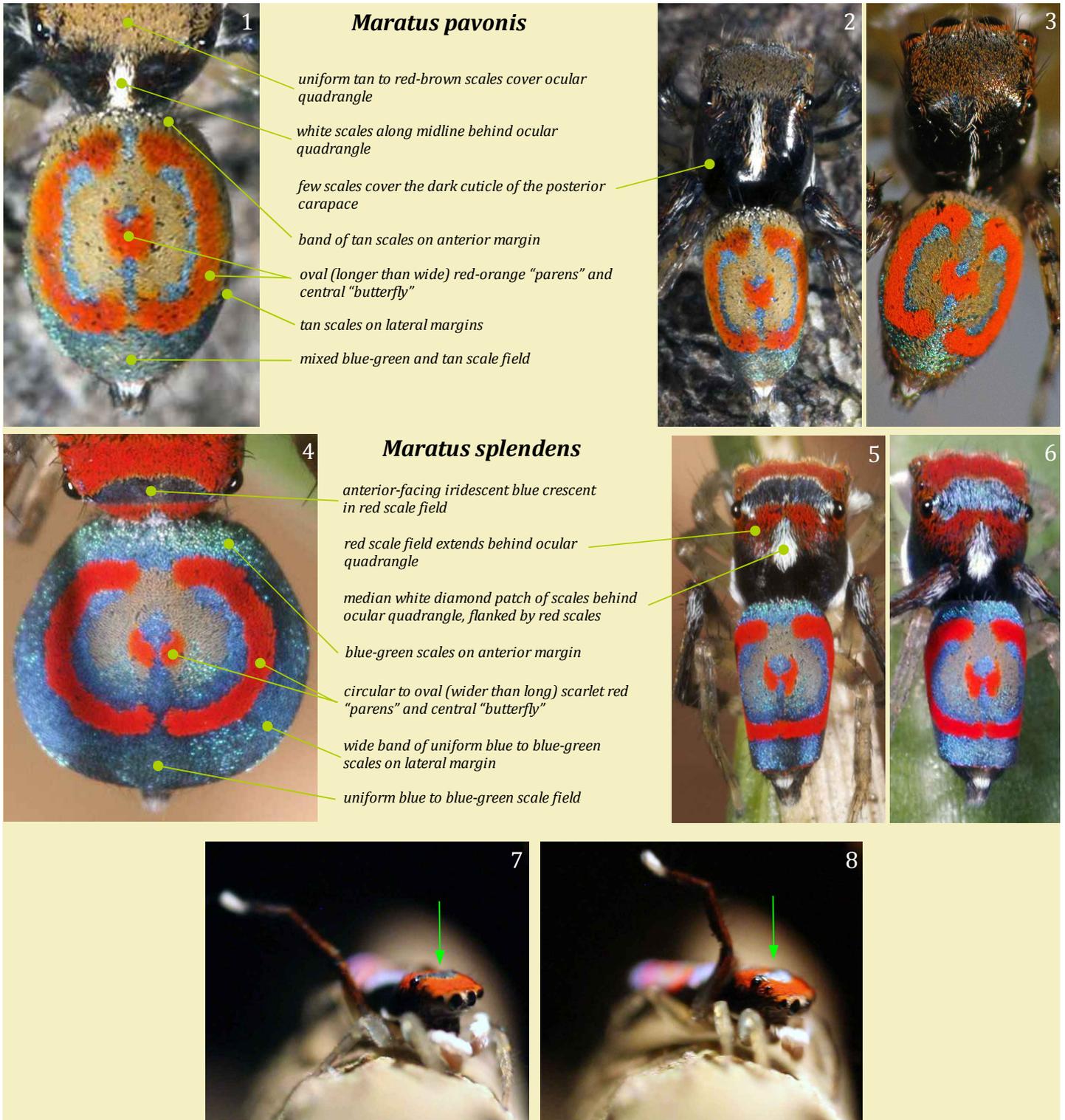


Table 2. Some field marks of adult male *M. pavonis* and *M. splendens*.

Characteristic	<i>M. pavonis</i>	<i>M. splendens</i>
Scale field of dorsal opisthosoma (fan)	Apart from a large red-orange, oval (longer than wide) pattern (“parens”) that is usually completely visible from above, dominated by a field of light-brown to tan scales	Apart from a scarlet red, circular to oval (wider than long) pattern (“parens”) that cannot be seen completely from above unless extended, dominated by a field of uniform iridescent blue to blue-green scales
Lateral margins of dorsal opisthosomal plate	Plate usually narrow with thick edges instead of flaps, but may have small, folding flaps; red-orange parens extend almost to lateral margins	Always bearing flaps covered with iridescent blue to blue-green scales; flaps expanded during display
Anterior marginal band of dorsal opisthosomal plate	Variable but broad and light-brown, tan or cream-coloured	Absent or thin with only a few white setae in front of a plate dominated by shiny blue-green scales
Posterior margin of dorsal opisthosomal plate	May have white to tan scales mixed in with iridescent blue-green scales (Tasmania)	Broad band of uniformly iridescent blue to blue-green scales extends from parens almost to or completely to posterior margin
Scalation of antero-dorsal carapace (ocular quadrangle)	Uniform brown to red-brown in front of PLE	Bright scarlet red, with broad, transverse band of blue iridescent scales with highly directional reflection due to structure
Marking of postero-dorsal carapace behind eyes	Mid-sagittal (median) line of white scales, of variable width, surrounded by dark brown to black carapace devoid of scales	Diamond-shaped mid-sagittal patch of white scales, surrounded on front and at sides by scarlet red scales
Banding of legs I, II, and IV	Regular, dark banding of leg segments, femora dark in front with white and blue iridescent scales (Tasmania); or colourless with little or no banding (Western Australia)	Translucent or colourless with no noticeable banding, or with light banding
Colouration of legs III	Brown to deep red or red orange in front (all areas); deep red with white stripe on dorsal patella, anterior dark, often bearing numerous iridescent blue scales (Tasmania)	Dark red-brown in front, black in rear, white stripe on dorsal patella
Pedipalps	Often raised bilaterally with adpressed distal tips below the clypeus, with anterior (“medial”) surfaces upright and covered with thick, bright white setae	Same as <i>M. pavonis</i>
Tarsi III	Covered with bright white setae, contrasting with dark setae of metatarsi	
Eye colour	Eyes of front row (AME, ALE) with distinctly green tint	
Marginal band of carapace	Complete marginal or basal band of white scales	

In male *M. splendens*, legs I, II, and IV were relatively transparent, without conspicuous markings or banding. Some *M. pavonis* from Western Australia (Figure 2, 1–2) were similar, but *M. pavonis* from Tasmania (Figure 2, 4–16) were darkly banded, often with dark, iridescent blue areas on the anterior femora of all legs. For general comparison, additional images of *M. pavonis* and *M. splendens*, respectively, are presented in Figures 2 and 3.

Figure 2. General appearance of *Maratus pavonis*. 1–2, displaying male and 3, female from Herdsman Lake, Western Australia. 4–5, males, 6, mating pair, and 7, displaying male from Mount Stuart, Tasmania. 8–9, displaying male, and 10–15, detail views showing the opisthosomal plate of a male from Stanley, Tasmania. One male from Western Australia (2) appears to have flaps that wrap around the lateral margins of the opisthosoma, whereas all of the males from Tasmania have curved dorsal plates. Photographs 1–3 © Farhan Bokhari, 4–8 © Kristi Ellingsen, used with permission.

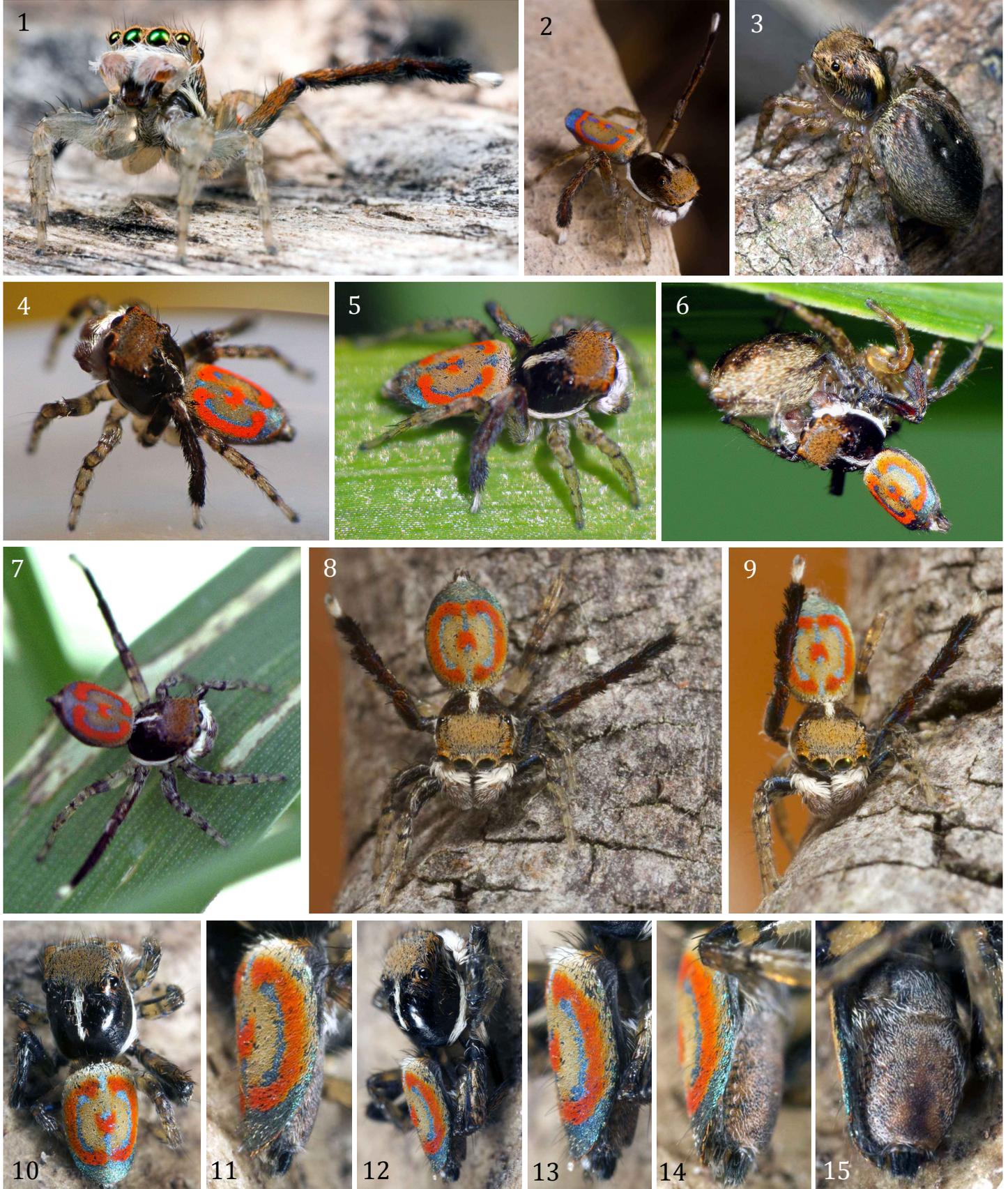
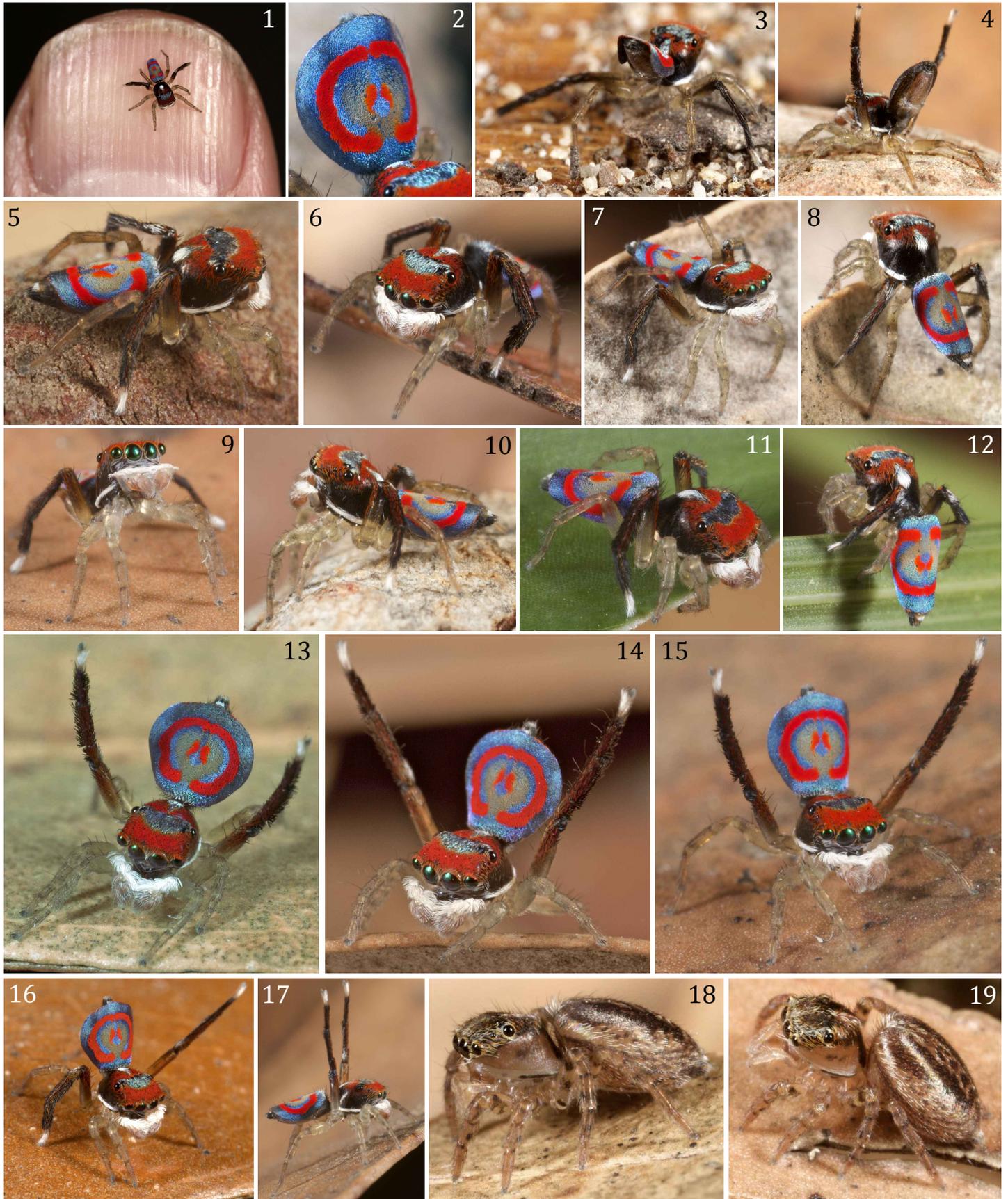


Figure 3. General appearance of *Maratus splendens* from Lane Cove National Park, Sydney, New South Wales. 1, adult male on thumb, to show scale, 2, detail of partly expanded fan of male, 3–4, males with a partly elevated opisthosoma seen from the rear, 5–12, males with folded or retracted fan, 13–17, males facing females in display positions, 18–19, two views of a female. The prevalence of iridescent blue or blue-green scales on the dorsal opisthosoma contrasts with the light brown or tan scale cover of *M. pavonis* (Figure 1).



Visual displays

Maratus males, like related euophryines (including *Saitis barbipes*; see Hill 2009), are equipped with long, dark legs III tipped with bright white tarsal setae, legs that can be extended and waved or lowered in front of a female. They can also move their pedipalps up and down. Like many if not most salticids (*e. g. Habronattus dossenus*, Elias *et al.* 2005, 2006a, and *Phidippus clarus*, Elias *et al.* 2010, Sivalinghem *et. al* 2010), they can vibrate the opisthosoma and legs, presumably to produce substrate-borne vibrations that can be detected by a female. The one feature that really distinguishes this genus, however, is clearly their ability to raise and to display colourful patterns associated with the dorsal opisthosoma (*fan*), to effect. We previously (Otto and Hill 2010) reviewed early reports related to the courtship behaviour of *Maratus*, including *M. pavonis*. None of these previous studies included measurement of timing, however.

Behavioural studies often create the false impression that animals follow a predictable sequence of activities leading to a specific outcome. For jumping spiders, it is certainly true that general patterns of courtship behaviour do exist, but they occur with a broad range of possibilities affected by the layout of plant configurations, the relative position of a female, and the behaviour or disposition of that female. What works in one situation may not work in another situation, but a male has a number of approaches related to getting and maintaining the attention of a female, obtaining the cooperation of a female, and finally completing the mating act successfully. Categorization can, nonetheless, provide a useful framework. Categories of display observed in this study are described qualitatively in Table 3.

Table 3. Categories of display by male *Maratus pavonis* and *M. splendens*. All displays were observed in both species, but differed in some details.

Display	Description	Occurrence
<i>pedipalp flicker</i>	pedipalps rotated so that distal parts are in contact and bright white medial (anterior) setae form a continuous line under the eyes; in this position they are moved up and down in unison (bilaterally), generally in a high position	observed in general contexts, presumably when not facing a female; as in many other salticids this may be a general advertisement to elicit movement by other animals in the surroundings
<i>single leg wave</i>	one (unilateral) leg III flexed and raised, or just raised, then extended and lowered to one side at a non-uniform rate of fairly continuous movement; may be repeated on one side or may alternate this display from side to side	may occur generally when female is not visible; may be a general advertisement to elicit movement by a conspecific or another animal
<i>opisthosomal bobbing</i>	near-horizontal opisthosoma moved or vibrated up and down rapidly	may occur when female is not visible or not making eye contact; when fan is raised this changes to lateral (side to side) movement of the fan
<i>fan dance</i>	opisthosoma raised and dorsal plate flattened, or (if present) flaps extended, opisthosoma moved laterally from side to side, legs III extended to near-vertical position and then lowered to form V-shape bilaterally, in V-shape metatarsi are often (but not always) flexed downward rapidly, then legs III are returned quickly to near vertical position; often accompanied by side to side stepping in synchrony with lowering of one leg III, or turning to face a moving female, may be repeated multiple times in a series	starts suddenly when the male sights and faces a female directly; can transition into semaphore and tapping
<i>semaphore</i>	<i>bilateral arm signals</i> ; legs III raised to near vertical position, then lowered gradually (continuous movement at variable rate) to a near horizontal, lateral position, then quickly raised again; generally includes bilateral pedipalp flicker; may be repeated multiple times	observed after fan dance and before tapping, apparently when male is still facing a female
<i>tapping</i>	with legs III in extended, lateral horizontal semaphore position, very quickly bobs entire body up and down (or back and forth), tapping (if in contact) legs III against the substrate as they are rapidly raised and lowered	occurs when very close to female, intensive vibrations appear to be a preamble to mounting and mating

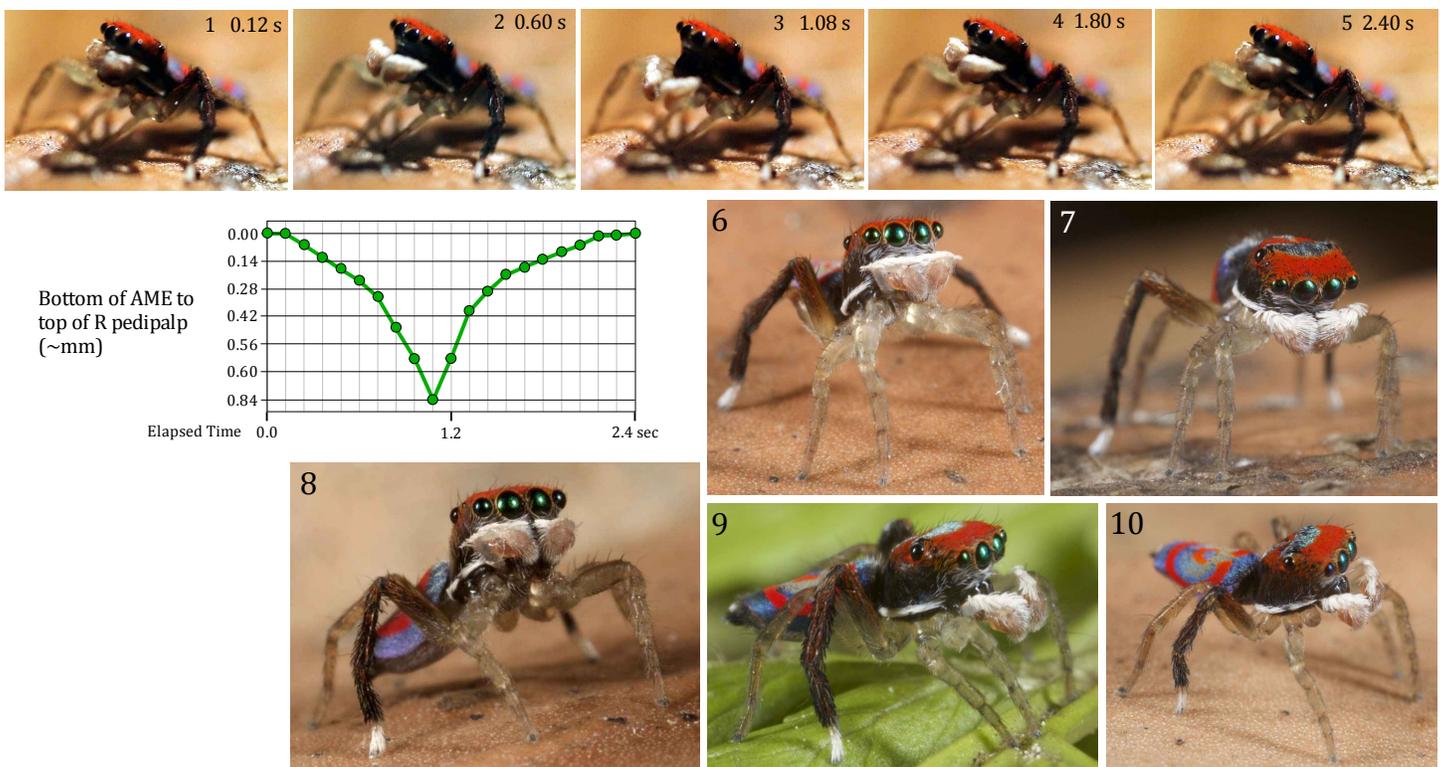
To facilitate the comparison of *M. pavonis* with *M. splendens*, each display will be described in a separate section, addressing both species.

Pedipalp flicker

Although many, if not most, salticids rapidly (“excitedly”) vibrate their pedipalps, some, including the amycine *Thiodina sylvana* (Hentz 1846) from the southeastern United States, do not. In any case the function of this movement is poorly understood. There are different patterns of decoration, posturing or movement associated with the pedipalps of different salticids. For example, movement of pedipalps in large salticids of the genus *Phidippus* can be used to present the iridescent colours of their chelicerae to an animal that they are facing. Both male and female *Anasaitis canosa* (Walckenaer 1837) rapidly rotate a patch of highly iridescent blue-white scales as they move about in leaf-litter, almost concealing the spider behind these moving spots of bright light.

Male *M. pavonis* and *M. splendens* hold the ends of the two pedipalps together, forming a bright horizontal bar of white setae (associated with the anterior margins of the pedipalps) just below the eyes. This posture is often maintained without movement of the pedipalps. Although this horizontal bar is found in other salticids, including *Hasarius adansoni* (Audouin 1826), it is not a characteristic of all *Maratus* (Hill 2009, 2010, Otto and Hill 2010). Pedipalp flicker involving up and down movement of the paired pedipalps at a rate varying from about 0.5 to 3/s has been observed in both *M. pavonis* and *M. splendens*, often in association with other displays (e. g., during a single leg wave, or a semaphore display). A slower cycle of flicker ($\sim 0.5/s$) by a male *M. splendens* is shown in Figure 4.

Figure 4. Bilateral pedipalp flicker by male *Maratus splendens*. The chart shows one complete cycle over 2.4 seconds, based on frames (25/s) from a video clip. To produce the data for this chart, frames were magnified and the distance between the bottom of the right anterior medial eye (AME) and the top of the right pedipalp was measured directly from each image. Selected frames from this sequence show lowering (1–3), followed by raising (3–5) of the pedipalps. Note how the bright white setae at the top (anterior margin) of the pedipalps was exposed to view as the pedipalps were lowered. In contrast, these were scarcely visible when the pedipalps were raised to the maximal extent (frames 1, 5). The lowest position in this sequence was (3). During the flicker cycle, movement of the paired pedipalps was continuous, but varied in angular velocity, which was greatest when the pedipalps were in a lower position. This created a “pulse” or visual flash effect. 6–10, detailed views of males showing how the palps are held together in front of the chelicerae.



Single leg wave

The extension and gradual lowering, or raising and lowering, of a single, laterally extended leg, has been observed generally in *Maratus*, even in the absence of a female (Otto and Hill 2010). Photographs of this display by *M. splendens* are shown in Figure 5. In Figure 6, two cycles of single leg extension, each about 2.5 s in duration, by a male *M. pavonis* are shown (first RIII and then LIII).

Figure 5. Photographs of *single leg wave* display by male *M. splendens*.

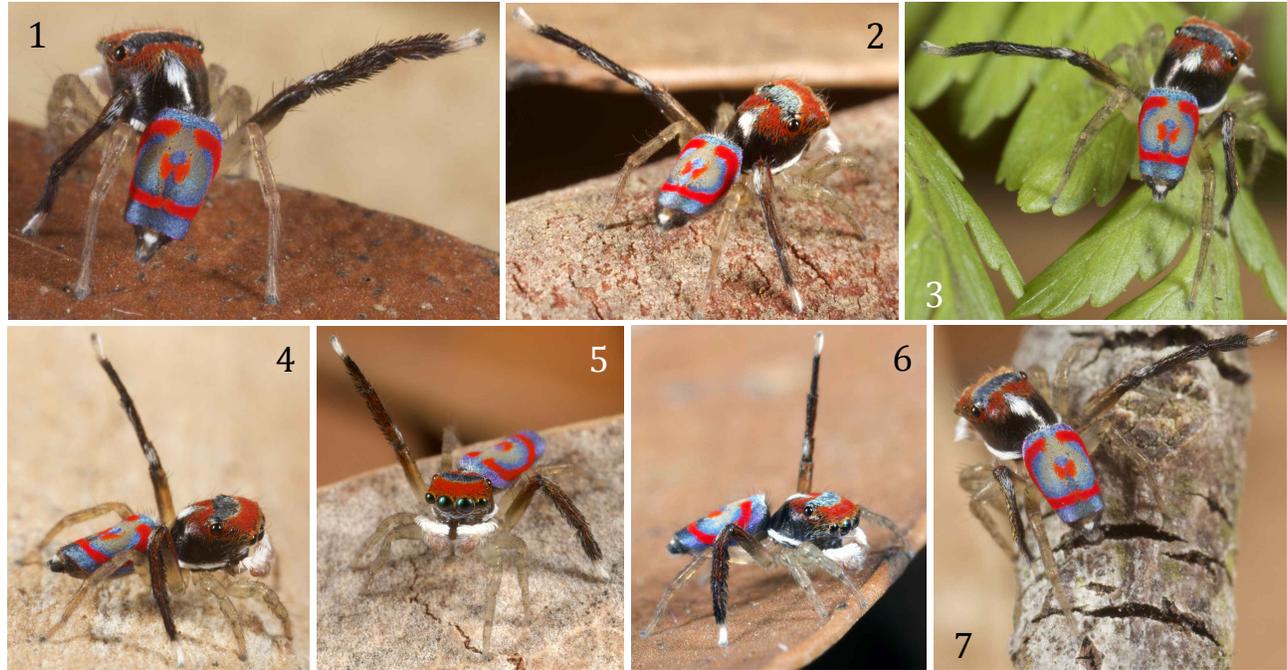


Figure 6. Single leg extension by a male *Maratus pavonis* from Mount Stuart, Tasmania. Selected frames from this sequence show flexion and raising of RIII (1–4), followed by extension and lowering of RIII (4–7), and a later phase of slower lowering of the laterally extended LIII (8–13). Flexion and elevation of each leg took place relatively quickly, followed by a longer period of interrupted (“jerky”) extension and lowering of the extended leg. The elevation of the long axis of each tibia above the horizontal plane of the carapace was estimated. Frames (30/s) from video clip © Kristi Ellingson, used with permission.

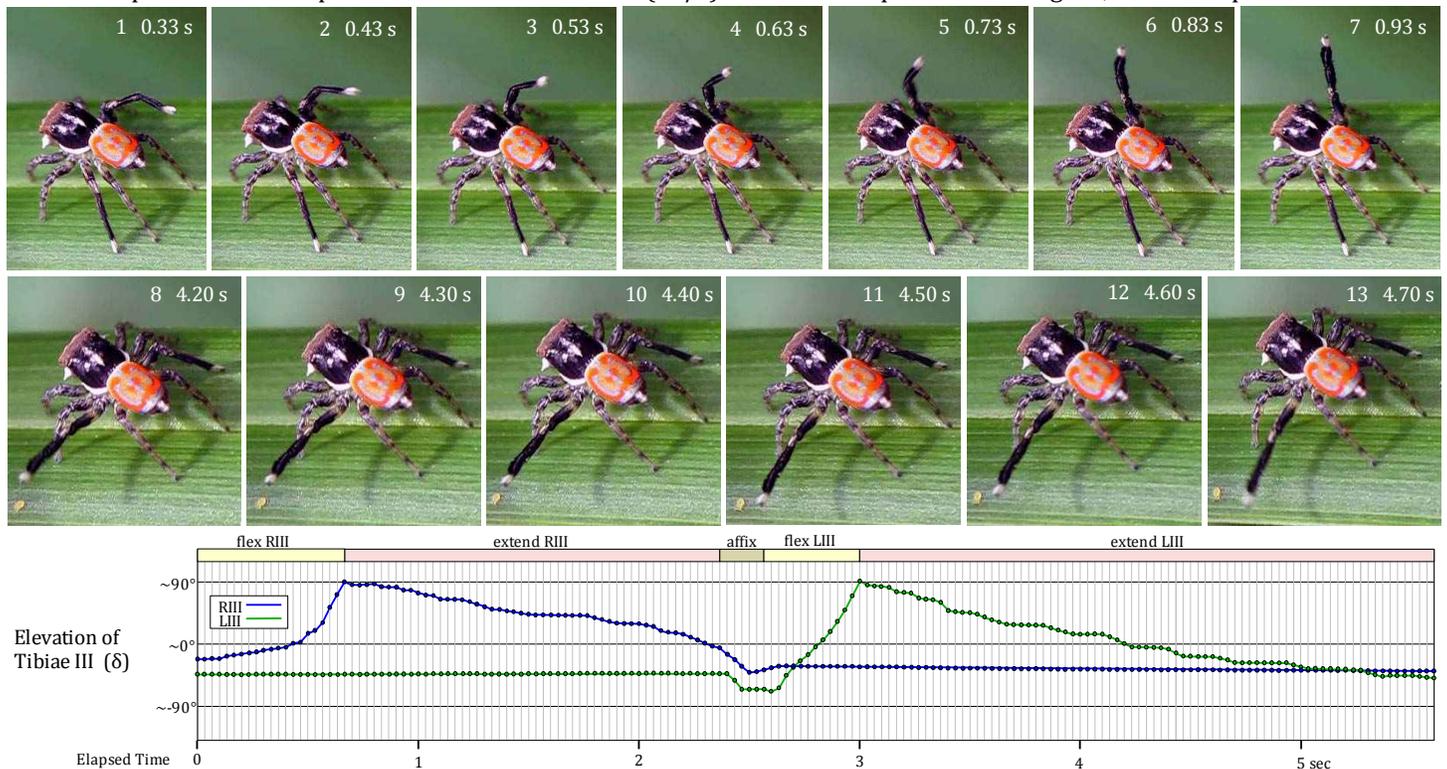


Figure 7 shows a similar display by a male *M. pavonis*, including one cycle of extension of RIII followed by two successive cycles of extension of LIII, each with the same temporal characteristics described in Figure 6. The slower, “jerky” or “interrupted” lowering of each extended leg can also be seen in these cycles. Elevation of each leg III for *M. pavonis*, as part of this single leg display, was generally accompanied by flexion at both the femuro-patellar joint (patellar flexion) and the tibio-metatarsal joint (metatarsal flexion), prior to extension and lowering of the respective leg (Figure 7, frame 4).

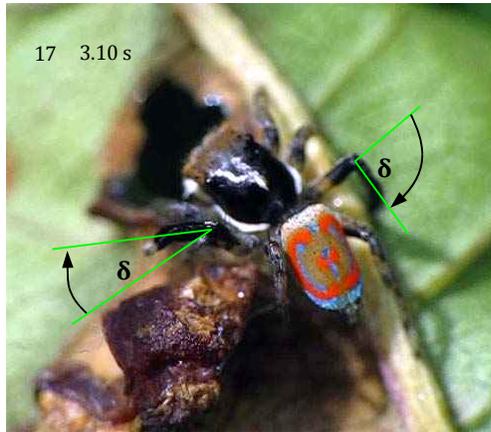
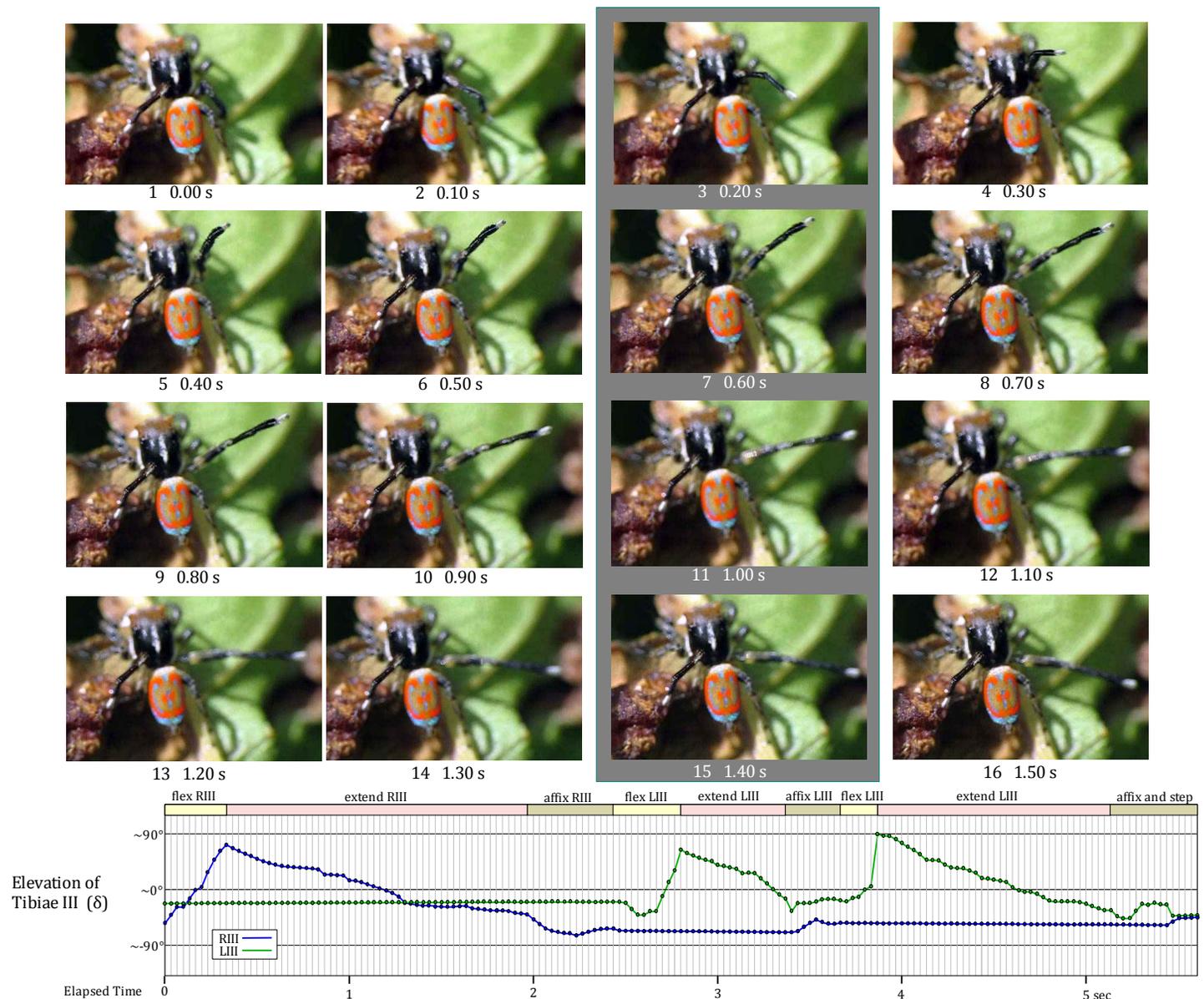
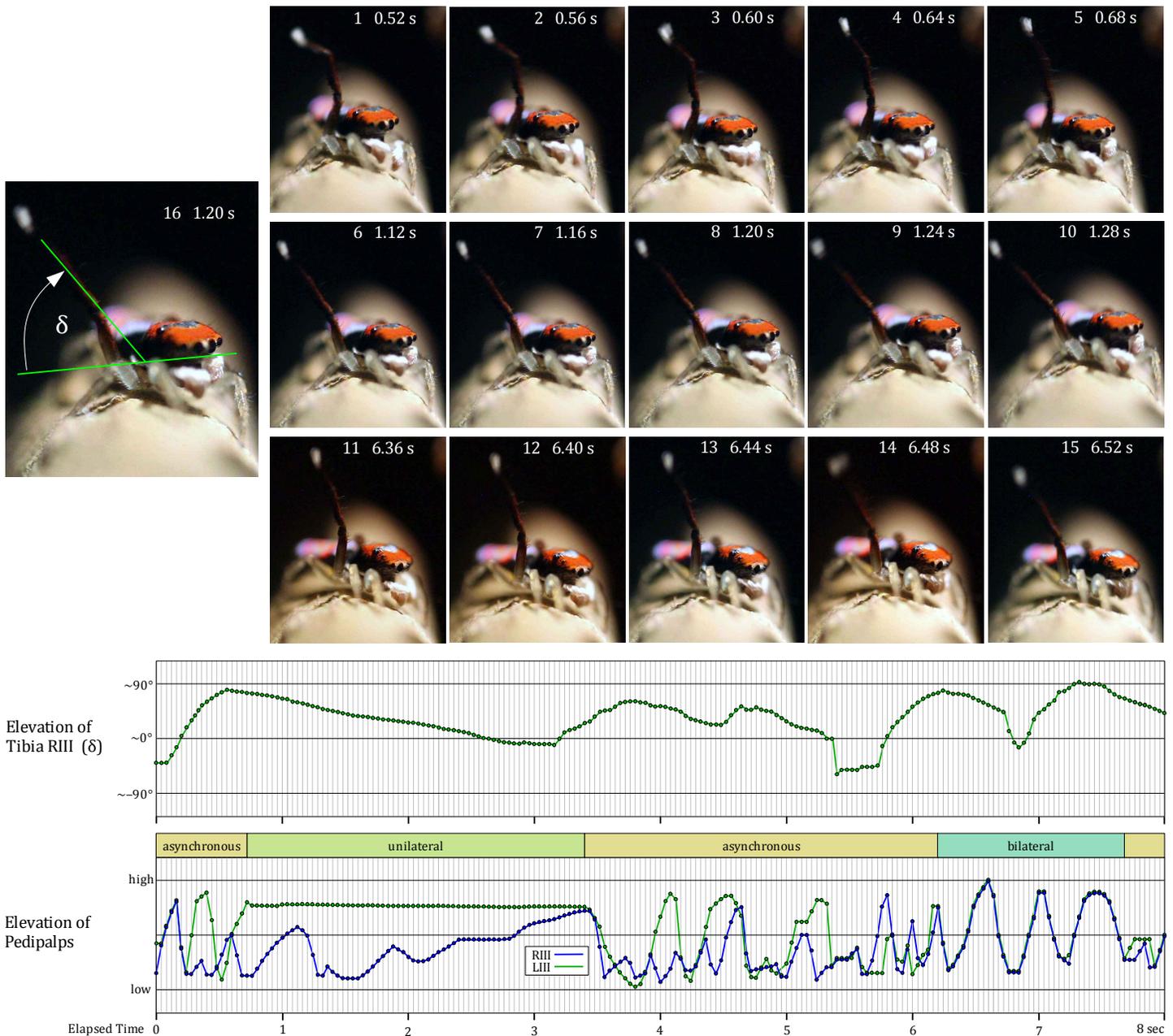


Figure 7. Single leg extension by a male *Maratus pavonis* from Mount Stuart, Tasmania. To more easily observe changes in position, you can follow a single column of frames (for example frames 3, 7, 11, and 15, highlighted, are separated by 0.40 s). To record the timing of movement, the angle between a horizontal plane (referent to the body of the spider) and each tibia III (δ) was estimated (17). Each leg III was unilaterally held in a flexed position at the femuro-patellar (“knee”) joint, and raised (1–4), then more slowly extended and lowered (4–16), and finally brought into contact (affixed) with the substratum in a normal standing position. This display generally alternated between RIII and LIII, although in the sequence shown here extension of RIII was followed by two extensions of LIII (17). Frames (30/s) from video clip © Kristi Ellingson, used with permission.



In contrast, in *M. splendens*, the spiders generally raised each leg III in a more extended configuration, with much less (if any) concurrent flexion at the femuro-patellar (“knee”) joint (Figure 8, 1–4; see Figure 6, 1–4, and Figure 7, 1–4, for comparison with *M. pavonis*), and movement of leg III was more continuous (less “jerky” in appearance). The sequence charted in Figure 8 depicts the raising and lowering of LIII 5 times over an 8 second interval, a behaviour that would be described by a human observer as *rhythmic waving* of this leg. This was accompanied by movement of the pedipalps at a rate of $\sim 2/s$. As noted above the chart, most of the time this was either unilateral (R pedipalp only) or asynchronous, and could be interpreted as sensory behaviour. Toward the end of this sequence, however, about 1.5 s of bilateral or synchronous pedipalp flicker was observed.

Figure 8. Single leg wave (RIII) display by a male *Maratus splendens*. Three different patterns of pedipalp movement are shown in this sequence: alternating or asynchronous movement (1–5), unilateral movement (with the right pedipalp, 6–10), and synchronous or bilateral movement (11–15). Bilateral movement may constitute a visual display. Asynchronous or unilateral movement of pedipalps may be chemosensory, and this included forward projection of pedipalps against the substratum, in addition to the vertical movement depicted in this chart. Frames (25/s) from video clip.



Salticids in general are very good at *multitasking*, and this can confuse the analysis of behavioural patterns. It is very likely that this male *M. splendens* was moving its pedipalps to “taste” the surface, and later for a pedipalp flicker display, quite independent of its execution of a series of single leg waves. Other, perhaps more impressive displays of multitasking in salticids include maceration and feeding on prey during a display, active movement during a display, and even mating (by females) while feeding (unpublished observations). The lack of synchrony between movement of leg LIII and the pedipalps in this example is good evidence for multitasking.

Opisthosomal bobbing

Opisthosomal bobbing refers to the raising and lowering of the opisthosoma when it is held in a near-horizontal position. Because it is not associated with visual display in the direction faced by a spider, it is likely to be related to the generation of acoustic or vibratory signals. Vibratory signals are so commonly encountered in salticids and other spiders (*e. g.*, Elias *et al.* 2003) that their absence might be considered a novelty. Examples of *bobbing* by are presented here for *M. pavonis* (Figure 9) and *M. splendens* (Figure 10).

Figure 9. Bobbing by a male *Maratus pavonis* from Stanley, Tasmania. Note the increase in the rate of opisthosomal bobbing from about 1/s to 3/s over the course of 6 seconds. Blurriness associated with each image was due to higher frequency vibrations of the opisthosoma that could not be measured with this technique. Because movement of the opisthosoma would not be readily visible in front of the spider, it is assumed that this represents an acoustic, and not a visual, display. At the end of this sequence the spider began a single leg extension (LIII) display. Frames (25/s) from video clip.

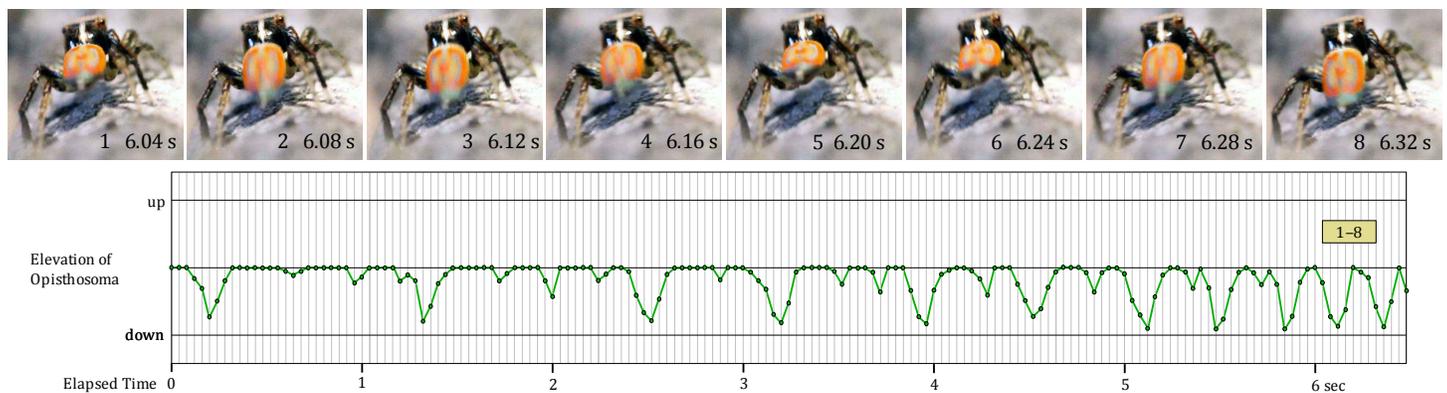
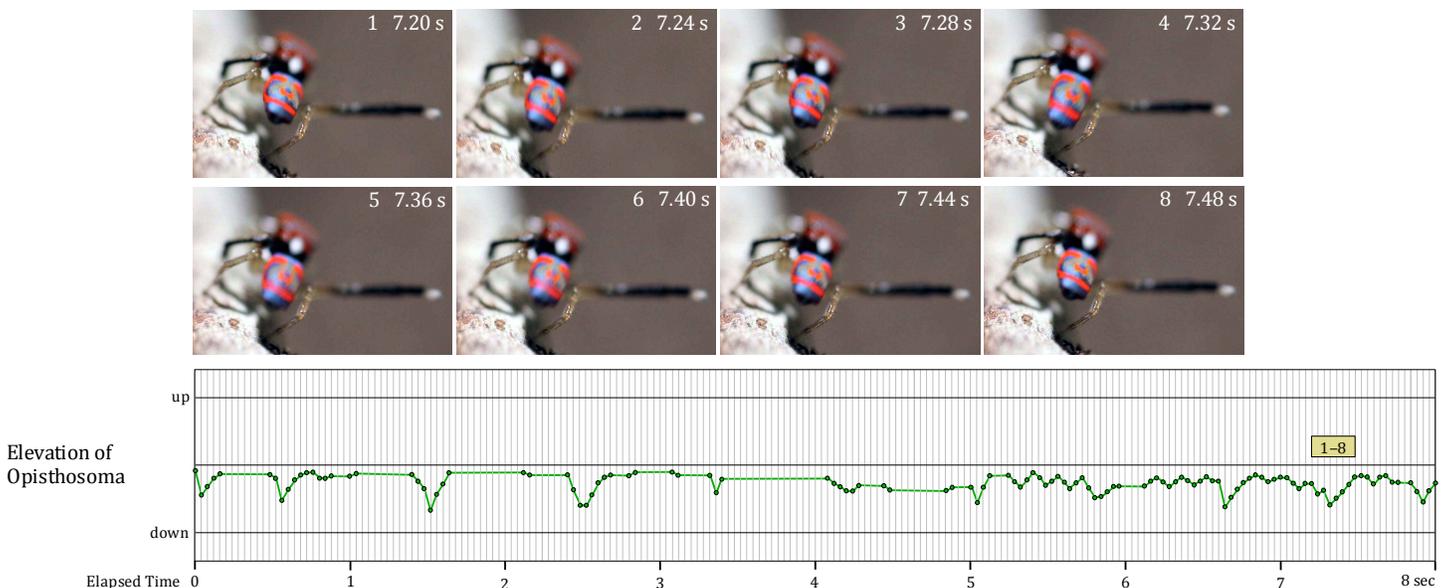


Figure 10. Bobbing display by a male *Maratus splendens*. The spider first raised and then extended RIII, then began to raise and lower the opisthosoma as shown here. Initially this movement was intermittent (~1/s), but later in the sequence (1–8) it was relatively continuous. Frames (25/s) from video clip.



Fan dance

The *fan dance* is the distinctive display of *Maratus* (and some other Australian euophryines presently placed in other genera). All other displays of these spiders can be found in other euophryines with long legs III (*e. g.*, *Saitis barbipes*, Hill 2009), but not the fan dance. This display of the elevated opisthosoma is what gives us good reason to refer to these salticids as *peacock spiders*. Photographs of male *M. splendens* engaged in this display are shown in Figures 11–12.

Figure 11. Three series (1–3) of photographs of male *M. splendens* engaged in a fan dance. The curved “V” shape shown in (1.1) is very typical of this display. Note the degree of expansion and rotation of the opisthosoma in (1.2) and (1.3). Usually, metatarsal flexion (3.1) preceded elevation of legs III into a more vertical position (3.2), followed by lowering of these legs prior to a subsequent flexion of the metatarsi (3.3). Flexion at the patella (1.2, femuro-patellar joint) was infrequently observed. Note the change in elevation of the spider from (2.1) to (2.2).

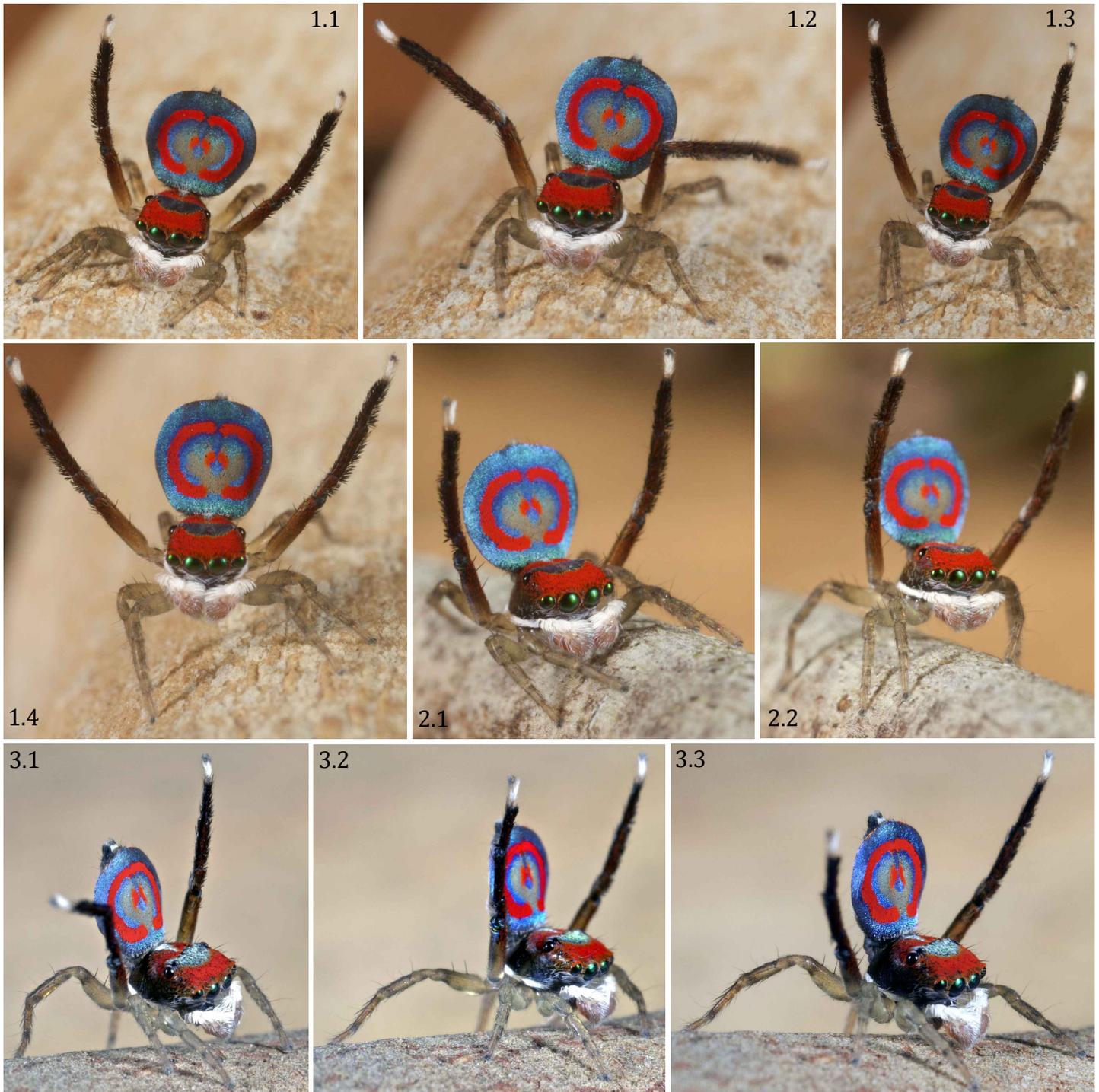
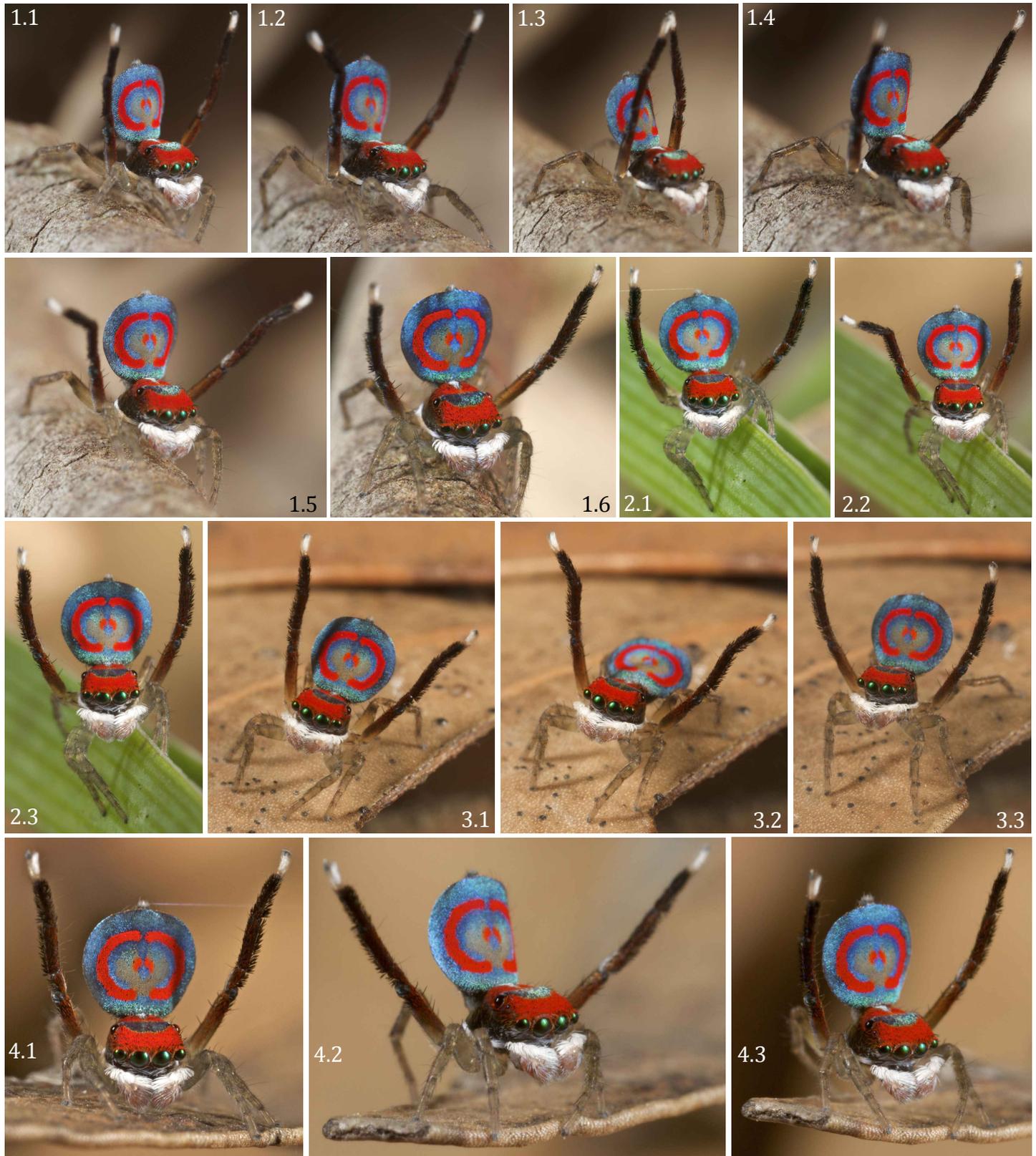


Figure 12. Four series (1–4) of photographs of male *M. splendens* engaged in a fan dance. In the first series are shown bilateral metatarsal flexion (1.1), maximal elevation of legs III after flexion (1.2), lowering of legs III to a typical “V” stance (1.3), and then a second bilateral metatarsal flexion (1.4). In (2.2), only metatarsus RIII was flexed. Sometimes only one metatarsus was flexed unilaterally, but more often left and right metatarsal flexion was only slightly asynchronous if not synchronous. The low angle of the opisthosoma shown in (3.2) was not generally observed in this display. In position (4.2), which was photographed approximately 2 minutes after (4.1), the arms were lowered to the more horizontal position associated with the *semaphore* display, then raised (4.3) four seconds later. Semaphore display may represent a kind of resting stage or transition between successive fan dances.



Temporal analyses of three different video clips that include the fan dance of *M. pavonis* are presented in Figures 13–15. Figure 13 shows the general features of this display, wherein legs III were separated laterally to a V-position, the metatarsi were rapidly flexed, and then legs III were rapidly returned to a near vertical position, then more slowly lowered once again to the V-position. Through a series of cycles, this *M. pavonis* continued to move its partly-elevated opisthosoma from side to side at about 10 cycles/s.

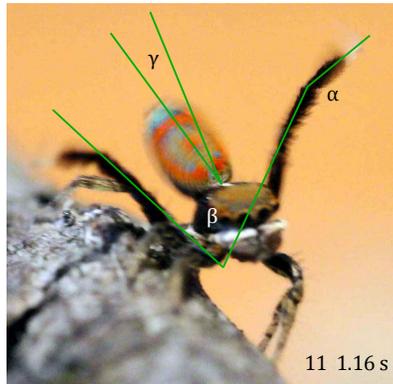
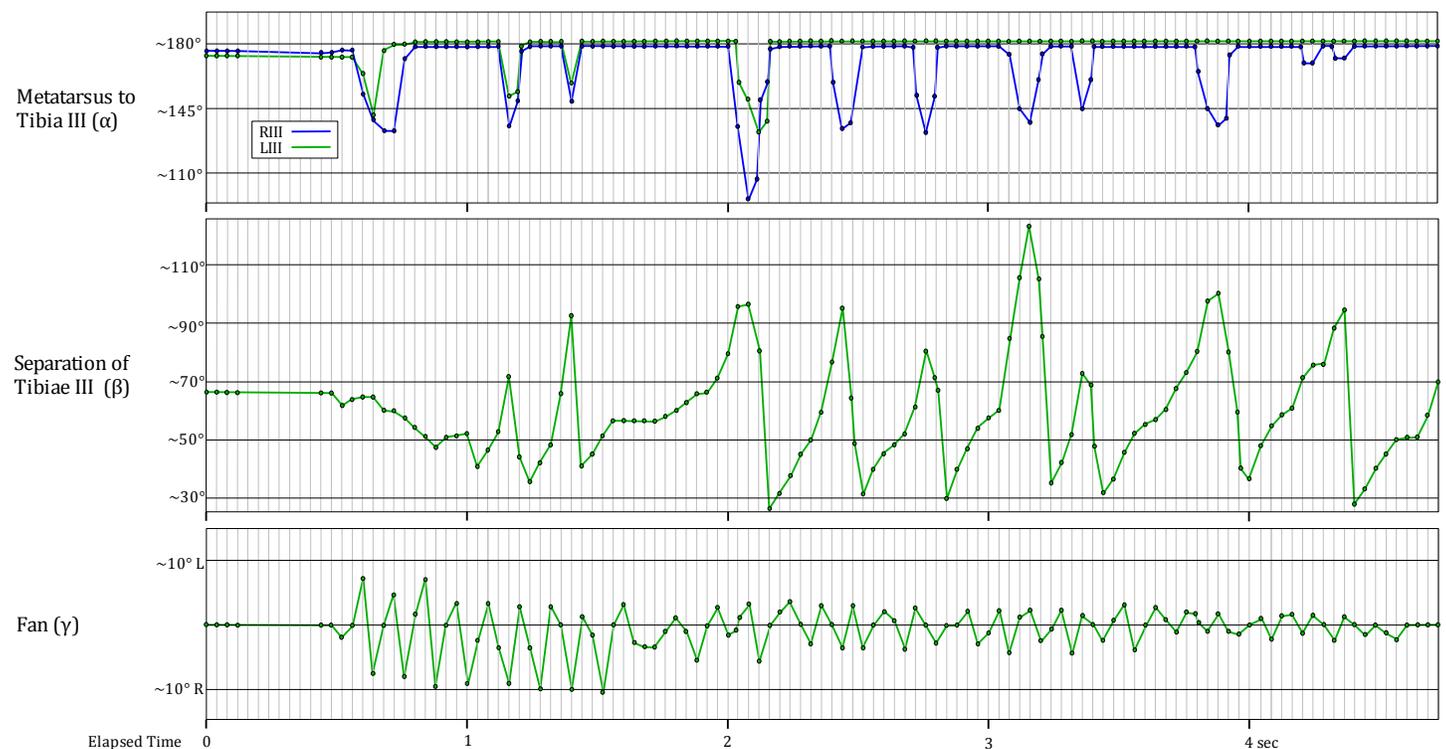
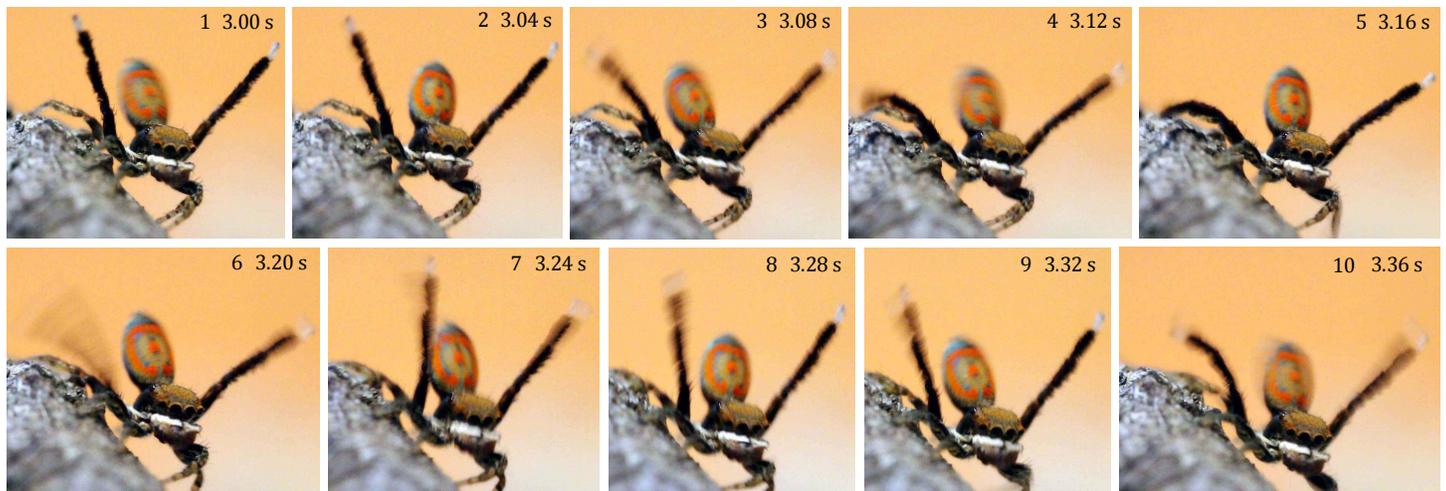


Figure 13. Fan dance of a male *Maratus pavonis* from Stanley, Tasmania. Initially (frame 11, at left), the metatarsi of both legs III were flexed. After 2 seconds, the metatarsus of RIII was flexed unilaterally (3–6, 10). Legs were rapidly brought together in a more vertical position after each metatarsal flexion (7), then were more slowly lowered prior to the next flexion. Waving of the partially erect opisthosoma was continuous, although the amplitude of this movement declined after the first 2 seconds. This difference can be seen in a comparison of (11), at left, to (9). There was no apparent relationship between waving of the opisthosoma and cycles of metatarsal flexion. Frames (25/s) from video clip.



In Figures 14–15, the elevation of each tibia III was measured separately. In the first sequence (Figure 14), a single leg wave (LIII) preceded the fan dance, which was very symmetrical. This was followed by transition to a *semaphore* display (see next section) with legs III held in a horizontal, extended position. Note that side to side (lateral) movement of the fan was only associated with the fan dance.

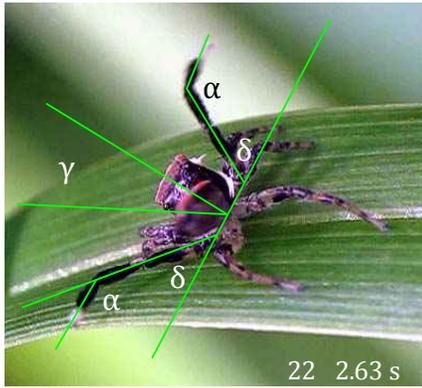
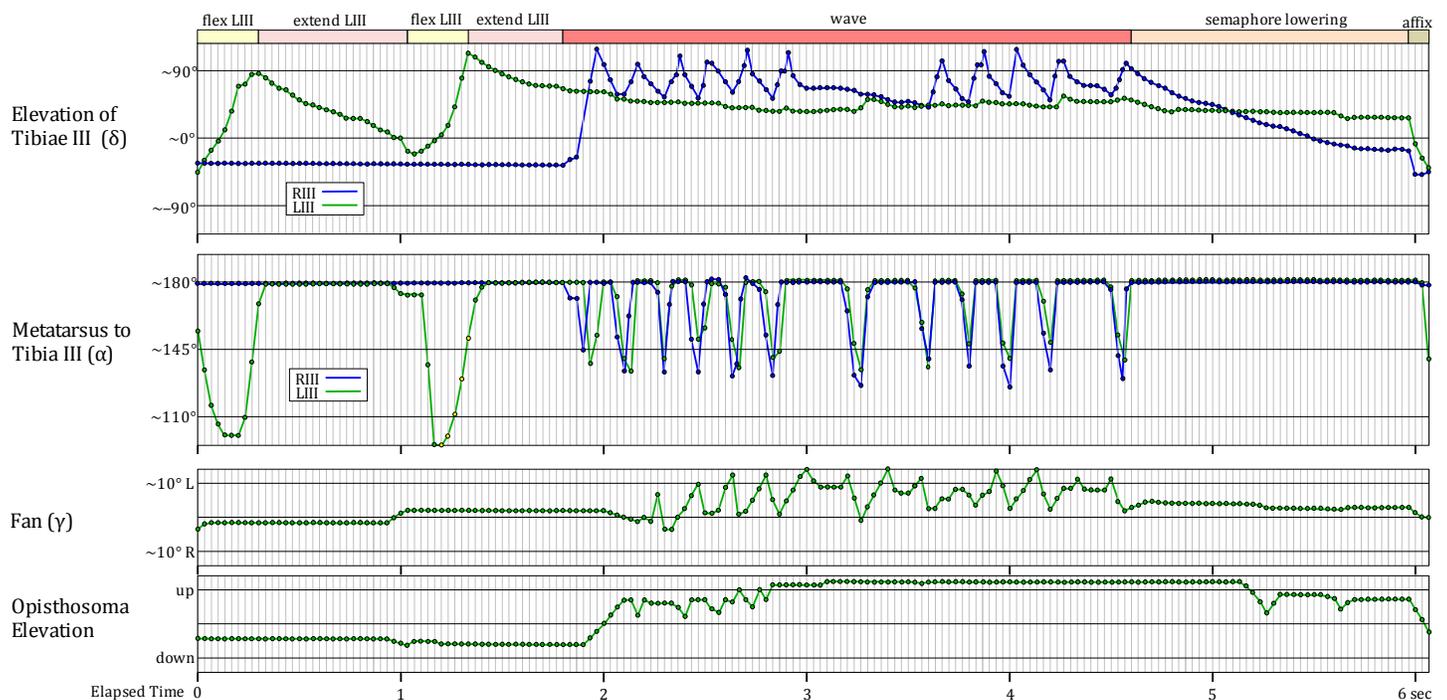
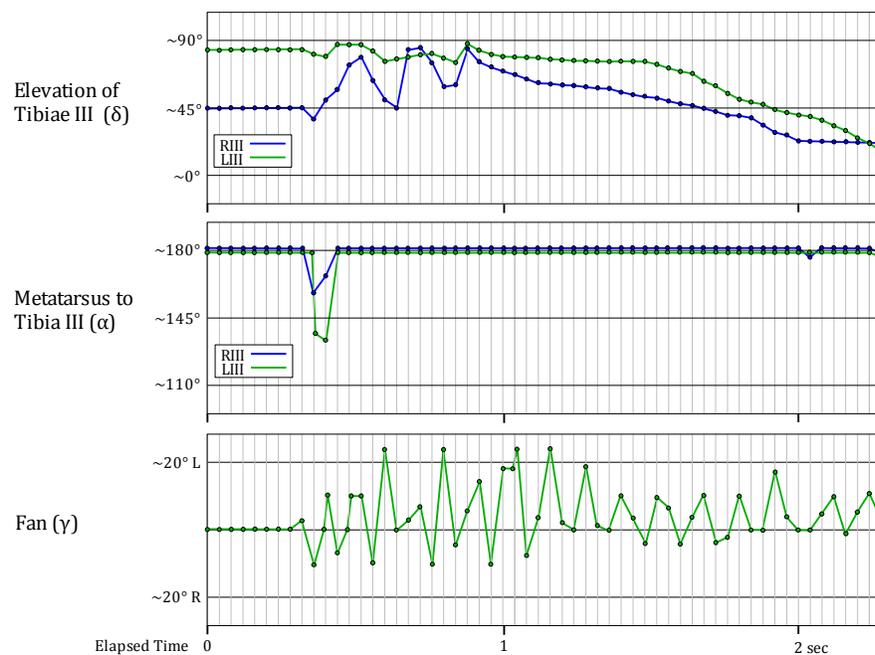
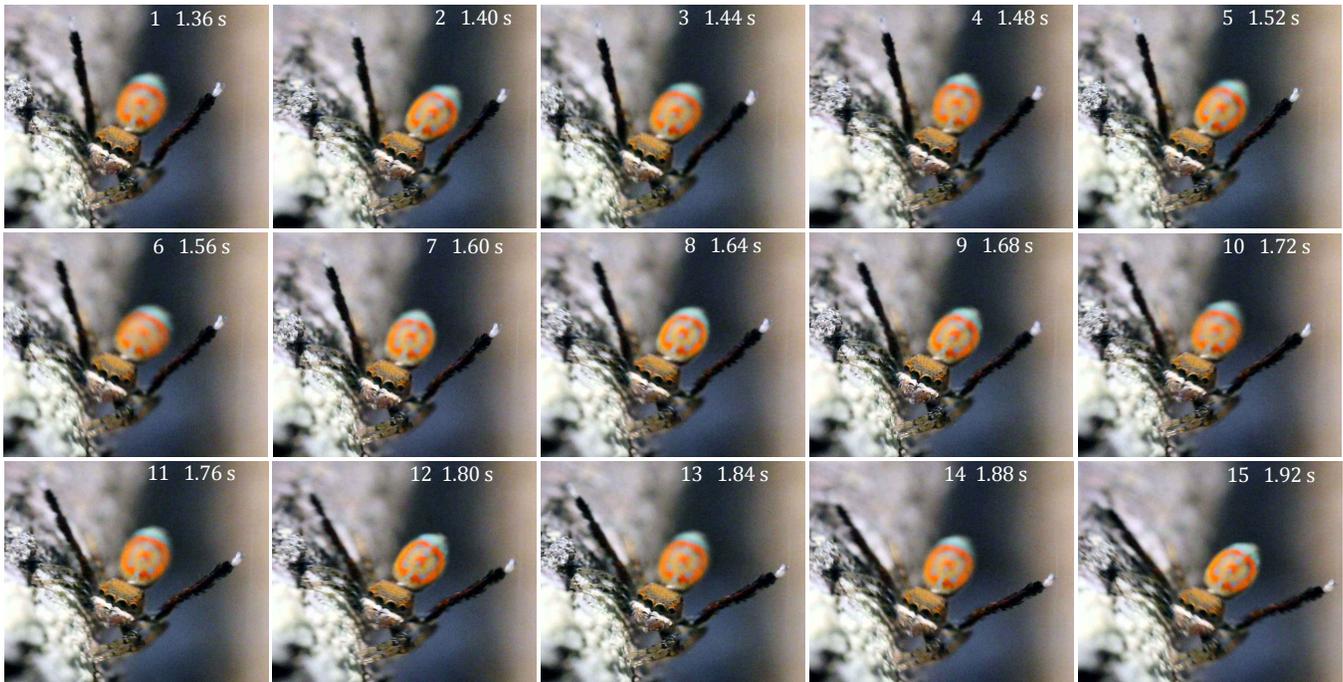


Figure 14. Display by a male *Maratus pavonis* from Mount Stuart, Tasmania. This sequence depicts a transition from single leg extension to a fan dance to semaphore positions over the course of 6 seconds. Selected frames from this sequence show the transition from single leg extension to fan dance as the opisthosoma was raised (1–7), subsequent waving with the opisthosoma held in an elevated position (8–14), and a semaphore display involving the gradual lowering of the laterally extended legs III (15–21). Note the bobbing (elevation changes) of the opisthosoma at the start of the waving display, and intermittently during the semaphore. Frames (30/s) from video clip © Kristi Ellingson, used with permission.



For the male *M. pavonis* shown in Figure 15, this lateral movement of the opisthosoma continued as the legs were lowered into a semaphore position. In addition, only one bilateral metatarsal flexion was seen in three cycles of waving with leg RIII.

Figure 15. Display by a male *Maratus pavonis* from Stanley, Tasmania. Flicker (flexion) of the metatarsus was only observed once, at the onset of waving. Separation of legs III during waving was accomplished primarily through movement of RIII. After the first second, both legs III were lowered as a semaphore, and the sequence shown here was followed by tapping and vibration of these lowered legs. Note the continuation of relatively large amplitude side-to-side movement of the fan as the legs were lowered (1–15, ~8 cycles/s). Frames (25/s) from video clip.



With a rate of about 3–5 cycles/s, each cycle including metatarsal flexion of about 0.1 s in duration, accompanied by ~8 cycles/s of lateral fan movement, the general appearance of this display to the human eye is one of very rapid, vibratory or oscillatory movement. The Tasmanian *M. pavonis* that were observed for this study continuously moved the opisthosoma laterally through a series of fan dance cycles, with a displacement that was estimated to be about 10–20° in either direction.

Three clips including the fan dance display of *M. splendens*, facing a female, are charted in Figures 16–18. In each case, both legs III were kept at about the same elevation, and only the separation between the two was charted, as estimated by the angle between tibiae III (β). As shown in Figure 16, the fan of *M. splendens* was only moved laterally during each separate cycle of the fan dance (identified by one flexion of the metatarsi). Also, the amplitude of this fan movement ($\sim 5^\circ$ in either direction) appeared to be significantly less than that observed in *M. pavonis*, although fan movement during each cycle of the fan dance was quite fast (~ 10 cycles/s). Note that the fan in this case was not fully extended.

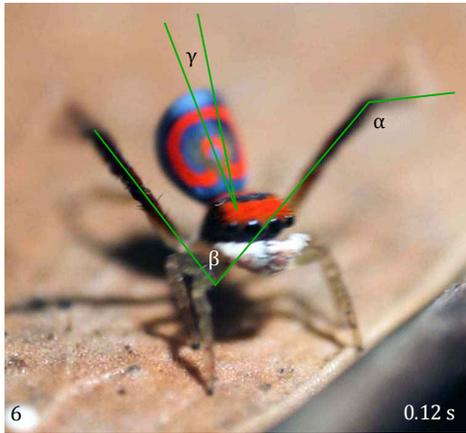
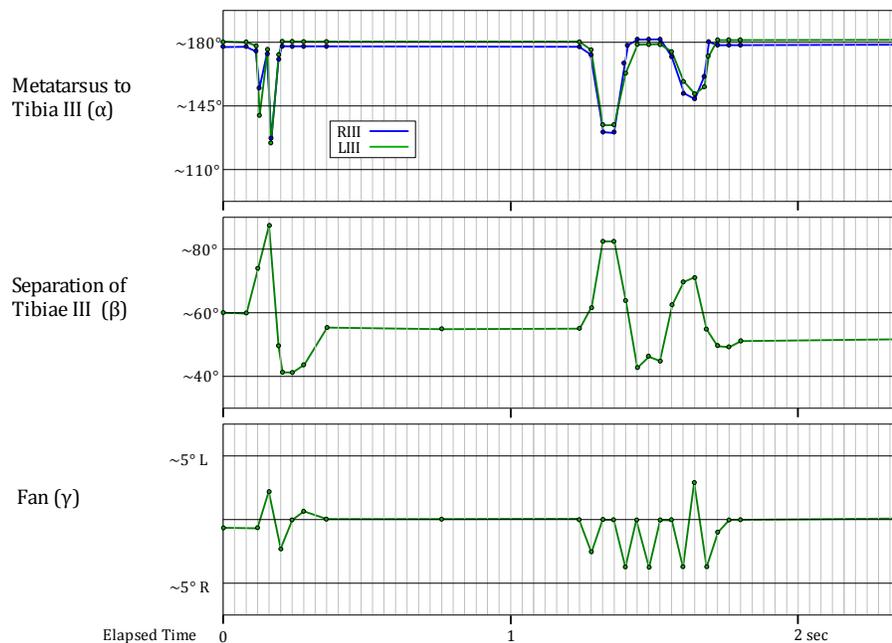


Figure 16. Fan dance of a male *Maratus splendens*, facing female. During this sequence the body was held erect above the surface, tilting only slightly to face the female. Pedipalps were held in front of the chelicerae, forming a white band in front of the clypeus. Three components of movement during the display were estimated by examination of individual frames, including γ (bottom chart), an estimate of the lateral rotation of the elevated opisthosoma or fan with respect to the pedicel. Representative frames from the first bout of display (1–5, below) show the relationship between these components: 1, starting position, with legs III spread in a V-shape. 2, opisthosoma moved to the spider's right as flexion of metatarsi III began. 3, flexion of metatarsi III. 4, legs III straightened out and brought back to a more vertical orientation. 5, legs III returned to a starting position (as in [1]). During each bout of movement, the abdomen (not fully raised or extended) was waved (lateral oscillation) at a frequency of about 10/s. Frames (25/s) from video clip.



Another way to describe this distinction is to say that, to a human observer, the fan dances of the *M. splendens* that were observed appeared as a series of isolated, clean or distinct, rapid signals, interrupted by intervals with no movement at all, and not as the kind of continuous or “excited” oscillation that characterized the fan dances of *M. pavonis*. These relatively long motionless intervals can also be seen in the sequences presented in Figures 17 and 18.

Figure 17. Fan dance of a male *Maratus splendens*, facing female. In this sequence, bilateral flexion of metatarsi III was more loosely coupled, as the right leg was moved in advance of the left (1–6). For this reason the angle between the tibia and metatarsus is charted separately for each leg III. As in the previous example, legs III were lifted into a more vertical orientation after each wave of the metatarsi, and side-to-side movement or oscillation of the partially extended and raised abdomen accompanied each bout of movement at a frequency near 10/s. Frames (25/s) from video clip.

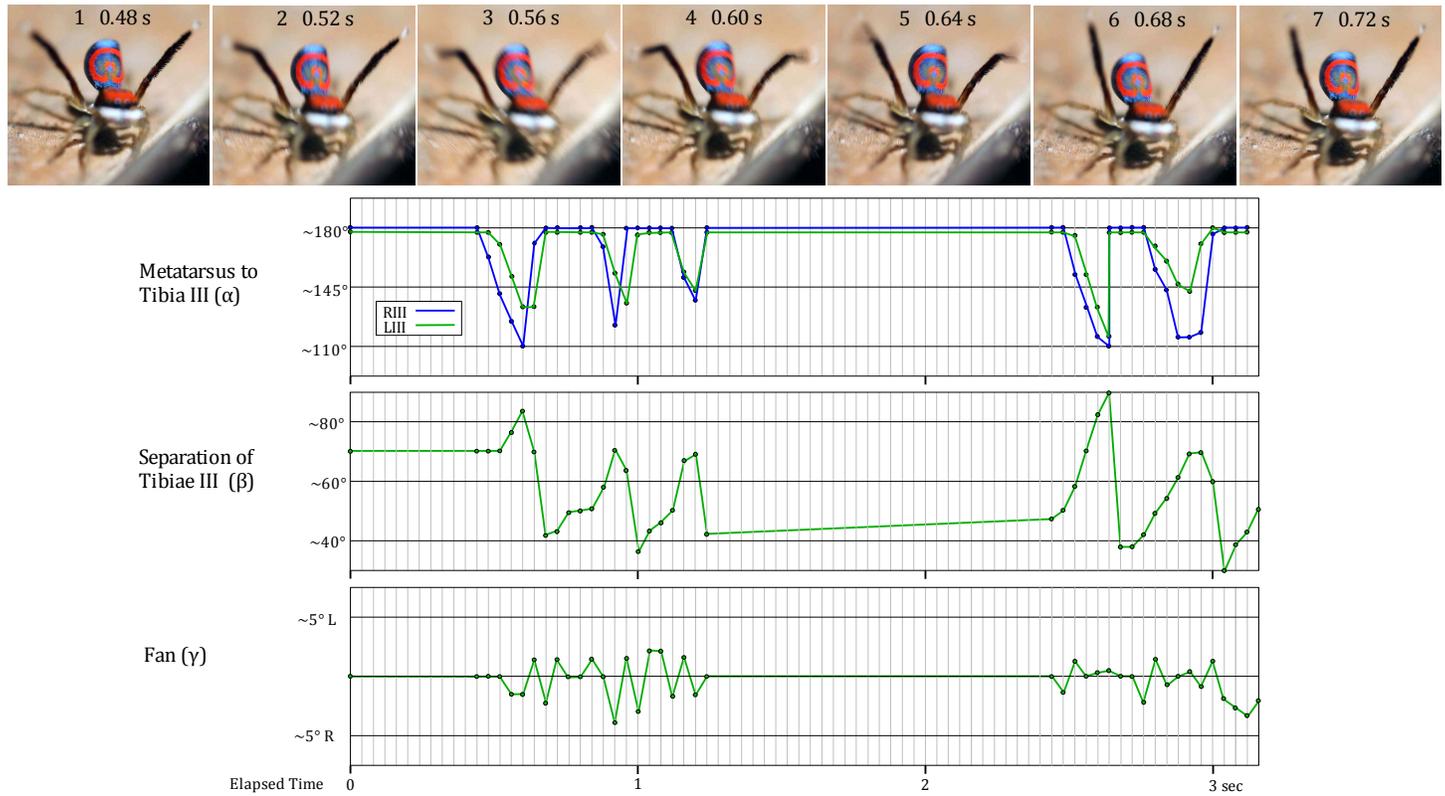
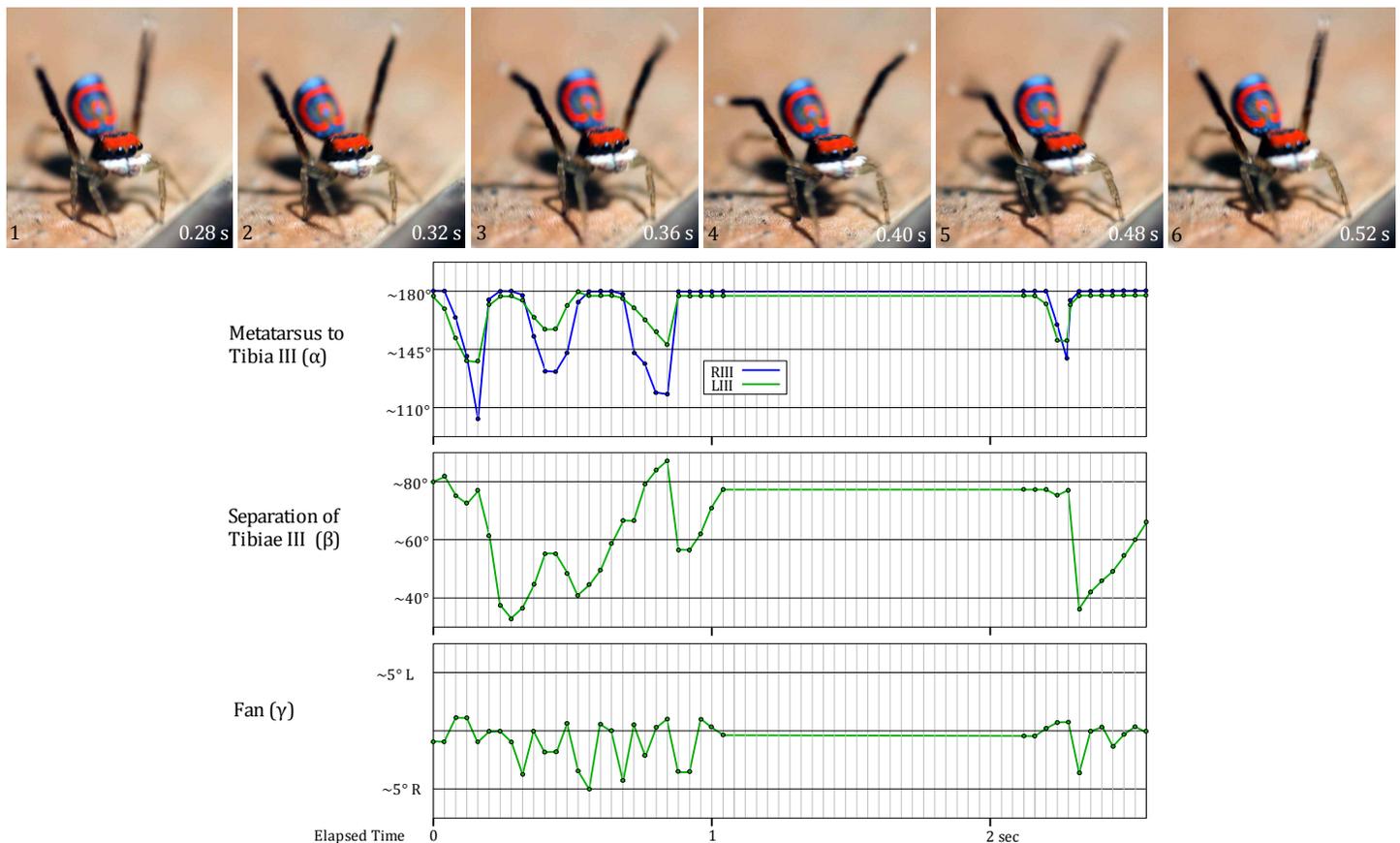


Figure 18. Fan dance of a male *Maratus splendens*, facing female. Frames (25/s) from video clip.



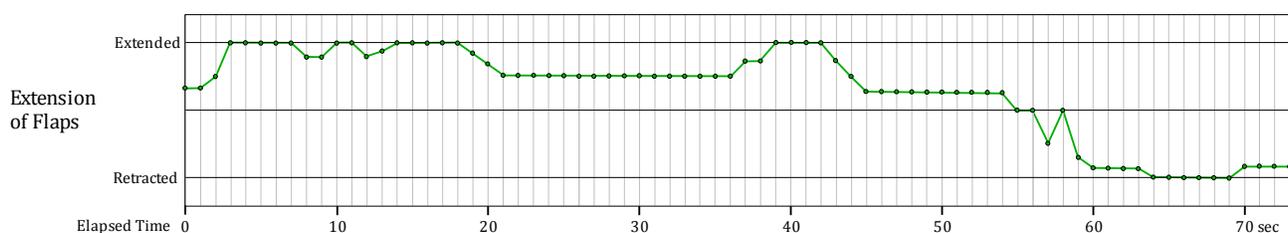
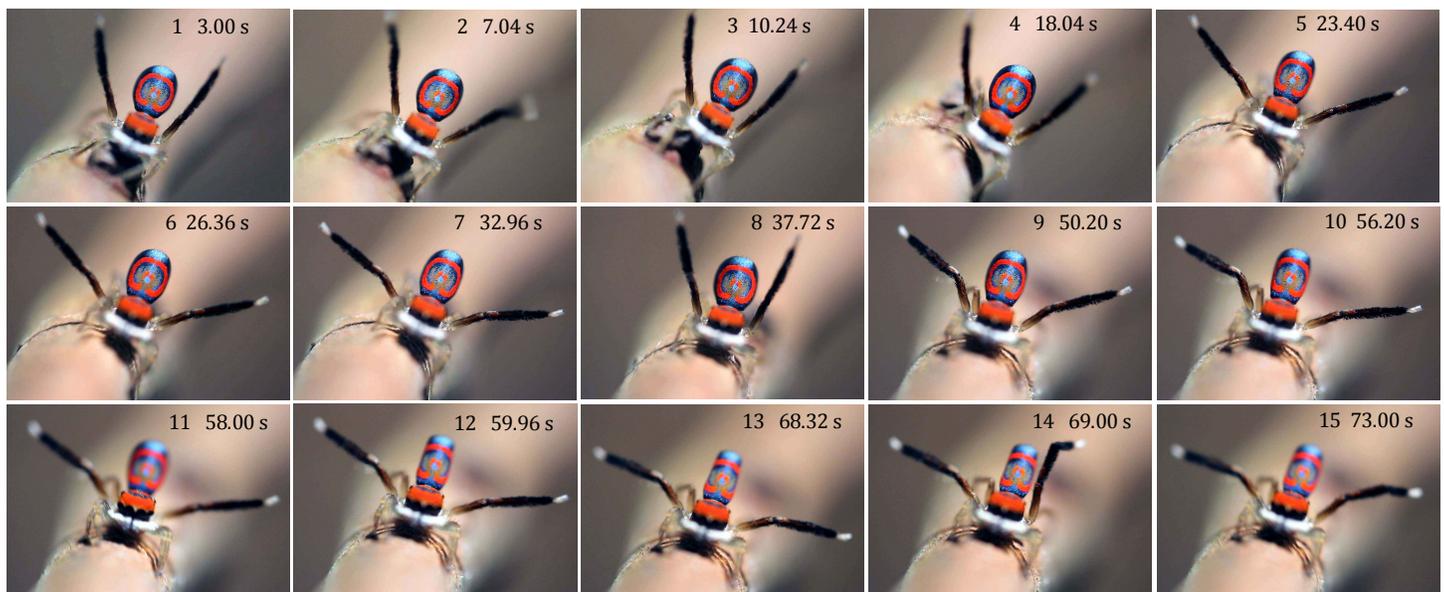
Side to side (lateral) stepping during the fan dance

Depending partly on characteristics on the substratum (e. g., branch width), and movement or proximity of the sighted female, *Maratus* (*pavonis* or *splendens*) may move or actively step from side to side during the fan dance. This movement was not a necessary part of the fan dance, however. This movement was generally synchronized with the waving of legs III. For *M. splendens*, this often appeared as a step to the left during one cycle of waving, followed by a step to the right during the next cycle of waving, and so on. Some of the *M. pavonis* tended to favor waving movement of one of their two legs III, irrespective of whether they were stepping to the right or left during a bout of waving. As first described by Dunn (1957; termed a *nautical roll*), there appeared to be a tendency in some *M. pavonis* to hold the leg (III) in the direction of side-stepping movement more vertically, as the contralateral leg III was waved vigorously. Again, the interrupted display of *M. splendens* created quite a different visual effect from the almost continuous movement of *M. pavonis* when they were stepping.

Elevation and extension of the opisthosoma during display

During the fan dance of *Maratus splendens*, the degree of elevation and extension (or inflation) of opisthosomal flaps varied. This may be related to a number of different factors, ranging from the ability of the male to sustain the extension of these flaps, or the level of arousal of the male in response to the behavior of the female. The opisthosoma can be rapidly inflated, but changes in the extent of this inflation are not part of display and generally take place over a much longer time frame as a male displays in front of a female, as shown here (Figure 19).

Figure 19. Extension of opisthosomal flaps during display by a male *Maratus splendens*. During a sequence of fan dance (1–4), followed by gradually lowering of legs III in a semaphore display (5–15), the opisthosomal fan was generally held erect, but the lateral flaps were slowly retracted. Throughout the entire sequence, the pedipalps were held in an elevated position and were not moved. As in several other waving display sequences, active waving of the metatarsus was often accompanied by side-to-side stepping or rotation of the prosoma. Note the very long time scale for these changes. Frames (25/s) from video clip.



Semaphore (bilateral arm signal) display

This is the “signature” *arm signal* display of male euophryines with long legs III (Hill 2009), making use of the length of these legs, and their characteristically white tarsi. In general, legs III are raised quickly to a near vertical position, then lowered slowly until they are fully extended in a lateral direction (Figure 20).

Figure 20. Five series (1–5) of photographs of male *Maratus splendens*, facing female, during a *semaphore* display. This display can be combined with some elements of the fan dance, such as elevation or inflation of the fan (e. g., 5.3), but this is not a necessary feature of the display as shown in (2.2). The defining feature of this display is the gradual lowering of legs III below the “V” stance typical of the fan dance, to a horizontal orientation. The “deemphasis” of the fan during transition to a semaphore display can be seen in the transition from (3.2) to (3.3), and from (4.1) to (4.3).



The *semaphore* display is often, but not always, associated with a more vigorous *tapping* display, described in the next section. Temporal studies of video clips including the semaphore display of *M. pavonis* and *M. splendens* are presented in Figures 21–22.

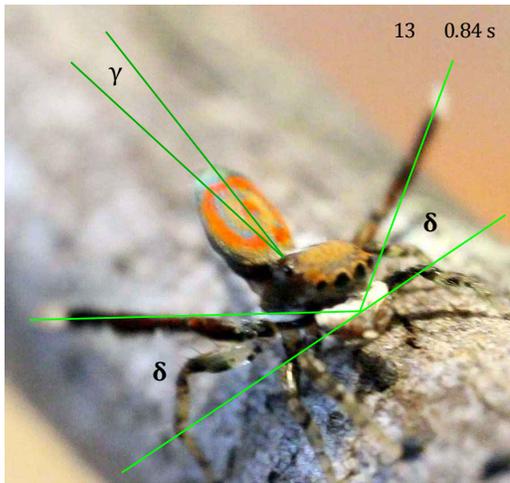
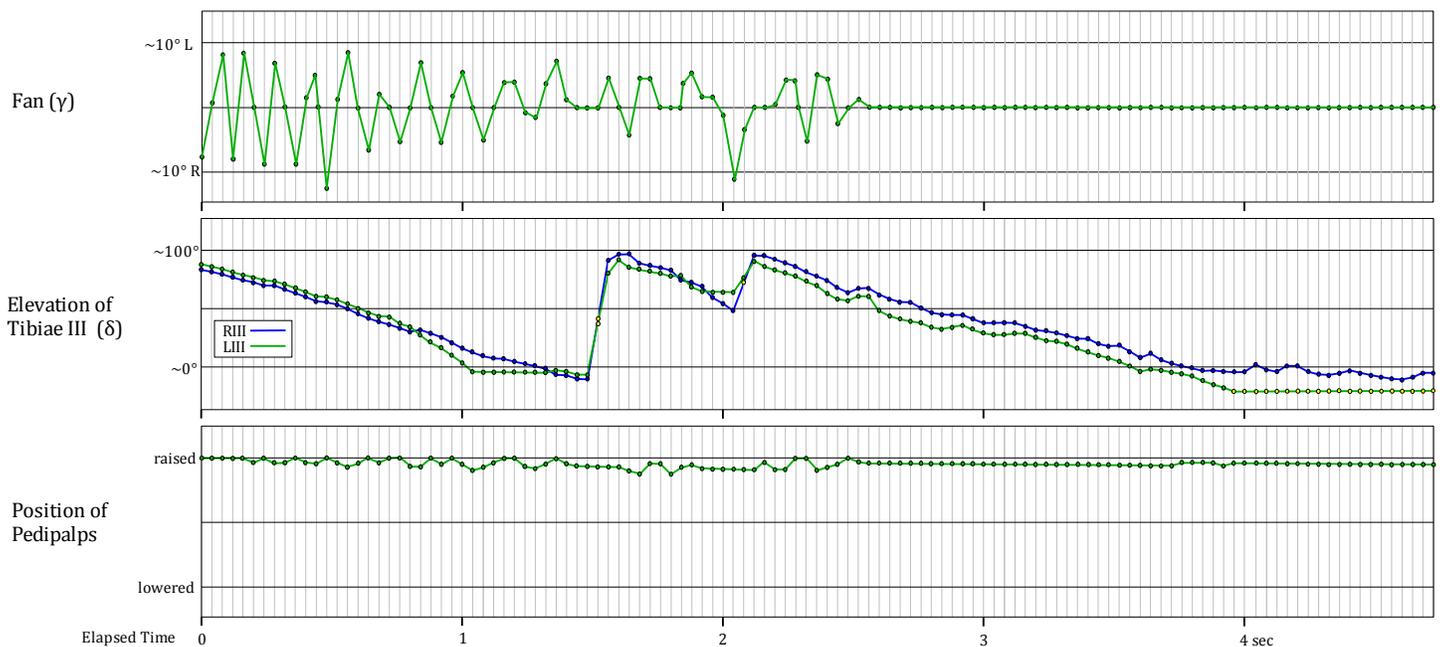
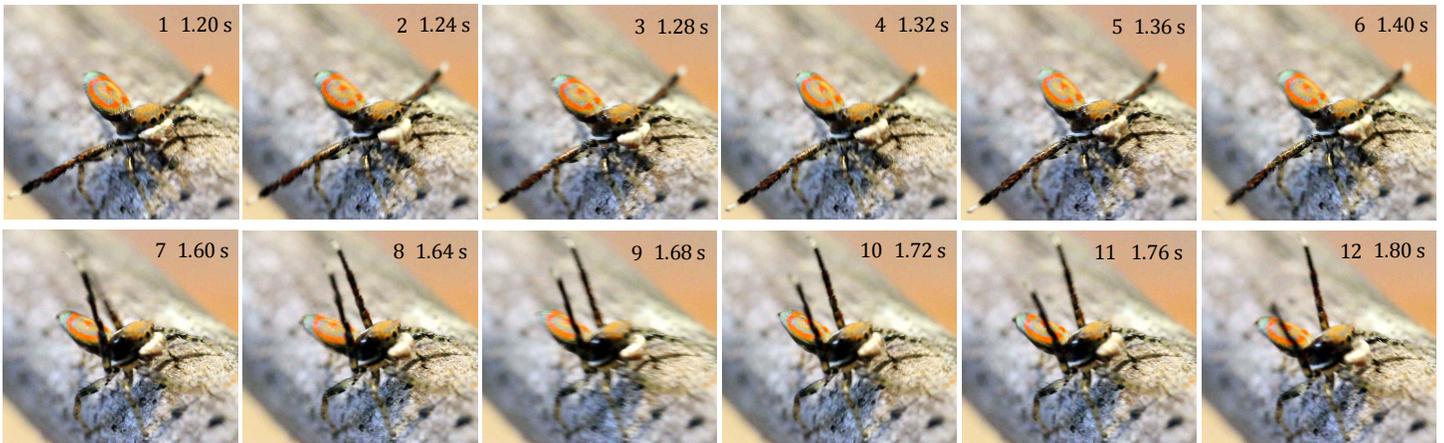


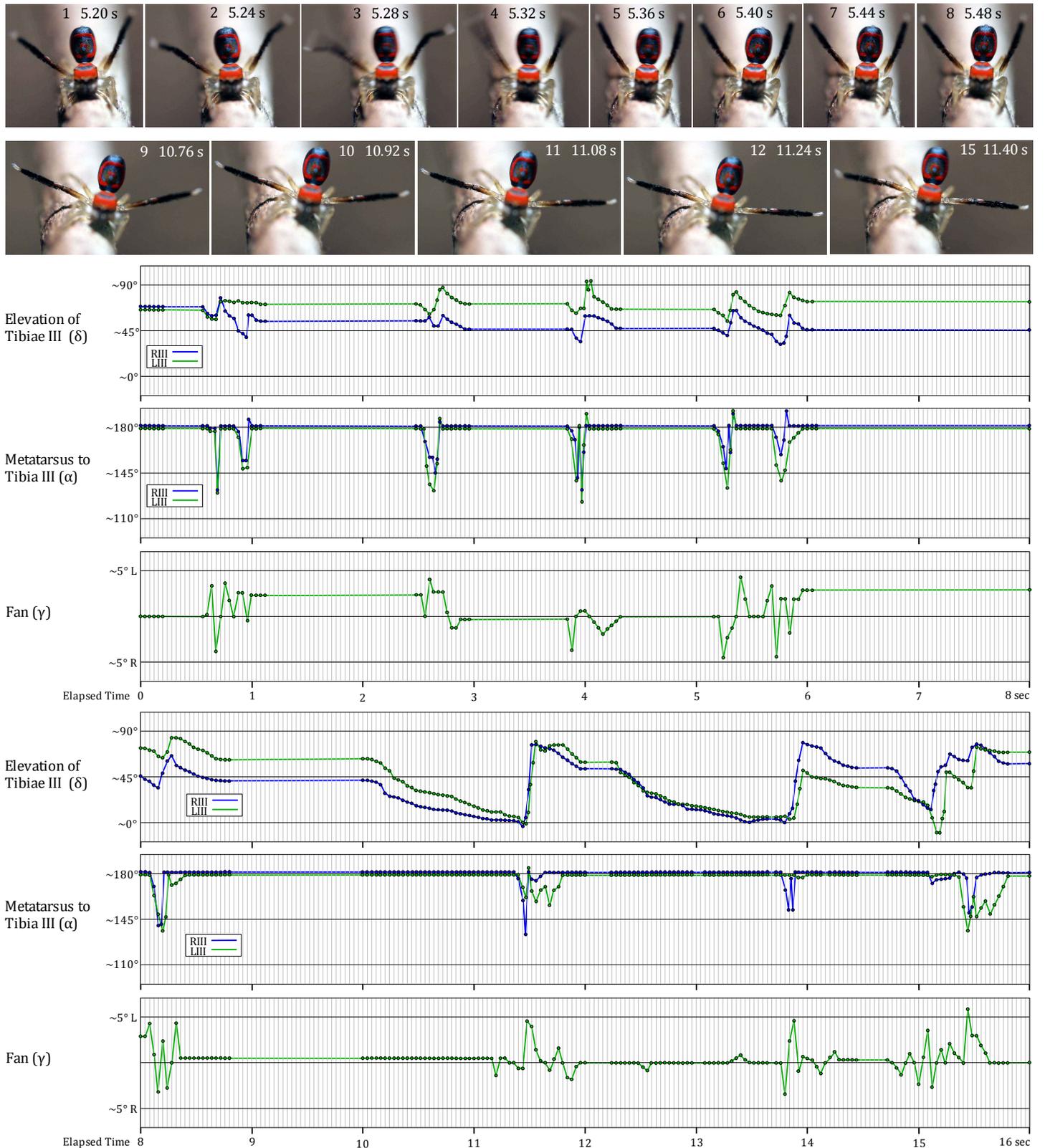
Figure 21. Semaphore display of male *Maratus pavonis* from Stanley, Tasmania, facing female. Laterally extended legs III were bilaterally lowered (1–6) and then rapidly raised to a vertical position (7) to begin a new cycle of lowering (7–12). For the first 2.5 sec of this sequence the partially erect fan was waved from side to side ($\sim 10/\text{sec}$), as the pedipalps were moved slightly up and down (pedipalp flicker) in a raised position (also $\sim 10/\text{sec}$). Pedipalp flicker like this was not generally observed during the fan dance. There was no metatarsal flexion in this sequence. Toward the end of this sequence, leg RIII was moved up and down slightly. On a surface, this could be associated with *tapping*. Frames (25/s) from video clip.



A longer (16 s) sequence for a male *M. splendens* is shown in Figure 22. This depicts a transition from a fan dance to a semaphore display, with movement of the fan appearing only intermittently as in previous examples for this species. This can be contrasted with the continuous movement of the fan in *M. pavonis*

as shown in Figure 21. Behaviour during the last 8 seconds of this sequence can be interpreted as regular alternation between a fan dance (with legs III elevated), followed by longer intervals including gradual lowering of legs III in a semaphore, and several intermittent motionless intervals. Each of these longer cycles can exceed 3 seconds in duration. If you can, it is useful to step through each chart “in time.”

Figure 22. Display by a male *Maratus splendens*. An intermittent series of fan dance displays (1–8) during the first 8 seconds of this sequence were followed by longer semaphore displays (9–13) during the next 8 seconds of this sequence. The blurred appearance of opisthosoma and legs III in some frames was associated with rapid vibration that could not be measured at this frame rate (25/s). Pedipalp movement was not charted as it was insignificant. Note that the 16 second time scale is shown in two parts.



Tapping display

Tapping with outstretched legs III is probably a generalized precursor to mounting and mating in euophryines with long legs III (Hill 2009). This is commonly associated with a bout of semaphore display, and can be viewed as a highly energetic (rapid vibration rate) display that generates, in addition to the visual effect, a lot of vibration in the substratum. The entire body of the spider may be moved up and down in contact with the surface, as the tips of the outstretched legs III beat against the surface. This behaviour has been observed for both *M. pavonis* and *M. splendens*. Some examples are presented here (Figures 23–24), but it should be noted that much of the tapping movement (perhaps in excess of 50 cycles/s) is far too fast to chart with 25–30 fps video.

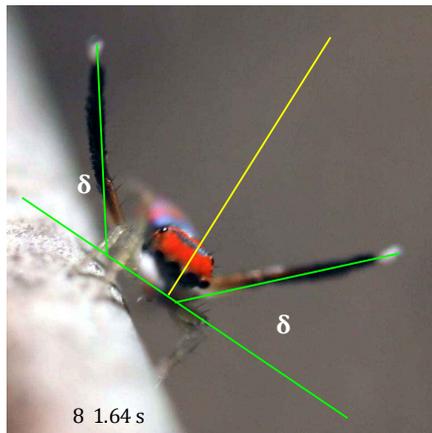


Figure 23. Semaphore and tapping display of male *Maratus splendens*, facing female. With pedipalps held in front of the clypeus, this spider rapidly bobbed up and down as it tapped the substrate with outstretched legs III (1–2), then quickly (3) raised legs III to a near vertical position (4–5), slowly lowering them as it flicked its pedipalps up and down (6–7) before the onset of a second bout of tapping. Tapping frequency appeared to be close to 15/sec, near the resolution of this video analysis. Note the change in elevation of the prosoma between (1) and (2), and the extent of lowering of the pedipalps between (6) and (7). In some cases (small yellow circles), the entire leg III could not be seen and its position was estimated from the blurry proximal segments of the respective leg. In the chart, turns by the spider are indicated with a (T). Frames (25/s) from video clip.

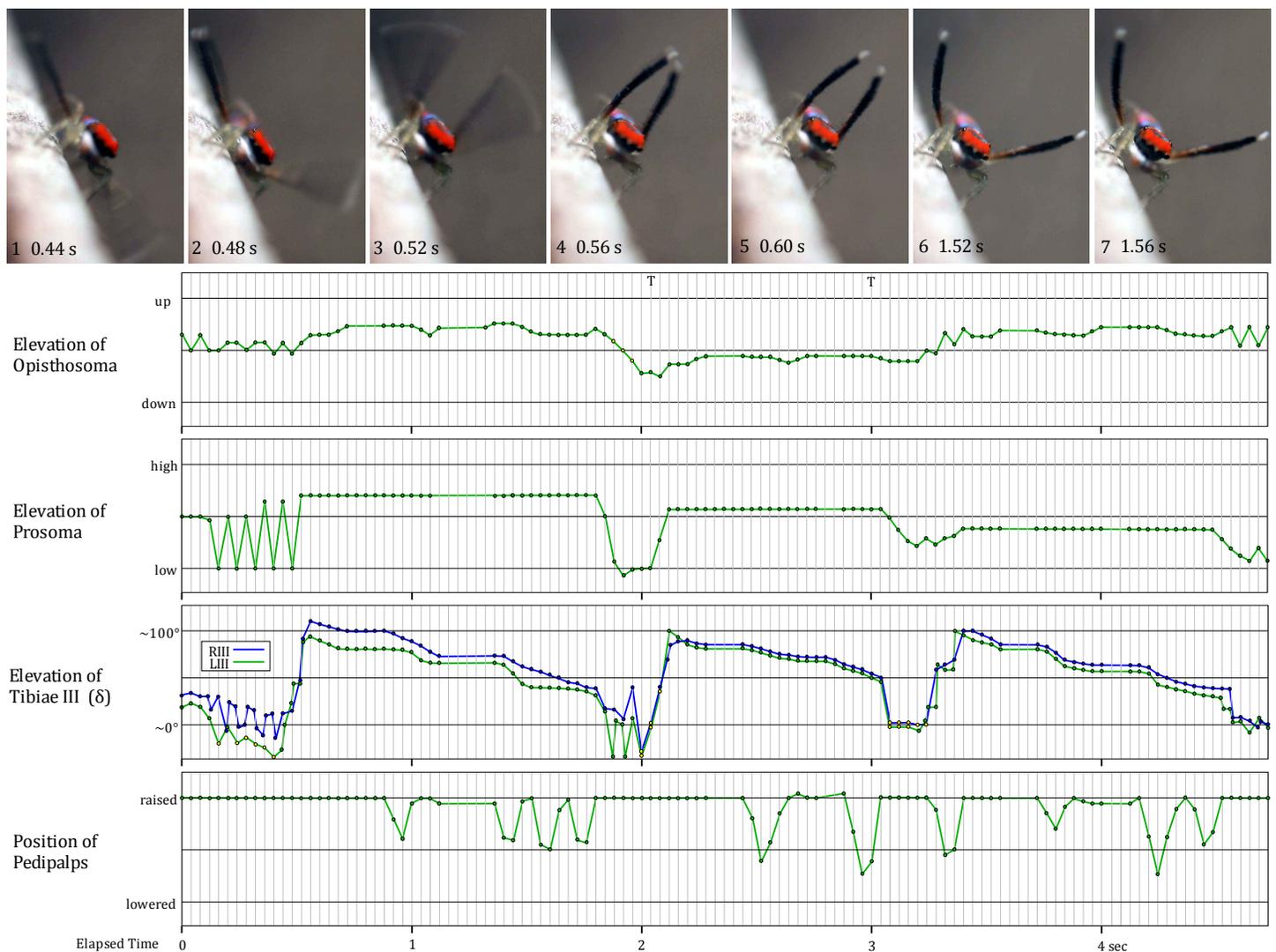
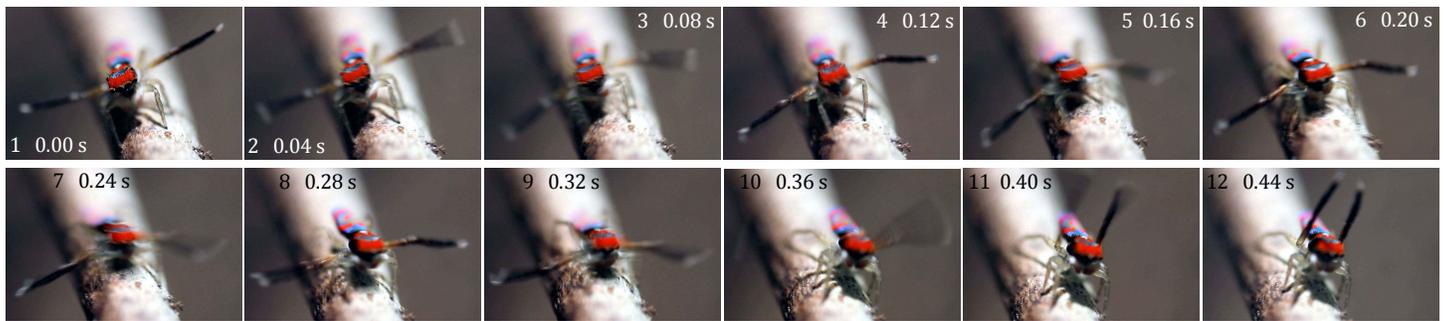


Figure 24. Part of a semaphore display by a male *Maratus splendens*. This sequence depicts a highly energetic (vibratory) tapping sequence, including rapid bobbing (~12 cycles/s) and vibration of the extended legs III. At this frame rate (25/s) the frequencies of vibration could not be measured. Note the relative depression of the body, and in particular the depressed opisthosoma, associated with rapid vibration of the extended legs III in frames 5, 7, and 9.



Discussion

Several behavioural differences may relate to the higher degree of development of the opisthosomal fan in *M. splendens*. The fan dance of male *M. splendens* included longer pauses with no movement, whereas the respective dance of the observed *M. pavonis* (from both the north and south of Tasmania) included almost continuous side to side movement of the opisthosoma. It appears that the size and brilliance of the display pattern is more important to *M. splendens*, and its rapid movement is more important to the success of *M. pavonis*. This hypothesis is consistent with an evolutionary continuum between a smaller dorsal plate, and a larger one with lateral extensions (or flaps). In addition, the single leg wave of *M. splendens* was relatively smooth when compared to the “jerky” or interrupted extension and lowering of a flexed (at the femuro-patellar joint) leg III by *pavonis*. The visual impression, for a human observer, was one of greater elegance or precision in the dance of *M. splendens*, and one of greater activity in the dance of *M. pavonis*.

Earlier descriptions of the courtship of *M. pavonis* and other *Maratus* were reviewed in a previous paper (Otto and Hill 2010), and behaviours previously reported for *M. pavonis* generally agree with the observations presented here. Of these earlier descriptions, the flexion of metatarsi III by male *M. amabilis* Karsch 1878 appears most similar to behaviour seen in the fan dance of both *M. pavonis* and *M. splendens*.

Dunn's (1957) description of the courtship of his *M. pavonis* was most poetic, as he gave this species the common name of Peacock Spider (*pavo* is Latin for Peacock). Some of his account, at least, bears retelling in this context:

It is noteworthy that the attitude adopted by the male was such as to display to the best advantage the more highly decorated portions of his body. The gaudy upper surface of the abdomen, the white-fringed palps, the long-haired third pair of legs, all were displayed to the clear view of the female, while the vibrations tended to attract the most attention possible to their charm. The abdomen was particularly striking when rays of sunlight, caught from different angles, were reflected more vividly from the brilliant colouration, bringing to mind the glory of the peacock's tail. It was, however, the habit of raising the abdomen as well as the colouration that suggested the specific name for this spider.

It is generally accepted that these male behaviours release (*releasers*) or elicit specific responses of females (*agents of sexual selection*) that observe them, perhaps in a predictable sequence. However, meaningful study of this interaction must include more observation of the responses of females than was possible here. There are a number of published studies of salticid courtship since the Peckhams' (1889) early work. Richman (1982) suggested that comparative studies could be useful to systematics. Several recent studies (*e. g.*, Elias *et al.* 2006a, Lim *et al.* 2008) have looked directly at the impact of display by a male salticid on the tendency of the female to continue to observe, or to subsequently mate with, a male.

A tale of two species

William Joseph Rainbow was an Entomologist with the Australian Museum when his description of *Attus splendens* (Sydney, Australia) was published (Rainbow 1896, Appendix 1). The name that he chose for this spider, *Attus splendens*, is a junior primary homonym for the *Attus splendens* described earlier, in 1883 by George and Elizabeth Peckham (Peckham & Peckham 1883), subsequently moved (Peckham & Peckham 1888) to the genus *Habrocestum*, well before Rainbow's use of *splendens* as a species-group name. The Peckhams' *splendens* (1883–1888) is now called *Habronattus decorus* (Blackwall 1846). Simon (1901) placed Rainbow's *splendens* in the genus *Saitis*, describing the *ovale median d'un rouge mat* that comprises the distinctive pattern of the dorsal opisthosoma of this spider.

R. A. Dunn much later (1947) identified a new species from Victoria, *Saitis pavonis*, as distinct from *Saitis splendens*. Dunn's key accurately depicted differences between the two, but may have been based solely on Rainbow's published description of *splendens*, as no additional characteristics of this species were described. Dunn's "co-type" (syntype) in the Museum Victoria (Appendix 2) closely agrees with his description of *pavonis*. Apparently because he placed a great deal of weight on the size of the opisthosomal flaps, Dunn did not think the two species closely related. In fact, he thought that his *pavonis*, without large flaps, was more closely related to *Saitis speciosus* (Pickard-Cambridge 1874; see description in Hill 2009 and Appendix 3). Collections that preceded Dunn's description (Appendix 3) placed spiders fitting Dunn's description in Rainbow's *splendens*.

Later still, Roewer (1951) changed the name of Rainbow's spider to *Saitis rainbowi*, presumably because of the status of Rainbow's *splendens* as a junior primary homonym. Although several recent, on-line catalogs (Platnick 2011, Prószyński 2011) have followed Roewer's replacement species-group name *rainbowi*, Żabka (1991) retained Rainbow's original name when he moved both *pavonis* and *splendens* into the genus *Maratus* Karsch 1878. Żabka's use of the original species-group name, *splendens*, is now justified by Article 23.9.5 of the current (2000) ICZN, which prohibits *automatic* (without a Commission ruling) replacement of a junior primary homonym when the respective names are *not considered congeneric after 1899*.

Curiously, Żabka had previously (1987) separated the genera *Lycidas* Karsch 1878 and *Maratus* Karsch 1878 on the basis of the presence of opisthosomal flaps in the latter. If *M. pavonis* and *M. splendens* are in fact closely related (and we believe that they are), then, in the absence of other significant differences, this distinction between *Lycidas* and *Maratus* may not be warranted. Based on its earlier appearance in the same publication (Karsch 1878), *Lycidas* would have precedence over *Maratus* as a genus-group name. Males of the type species for *Lycidas* (*L. anomalus* Karsch 1878, a single male specimen redescribed by Żabka 1987) have a dorsal opisthosomal plate and may represent one of the spiders that found by one of us (Jürgen Otto) in Sydney, the type locality (Hill 2009, Figures 28–29). There may be many related Australian euophryine salticids without dorsal plates or flaps that have never been described, and the relationship of these to the European *Saitis barbipes* (Simon 1868), the type for *Saitis* Simon 1876, should also be reexamined in a more comprehensive review of the Australasian euophryines, particularly those with long legs III that could be considered part of a "*Saitis* Group."

Maratus pavonis and *M. splendens* appear to be closely related, but there are also consistent differences that allow one to identify these as separate taxonomic species. Although Dunn's specimen of *M. pavonis* in the Museum Victoria (Appendix 2) does not have significant opisthosomal flaps, other spiders that agree with *M. pavonis* in most other characters may indeed have these flaps or lateral extensions to a variable extent, or at least a dorsal plate that can be folded around the lateral sides of the opisthosoma and then flattened as it is elevated for display (Waldock 1993, 2007, Bokhari 2009, Cam 2009c, Appendix 3). Morphologically, lateral flaps may simply represent the lateral edges of a larger variety of dorsal plate that can be folded around the opisthosoma. Although all of the *M. splendens* described here had these flaps,

none had flaps anywhere near as large as those described and figured by Rainbow (1896; see Appendix 1). It is noteworthy that *M. splendens* has only been found in the vicinity of Sydney, Australia, whereas *M. pavonis* is known from many localities ranging from Western Australia to the southernmost reaches of Tasmania. It is beyond the scope of the present study to determine whether or not the two should be considered representatives of separate *biological species*, and more extensive collections, studies of genitalic morphology, or detailed gene-sequencing studies may be able to shed some light on the actual relationship between the two groups and their geographical forms or potential for hybridization.

It is possible that future studies will reveal a more complex relationship that defies our simple concept of biological species. Geographic variation in both appearance and display behaviour of male *Habronattus pugillis* Griswold 1987 has been studied more extensively than that of any other salticid, and the emerging picture of geographic variation in this nominal species, particularly in the males, is complex (Masta 2000, Maddison and McMahon 2000, Masta and Maddison 2002, Hebets and Maddison 2005, Elias *et al.* 2006c). Hedin and Lowder (2009), in a phylogeographic study of three closely related *Habronattus* species, found that it was difficult to establish the monophyly of nominal species, apparently because of hybridization and gene introgression between species.

Acknowledgments

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This paper is respectfully dedicated to R. A. Dunn, formerly Honorary Arachnologist at the National Museum of Victoria (now the Museum Victoria), and his poetic vision of the *Peacock Spider*.

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<http://www.flickr.com/photos/wildernesscam/3970067458/>
- Cam. 2009b.** Male coastal peacock jumping spider courtship display.
<http://www.flickr.com/photos/wildernesscam/3955630036/>
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Appendix 1 — Original description of *Attus splendens* by W. J. Rainbow

Rainbow, W. J. 1896. Descriptions of some new Araneidae of New South Wales. No. 7. Proceedings of the Linnean Society of New South Wales 21: 628–633.

p. 628

DESCRIPTIONS OF SOME NEW ARANEIDAE OF NEW SOUTH WALES. No. 7.

By W. J. Rainbow
(Entomologist to the Australian Museum)

(Plate XLIX., figs. 1, 2, 3, 3a)

The present paper contains descriptions of three species new to science, and which, taken collectively, must form a valuable addition to our knowledge of the Araneidan fauna of this continent. ... The most important of the present series, however, is a new species of "flying" spider, for which I propose the name *Attus splendens*. In 1874 the Rev. O. P. Cambridge, F.Z.S., described and figured in "Annals and Magazine of Natural History,"* an Attid for which he proposed the name *A. volans*. From that singular spider the one now described, although possessing a remarkable affinity, is nevertheless sufficiently distinct to warrant the creation of a new species. Each is beautifully coloured, but the scheme of ornamentation is widely different. In *A. volans* the caput is ornamented with three longitudinal bars of soft greyish-green and two of scarlet, whereas *A. splendens* has a curved transverse bar of scarlet but no longitudinal bands; then again the scheme of ornamentation on the abdomen of each is also different. But the chief reasons for describing this species, and which must have the weightiest considerations in such cases, are to

* Vol. xiv. 4th Series, pp. 178-180, Plate xvii, figs 4-4d.

p.629

be found in the fact that not only are the copulatory organs somewhat more complicated than in *A. volans*, but the legs of *A. splendens* are more numerously spined. When immersed in spirit the bright colours entirely disappear, but upon being withdrawn from the tube, and exposed to the atmosphere, the spider soon redisplay its gorgeous livery. ...

p. 632

Family SALTICIDAE
Genus *Attus*, Sim.
Attus splendens, sp. nov.
(Plate XLIX. figs 3, 3a.)

♂. Cephalothorax 2 ½ mm. long, 2 mm. broad; abdomen 2 ½ mm. long, 2 mm. broad.

Cephalothorax steel-blue, broad, glossy. *Caput* steel-blue banded across the front with a broad curved bar of bright scarlet granules and scale-like hairs, the curvature directed forwards; in front, and surrounding the anterior row of eyes, there is a brush of short tawny hairs. *Clypeus* broad, high, rather flat, narrowest at its posterior extremity; at the junction of the cephalic and thoracic segments there is a broad but somewhat shallow depression, surrounded by a series of four white tufts or hairy brushes, the outer margins of which are surrounded with tawny hairs; sides steel-blue moderately clothed with tawny hairs.

Marginal band fringed with hoary pubescence.

Eyes arranged in three rows, and nearly forming a square, those of the front row of a bright emerald green; of these the two median eyes are sensibly the largest; the two comprising the second row are much the smallest of the group and are also of a bright emerald green; the third row are somewhat smaller than the lateral eyes of the anterior series, and are of an opaline tint.

Legs moderately long and strong, yellow-brown, clothed with hoary hairs, and armed with short stout spines; relative lengths 3, 4, 2, 1.

Palpi concolorous, short; radial joints rather longer than cubital, thickly clothed with long white hairs on the upper surface, and very sparingly clothed with exceedingly short white hairs on the under side; copulatory organ a large, oblong corneous lobe hollowed on the under side and rather complicated.

p. 633

Falces dark brown, conical, divergent at apex, seated well back behind the frontal margin.

Maxillae, labium, and sternum concolorous.

Abdomen oblong, narrowest in front, slightly overhanging base of cephalothorax, truncated at posterior extremity; upper side furnished (as in *A. volans*, Camb.) with an epidermis, which is continued laterally on either side to an extent considerably exceeding the width of the abdomen, and of an elliptical form; the outer portion of this epidermis on either side is capable of being depressed and folded round beneath the abdomen, or elevated and expanded to its full width after the manner of wings. The whole of the epidermis is densely covered with short and scale-like hairs, which give the different tints and hues to the abdomen; in the front and at the sides the colour is bright green; upon the upper surface there is a large oval ring of scarlet, the inner margins of which are bordered with bright green granules; in the centre there is a large patch of reddish-grey, surrounding a smaller and somewhat oval patch of scarlet; immediately below posterior margin of the scarlet oval ring there is a short, broad transverse patch covered with green granules, and fringed sparingly at ultimate extremity with scarlet scale-like hairs; lateral flaps furnished with bright green granules and scale-like hairs, becoming less brilliant towards their ultimate extremities; under side of a greenish grey colour, thickly clothed with short scale-like hairs.

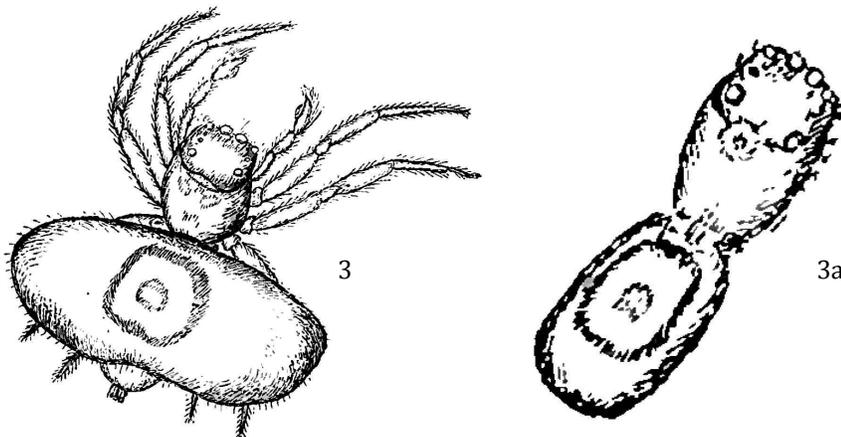
Hab.—Sydney.

EXPLANATION OF PLATE.

Fig. 3 — *Attus splendens* ♂.

Fig. 3a — “ “ showing epidermis folded under.

Plate XLIX. figs 3, 3a



Appendix 2 – Dunn's syntype of a male *Maratus pavonis* from the Museum Victoria

Dunn, R. A. 1947. A new salticid spider from Victoria. *Memoirs of the National Museum of Victoria* 15: 82–85.

Dunn (1947) reported that “A co-type has been lodged with the National Museum, Melbourne.” These photographs of that specimen (a syntype) were furnished by the Museum Victoria. This small (4 mm) specimen is in very good condition, in part because it was supported carefully on a small pin. As a result, all of the scalation characteristic of *Maratus pavonis* (Dunn 1947), including the broad band of cream to tan-coloured scales on the antero-dorsal opisthosoma, is still intact. Close examination of image (1) will reveal the presence of small, folded lateral opisthosomal flaps, although these could represent an artifact of shrinkage in ethanol. This was the only specimen that Dunn submitted to a museum at the time that he gave the name *Saitis pavonis* to this spider, although he placed 6 other specimens, also collected in a suburb of Melbourne, Victoria, in private collections.



Appendix 3 – Report on historic collections of Australian *Maratus* or *Saitis* from the Museum of Comparative Zoology (MCZ) at Harvard University

Based on a report by Jerzy Prószyński (1971, p. 466) that the Peckham Collection at the Milwaukee Public Museum contained a *Saitis splendens* (Rainbow 1896), we were able to track down this collection of related Australian spiders at the Museum of Comparative Zoology (MCZ) at Harvard University, the current repository for the Peckham Collection. This was part of our search for specimens of *Maratus splendens* (Rainbow 1896), but we were unable to find any specimens that agreed definitively with the description of that species, particularly with respect to the crescent band of blue iridescent scales between and in front of the PLE. On the other hand, there was considerable variation in the degree of development of the lateral extensions of flaps associated with the dorsal opisthosomal plate, and the elongation of that plate, for spiders that could otherwise be identified as *M. pavonis*. Many of the specimens listed here were collected at a later date, and are in noticeably better condition as a result. The older specimens of the Peckhams are in relatively poor condition, missing many setae or scales that could be of importance in their positive identification. A brief description, including a new classification (**bold**), of each of 14 lots of specimens is listed here, according to MCZ specimen or accession number.

MCZ 101157 ***Maratus pavonis*** (Dunn 1947)

6♂, 2♀

Collector: Rainbow

Label: *Maratus (Saitis) splendens (rainbowi)* Rainbow

Peckham Collection

Australia: Victoria: Murray River, near Kerang

These are fairly “typical” *M. pavonis*, and the white mid-line stripe of the postero-dorsal carapace is visible in at least 2 of the males. Some appear to have the thicker band of tan scales on the anterior margin of the opisthosoma. If Rainbow was indeed the collector, as the label suggests, then he, as well as the Peckhams, must have considered spiders now associated with Dunn's *pavonis* to be *splendens*.



MCZ 101158 *Maratus pavonis* (Dunn 1947)

6♂

Collector: Rainbow

Label: *Maratus (Saitis) splendens (rainbowi)* Rainbow

Peckham Collection

Australia: Victoria: Murray River, near Kerang

These males appear to have a more ovoid opisthosoma, but generally no significant flaps.

**MCZ 101159** *Maratus pavonis* (Dunn 1947)

1♂

Label: *Maratus (Saitis) splendens (rainbowi)* Rainbow

Peckham Collection

Australia: New South Wales: Sydney

This single specimen is from Sydney, and all specimens of *M. splendens* that are known are from that area. It also has a relatively wide opisthosomal plate, although this does not appear to separate this from other *M. pavonis*. It has the scale field of the ocular quadrangle that is characteristic of *M. pavonis*, and the anterior border of the crescent of iridescent blue scales in front of the posterior lateral eye (PLE) of *M. splendens* is not present.



MCZ 101160 *Maratus pavonis* (Dunn 1947)

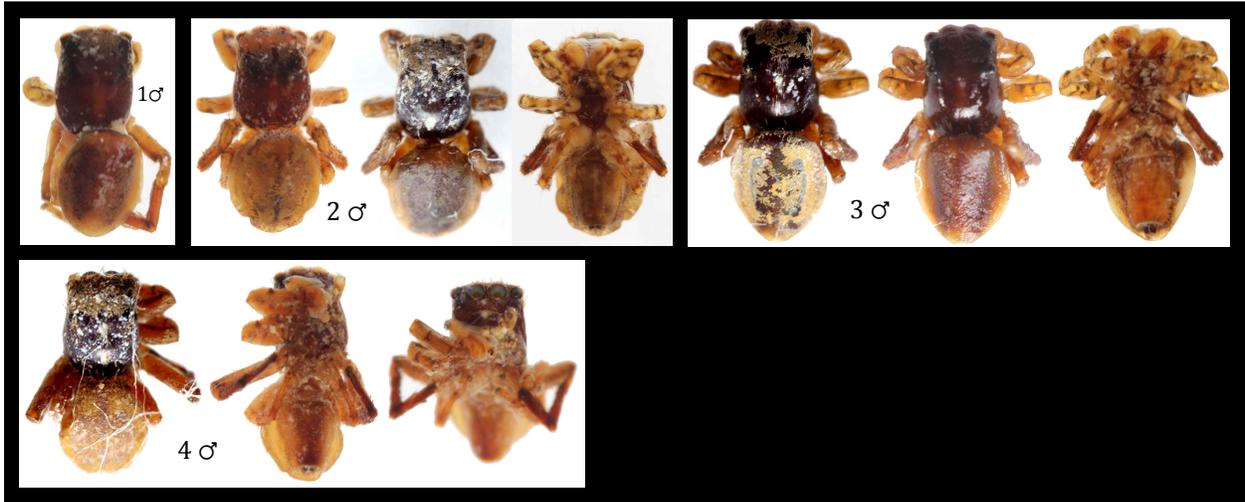
4♂

Label: *Maratus (Saitis) splendens (rainbowi)* Rainbow

Peckham Collection

Australia: Victoria: Melbourne

This lot of males, from the type locality of *M. pavonis*, is characterized by fairly wide opisthosomal plates that in at least one case could be considered to have lateral “flaps.” At the same time, several have scales of the definitive white mid-line stripe of the posterior carapace, the wider anterior marginal band of tan scales on the opisthosoma, and also the uniform field of scales in the area of the ocular quadrangle.

**MCZ 101161** *Maratus pavonis* (Dunn 1947)

2♂

Label: *Maratus splendens* Rainbow, *Habrocestum opalescens*

Peckham Collection

Australia: Victoria: Melbourne

These specimens from the Peckham Collection appear to solve the mystery of “whatever happened to the *Habrocestum opalescens*, nov. sp. listed (but not described) in Hogg’s (1900) paper on the spiders of Victoria (p. 77)?” Hogg (1900, p. 70) wrote: *I am not, however, publishing descriptions of any new Saltigrade spiders, as we are awaiting fresh classifications of this group, the Attidae, from M. Eugene Simon, in France, and Dr. and Mrs. Peckham, in America, who have been engaged on them for some time past.* If Hogg had provided a description of his new species from Victoria, we could now be calling this spider *M. opalescens* (Hogg 1900). These are typical *M. pavonis*. One still has a few remaining scales of the white mid-line carapacial line.



MCZ 101290 *Saitis speciosus* O. Pickard-Cambridge 1874

3♂, 5♀

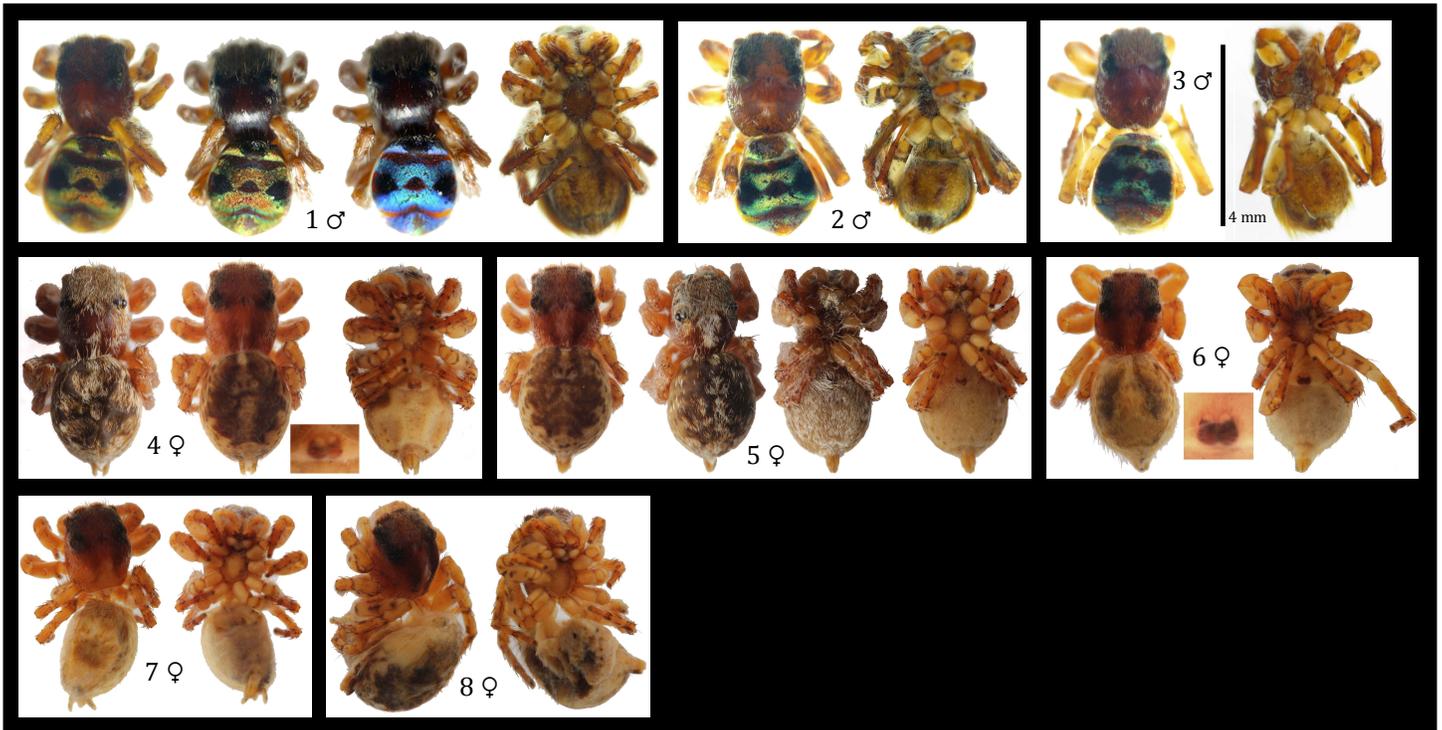
Collector: W. M. Wheeler, 22 OCT 1931

Label: *Maratus (Saitis) volans*, cf.

Rottnest Island Expedition: Harvard Australian Expedition

Australia: Western Australia

One of us (Hill 2009) recently republished the original description of this relatively well-known Australian spider. O. Pickard-Cambridge (1874) reported this spider from 'the Swan River, New South Wales,' but the Swan River actually flows through the city of Perth, Western Australia, and it is likely that his specimen was from that area. The colours reported by O. Pickard-Cambridge (1874, *scarlet maroon and brilliant emerald green*) accurately reflect those of specimens in alcohol, but surface drying (1, third view) is necessary to bring out the brilliant blue and orange colours of the scales. Cam (2009a, 2009b) described the courtship of this "Coastal Peacock Spider," which is very close to that of *Maratus*, and there is much opinion that it should be included in that genus. Žabka (1991, Fot. 21, p. 23, photograph by D. Knowles) actually called this spider a *Maratus*, but did not formally rename it. In fact, he listed *Saitis speciosus* as *incertae sedis* in the same paper (p. 64, entry 303).



Here we include, for comparison, a recent photograph of this distinctive spider from the coastal dunes of Western Australia © by Ron K. Kinsey (used with permission). In Western Australia, this spider is known as the Coastal Peacock Spider. It (~4.5–5 mm) is rather larger than *M. pavonis*. The females appear to bear a "death's head" symbol on the dorsal opisthosoma.



MCZ 101291 *Maratus volans* (O. Pickard-Cambridge 1874)

1♂

Label: *Maratus (Saitis) volans*

Peckham Collection

Australia: New South Wales: Sydney

This specimen, in very poor condition, represents the best known *Maratus* from the locality where it is best known.

**MCZ 101292** *Saitis speciosus* O. Pickard-Cambridge 1874 (and one unknown species)

3♂, 4♀

Collector: P. J. Darlington, 9 OCT 1931

Label: *Maratus (Saitis) sp.*

Geraldton Expedition: Harvard Australian Expedition

Australia: Western Australia

This is another lot of the Coastal Peacock Spiders. Specimens (1–6) can be readily identified as *S. speciosus*, but (7) is quite different. The smaller size (the *S. speciosus* are ~4.5 to 5.0 mm), the shape of the epigynum, and the tapering (not curved) posterior margins of the carapace all mark this as an unrelated salticid in this group.



MCZ 101293 *Maratus pavonis* (Dunn 1947)

1♂

Collector: P. J. Darlington, 10 NOV 1931

Label: *Maratus (Saitis) volans*, cf.

Pemberton Expedition: Harvard Australian Expedition

Australia: Western Australia

This is a very typical *M. pavonis* by all appearances (including scales of ocular quadrangle, anterior marginal scales of opisthosoma), but has a very wide dorsal opisthosomal plate nonetheless. Dunn (1947) did not provide a very good illustration of the pedipalps of this spider, so the several views given here may be of use.

**MCZ 101294** *Maratus amabilis* Karsch 1878

1♂

Collector: W. M. Wheeler, 23 DEC 1931

Label: *Maratus (Saitis) volans*, cf.

Harvard Australian Expedition

Australia: New South Wales: Wentworth Falls, 2800 ft.

This is Karsch's (1878) type species for the genus, *Maratus amabilis*, from the Blue Mountains on the outskirts of Sydney where the specimen that Karsch described was originally collected, and more recently rediscovered (Otto and Hill 2010).



MCZ 101295 *Maratus* sp. (“Darlington's Peacock Spider”)

1♂

Collector: P. J. Darlington, 10 NOV 1931

Label: *Maratus (Saitis) volans*, cf.

Pemberton Expedition: Harvard Australian Expedition

Australia: Western Australia

This apparently unnamed spider was figured and attributed to *Maratus*, but not given a specific name, by Žabka (1991, Fot. 20, p. 23, photograph by D. Knowles). Since P. J. Darlington collected this specimen as well as MCZ 101302 (below), we would like to honor him here with the common name of “Darlington's Peacock Spider.” Dr. Philip Jackson Darlington Jr. (14 NOV 1904–16 DEC 1983) was one of the great naturalist-explorers of the 20th Century.



We include a recent photograph of this spider from Western Australia © V. W. Framenau (used with permission). Like *M. amabilis*, this spider has a large dark spot at the center of each lateral flap (not shown in this photograph, as the flaps are folded). It is unfortunate that such a readily-identified spider has gone without a formal name for 20 years after Marek Žabka first figured it!



MCZ 101296

***Saitis speciosus* O. Pickard-Cambridge 1874**

1 ♀

Collector: P. J. Darlington, 24 OCT 1931

Label: *Maratus (Saitis)* sp.

Rottnest Island Expedition: Harvard Australian Expedition

Australia: Western Australia

This is a single adult female in very good condition. As in previously figured specimens, the epigynum is simple but easy to observe here, and the dorsal scalation of the opisthosoma is distinctive.



MCZ 101302

***Maratus* sp. ("Darlington's Peacock Spider")**

1 ♂

Collector: P. J. Darlington, OCT 1931

Label: *Maratus (Saitis) volans*, cf.

Margaret River Expedition: Harvard Australian Expedition

Australia: Western Australia

This is the same species as MCZ 101295. The black spots on the large flaps can be seen clearly here. As with *S. speciosus*, the surface of a specimen must be dried to observe the true colour:



MCZ 101304 *Maratus pavonis* (Dunn 1947)

1♂

Collector: P. J. Darlington, 20 OCT 1931

Label: *Maratus (Saitis) volans*, cf.

Harvard Australian Expedition

Australia: Western Australia: Penha

This is another one of the Western Australian *M. pavonis* that appears to have small flaps. One wonders whether these would still be apparent if the spider had recently fed.

