

Courtship display by a peacock spider, *Maratus constellatus* (Araneae: Salticidae: Euophryini: Australphryni)

David E. Hill¹ and Jürgen C. Otto²

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

² 19 Grevillea Avenue, St. Ives, New South Wales 2075, Australia, *email* jurgenotto8@gmail.com

Maratus constellatus Schubert 2020 was recently described from two males collected in the arid scrubland of Kalbarri National Park in Western Australia (Schubert 2020). Based on the presence of lateral opisthosomal flaps, this spider was initially associated with *M. harrisi* Otto & Hill 2011, in the *harrisi* group of the genus *Maratus*. However the apex of the embolus is of the same shape as that of other Western Australian spiders in the *flavus*, *mungaich* and *vespa* groups, and we have placed this spider in the *flavus* group with *M. flavus* Otto & Hill 2018, that it most closely resembles (Otto & Hill 2021). *M. constellatus* was not included in a recent study of peacock spider phylogeny (Girard et al. 2021).

Neither the courtship display of the male *M. constellatus*, nor the female, has been previously described. Here we provide a description of the male courtship display of this species, and we document the appearance of females and juveniles, based on spiders collected at the type locality, or reared from the eggs of those spiders, and subsequently reared to maturity in the laboratory.

The only known locality for *Maratus constellatus* is geographically removed from the range of all other members of the *flavus* group, all endemic to the southwestern corner of Western Australia. Males share many features with other *Maratus*, but bear a very distinctive pattern of scales on the dorsal opisthosomal plate (fan), evocative of a starry sky (Figure 1). When the opisthosoma is raised during courtship display, a short flap on either side of the fan, normally folded around the side of the opisthosoma (Figure 1.3), is extended.

Courtship display. Display by male *M. constellatus* can be separated into three different stages which will be described below: 1) *single leg wave* with a single extended leg III, 2) a side-to-side *fan dance* with the fan elevated as one extended leg III (the leading leg) is waved, and 3) *semaphore signalling* in place, with both legs III extended and alternately raised and lowered in unison. When a male courts a female, the fan dance often alternates with semaphore signalling. In addition, the fan dance sometimes includes the extension of both legs III, and semaphore signalling sometimes includes elevation of the fan (Figure 2). The semaphore signalling in this species is similar to what we have previously described for both *M. flavus* and *M. boranup* Otto & Hill 2018; in fact the latter species does not appear use the fan at all (Otto & Hill 2018). These semaphore displays are bilaterally symmetric, unlike the unusual assymetric positions assumed by a courting male *M. speciosus* (O. Pickard-Cambridge 1874) (Hill & Otto 2014). As in other *Maratus*, females appear to display rejection of a male with their opisthosoma and legs III elevated. Our interpretation of the role of these displays is based on observation of video clips of males and courted females under simulated natural conditions in the laboratory.



Figure 1. Some external features of the adult male *Maratus constellatus*. Many characters (e.g., the triangular anal tuft and the thoracic tract of scales) are shared with a number of other *Maratus* species. Stripes in the eye region and ornamentation of leg III resemble corresponding characters of *M. flavus*. However males can be easily identified by the distinctive pattern of scales on the dorsal opisthosomal plate.



Figure 2. Three sequential photos showing a display that combined semaphore signalling with extended legs III (with no lateral movement), with the elevated body and fan of the fan dance.

Single leg wave. The male may extend and wave a single leg III, either when a female is distant, or cannot be seen (Figure 3). This may function to elicit a response by a female in the vicinity, allowing her to be found by the male. This can be viewed as a kind of advertisement by the male. Similar behavior has been observed in other *Maratus* species.



Figure 3. Single leg wave, with one leg extended, by two different male *Maratus constellatus*.

Fan dance. In many *Maratus* species, display of the elevated fan appears to represent the most important courtship display of the male, often closely observed in all of its details by the female. *M. constellatus* also has a distinct fan dance, but this display alternates with semaphore signalling, which may be more of a determinant in the success of the male.

During a fan dance (Figures 4-8) the fan is elevated with flaps extended as the male steps from side to side (right-to-left alternating with left-to-right) in front of a female. Only one leg III, the leading leg, is extended, and this is alternately flexed and then extended as the male makes one step to the side. As the leading leg is flexed, the fan tends to rotate by several degrees in a retrograde direction, then rotates back by several degrees in the direction of the step as the leading leg is extended. This represents a low-amplitude fan wave at same frequency as the steps. In the examples shown here (Figures 5-8) the rate of stepping (and left-right or right-left fan waves) varied from 5.0-8.3 Hz.

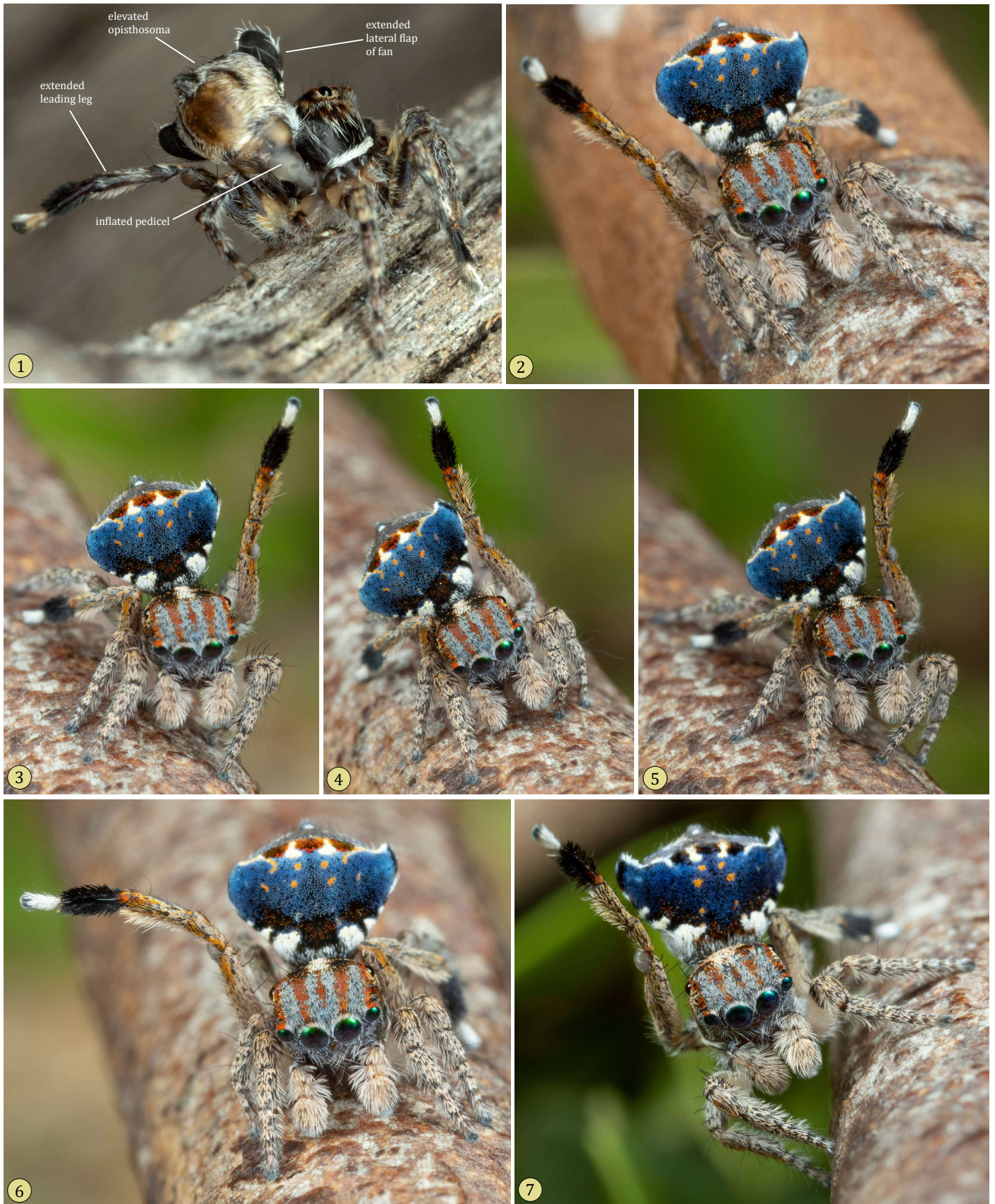


Figure 4. Fan dancing by male *Maratus constellatus*. During this display the fan is elevated with flaps extended as the spider steps from side to side in front of a female. While side-stepping, only the leading leg is alternately flexed (1, 5, 6), and then extended in a vertical position (2-4, 7).

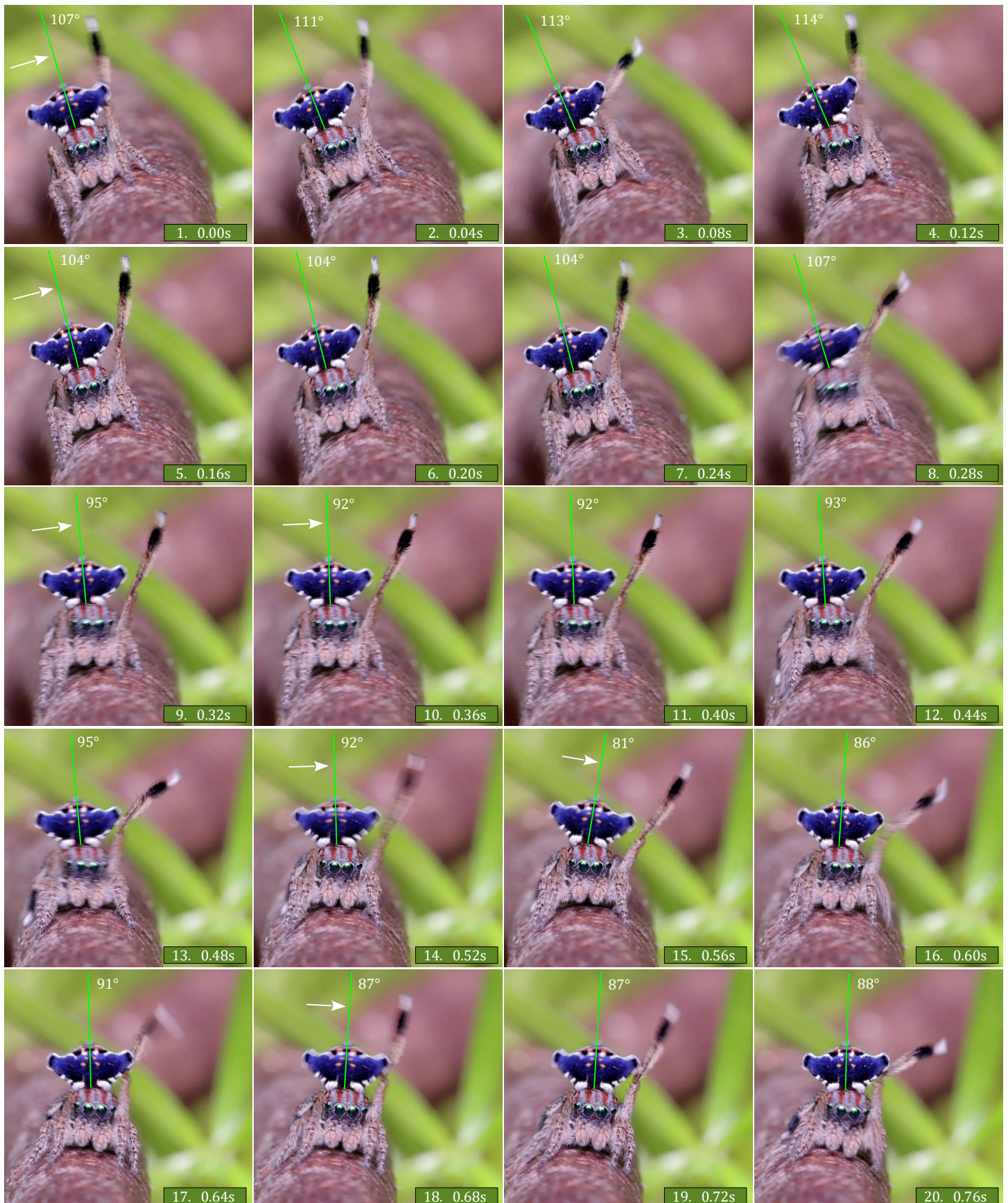


Figure 5 (continued on next page). Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (small steps accompanied by leading leg and low-amplitude fan wave at 6.7 Hz). Arrows indicate prograde (in the stepping direction) rotation of the fan relative to the previous frame. At other times fan rotation was slightly retrograde.

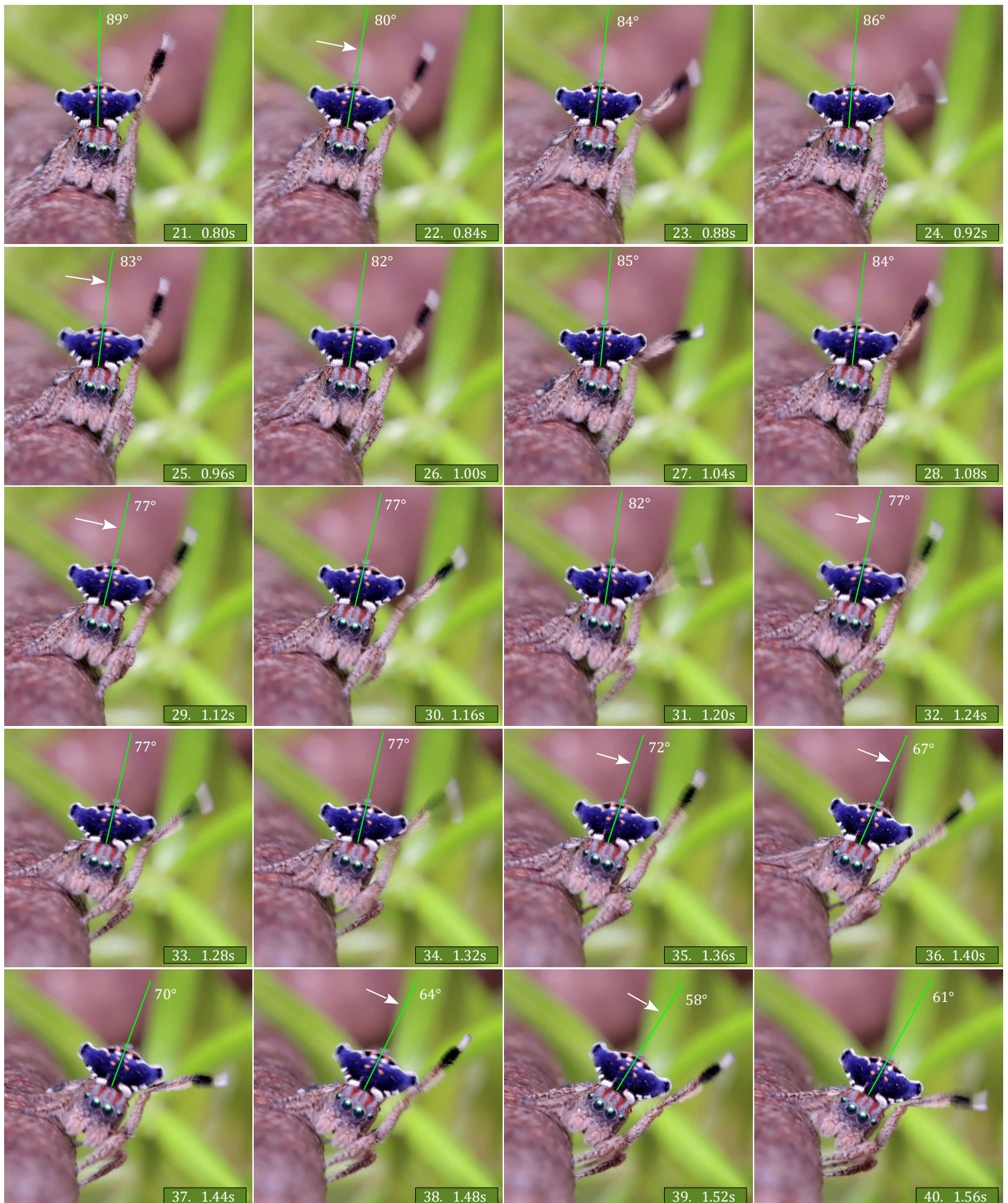


Figure 5 (continued from previous page). Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (small steps accompanied by leading leg and low-amplitude fan wave at 6.7 Hz).

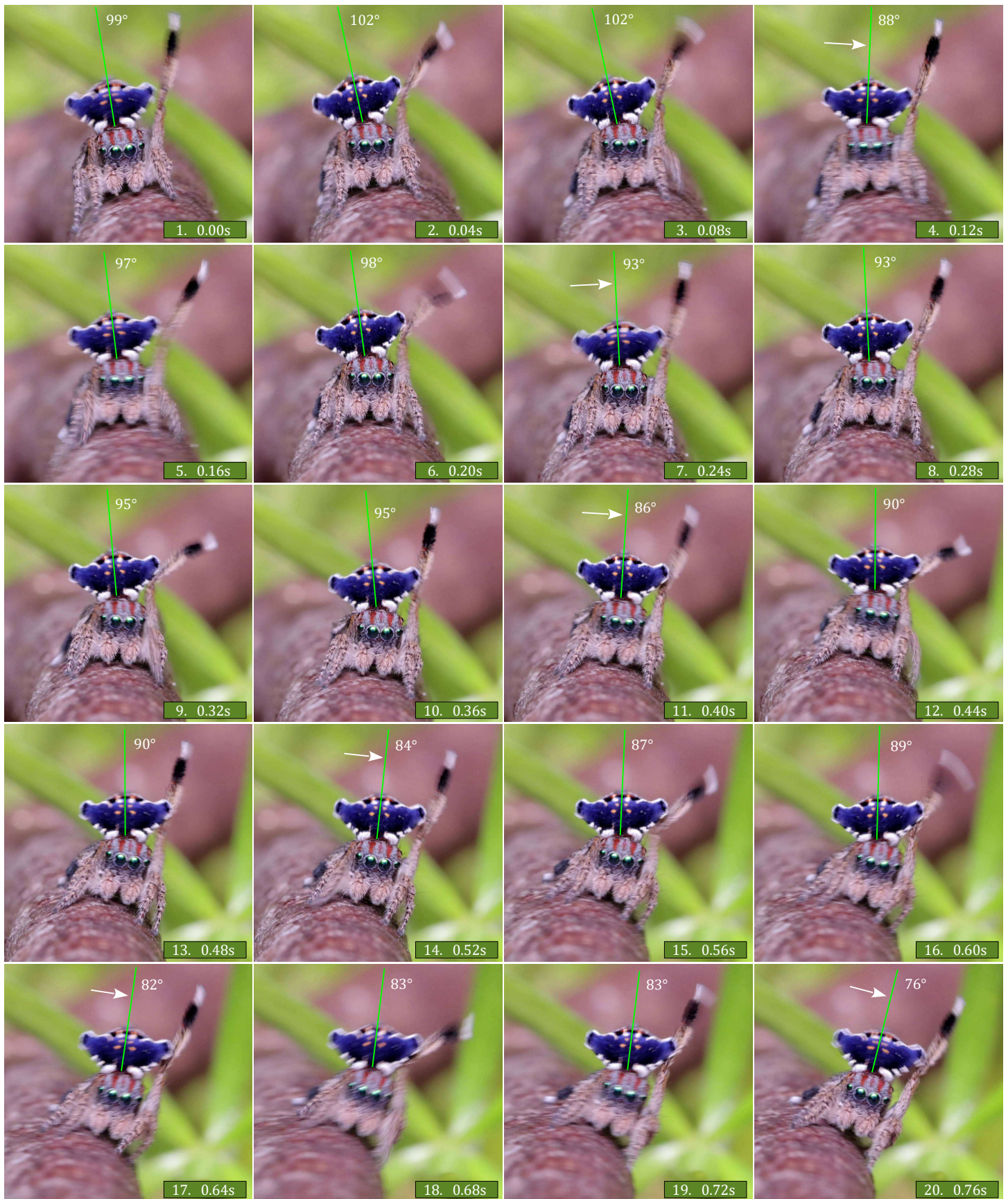


Figure 6 (continued on next page). Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (small steps accompanied by leading leg and low-amplitude fan wave at 8.3 Hz). Arrows indicate prograde (in the stepping direction) rotation of the fan relative to the previous frame. At other times fan rotation was slightly retrograde.

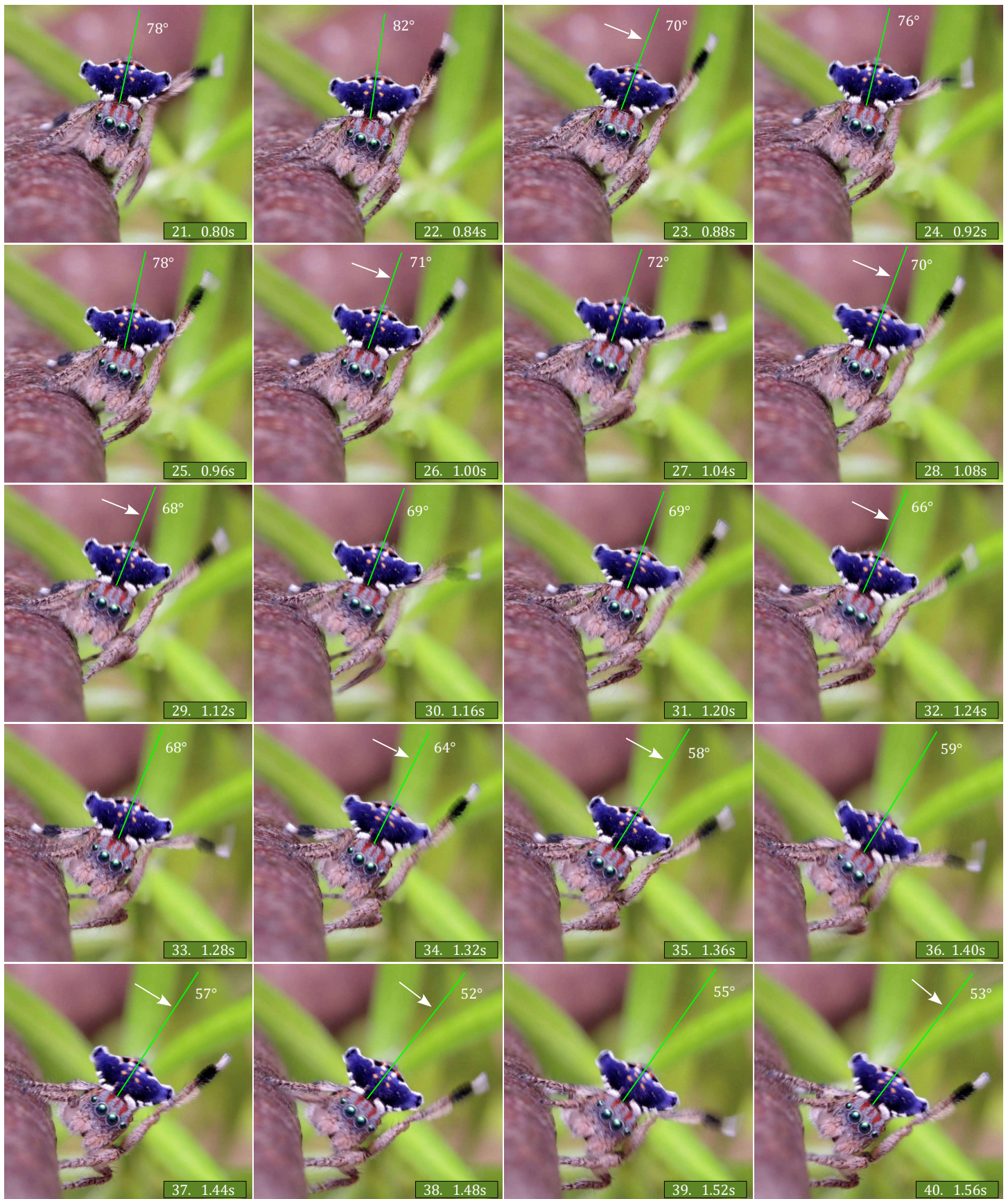


Figure 6 (continued from previous page). Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (small steps accompanied by leading leg and low-amplitude fan wave at 8.3 Hz).

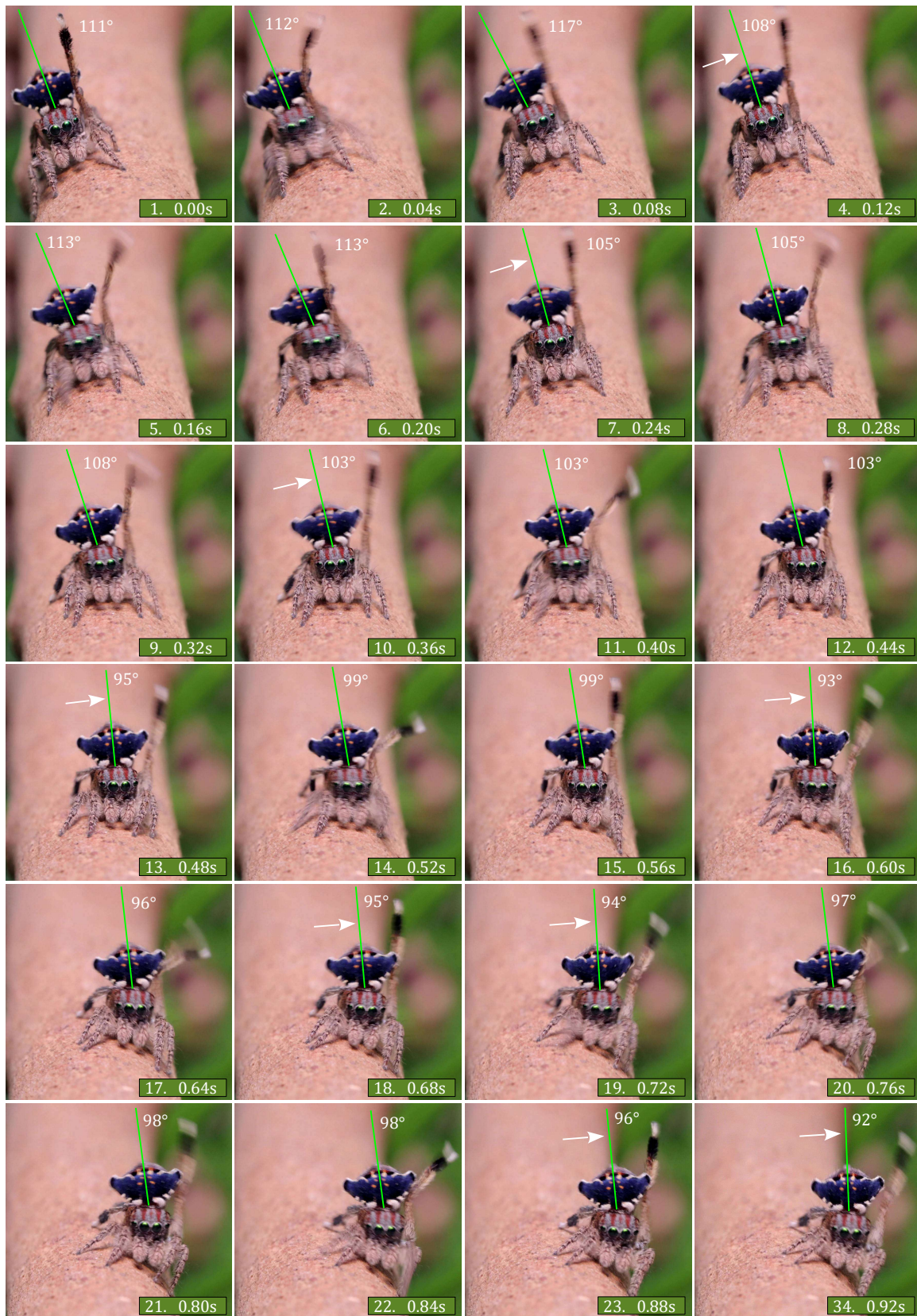


Figure 7. Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (small steps accompanied by leading leg and low-amplitude fan wave at 8.3 Hz). Arrows indicate prograde rotation of the fan (in the stepping direction) relative to the previous frame. At other times fan rotation was slightly retrograde.

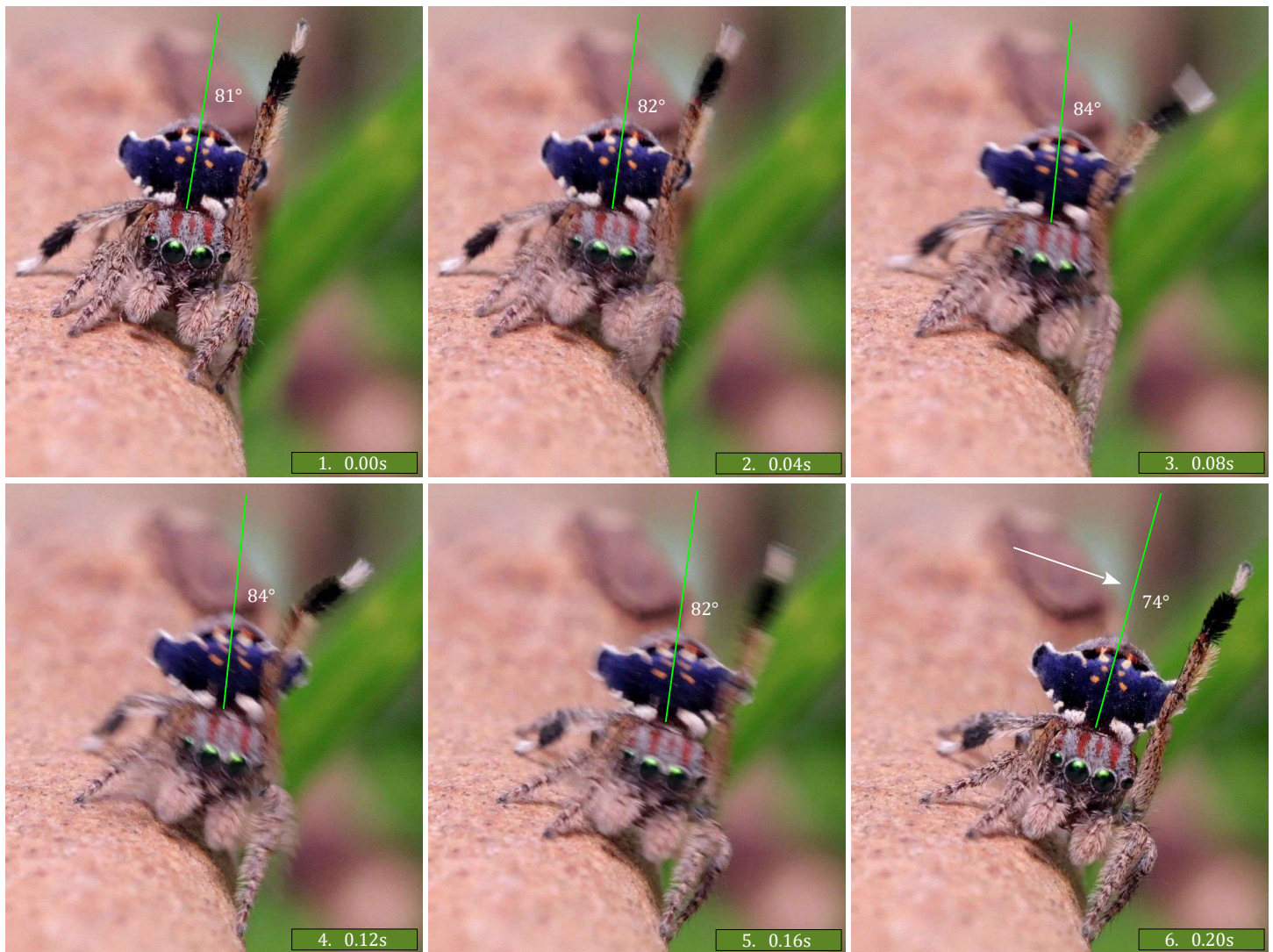


Figure 8. Sequential frames from a 25 fps video of a male *Maratus constellatus* fan dancing in front of a female (one small step accompanied by one leading leg and one low-amplitude fan wave at 5 Hz). Note the low-amplitude (3°) retrograde rotation of the fan as the leading leg was flexed (1-4), followed by 10° prograde rotation of the fan as the leading leg was straightened out to complete this step to the spider's left side. The higher magnitude prograde rotation was the result of the fact that this spider was stepping around the stem, and on a flat surface lower magnitude retrograde and prograde rotation of the fan during each wave should be comparable.

Semaphore signalling (Figures 9-11). Males produce a semaphore (flag) signal with both legs III extended in a vertical position, and then lowered symmetrically in a discontinuous series of steps to a horizontal, or even lower (if possible), position. The opisthosoma is lowered during this display, and the entire spider tends to assume a low position. From the low position these legs may be quickly elevated to a vertical position, to begin the next cycle of signalling. A single cycle of lowering legs III over a 3.2 s interval, followed by elevation in less than 0.04 s (in a single frame at 25 fps) is shown in Figure 10, and charted in Figure 11. When close to a female, a male may engage in semaphore signalling during pursuit from either the front or the rear. This display usually occurs *in place*, with no stepping, but it may also be interrupted as the spider moves quickly to a new position relative to the female.



Figure 9. Semaphore signalling with extended legs III. **1,** Approaching a female from the rear, as the female elevates legs III in a rejection display. **2,** Approaching a female from the front. **3-10,** Other positions assumed during this symmetrical display.

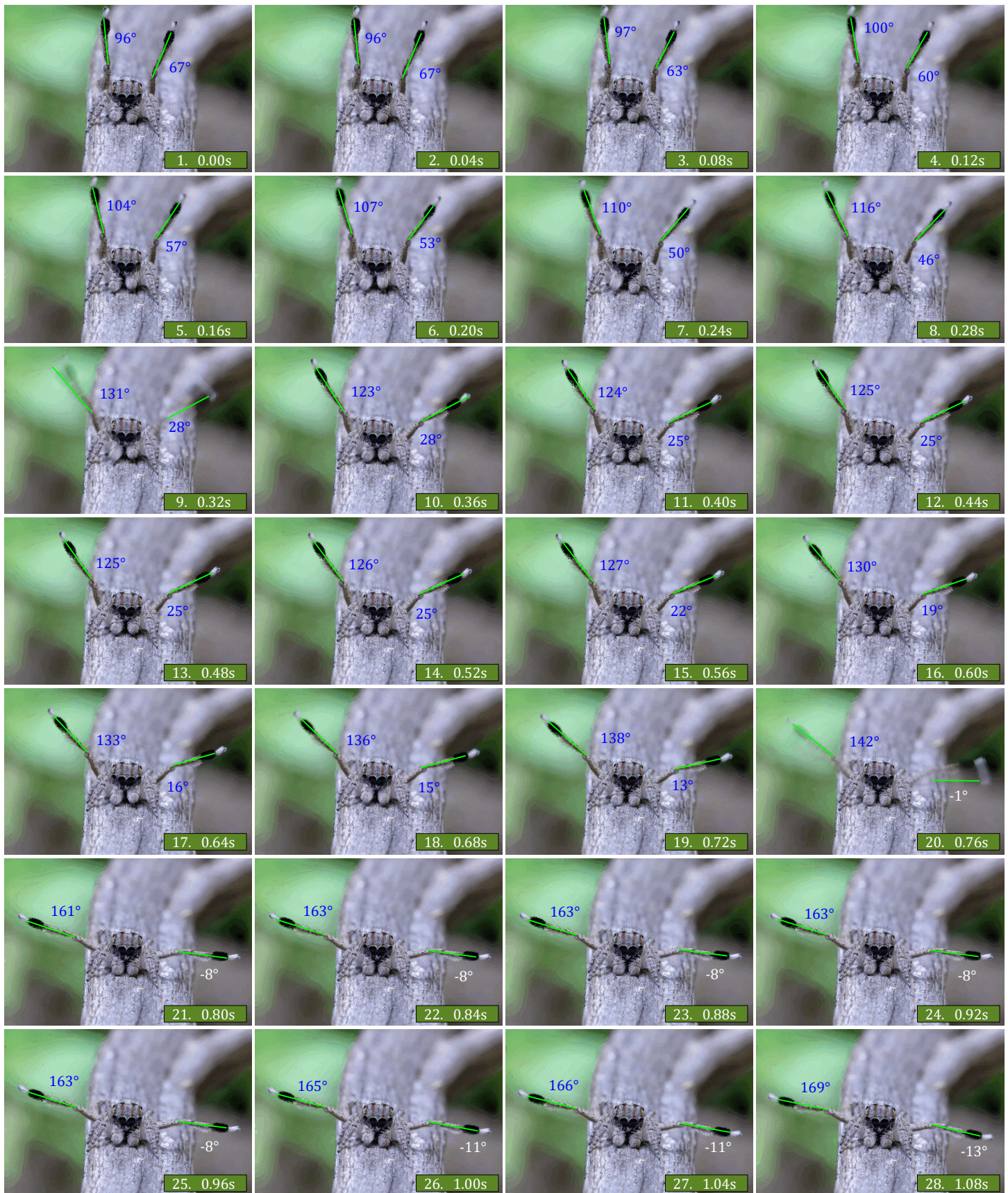


Figure 10 (continued on next page). Sequential frames (25 fps) from a semaphore display. Leg elevations above the horizontal are shown in blue, below the horizontal in white. Legs III were lowered in a series of steps over the first 3.2 s, then raised suddenly (frame 82). The entire sequence is charted in Figure 11.

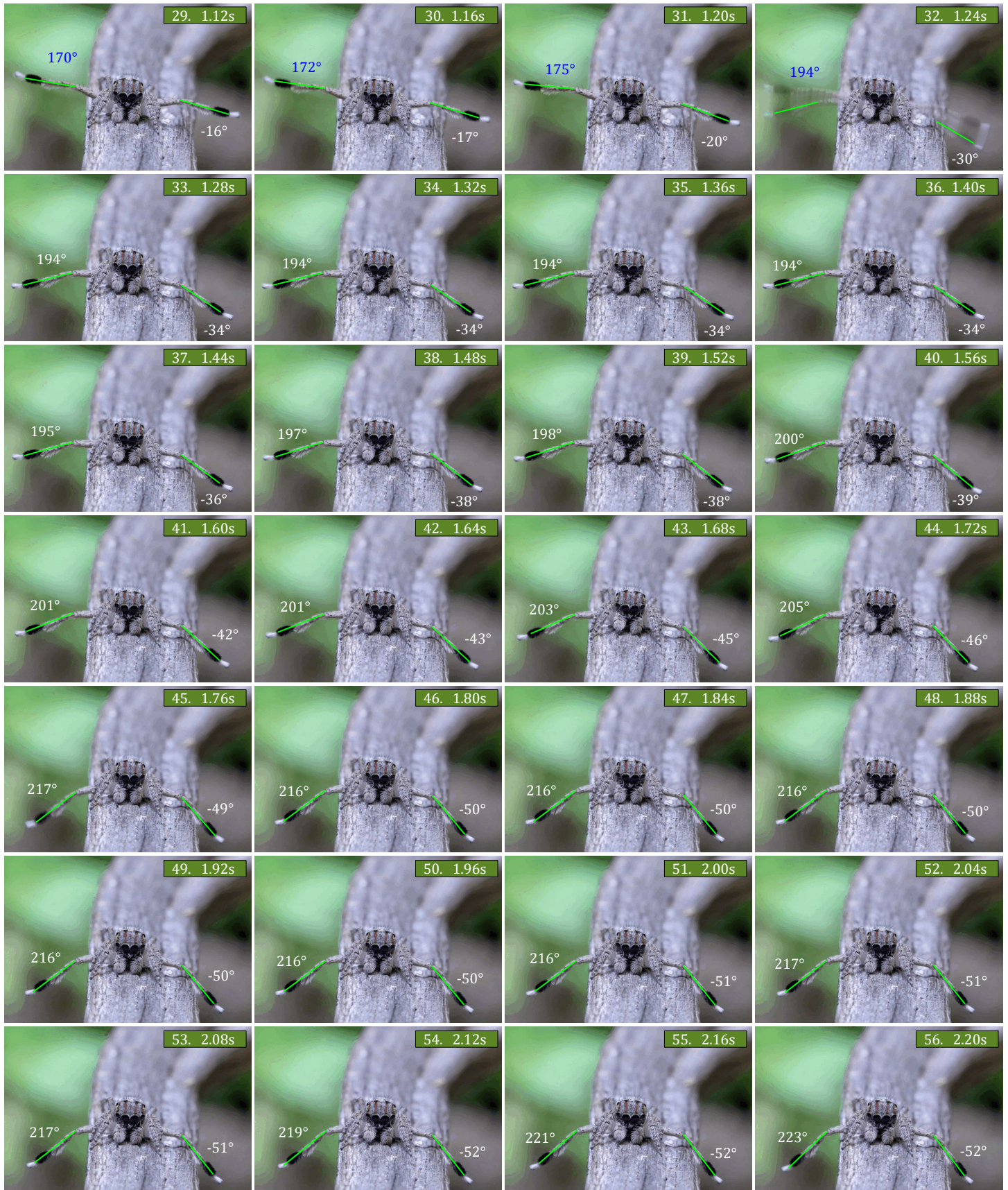


Figure 10 (continued from previous page, continued on next page). Sequential frames (25 fps) from a semaphore display.

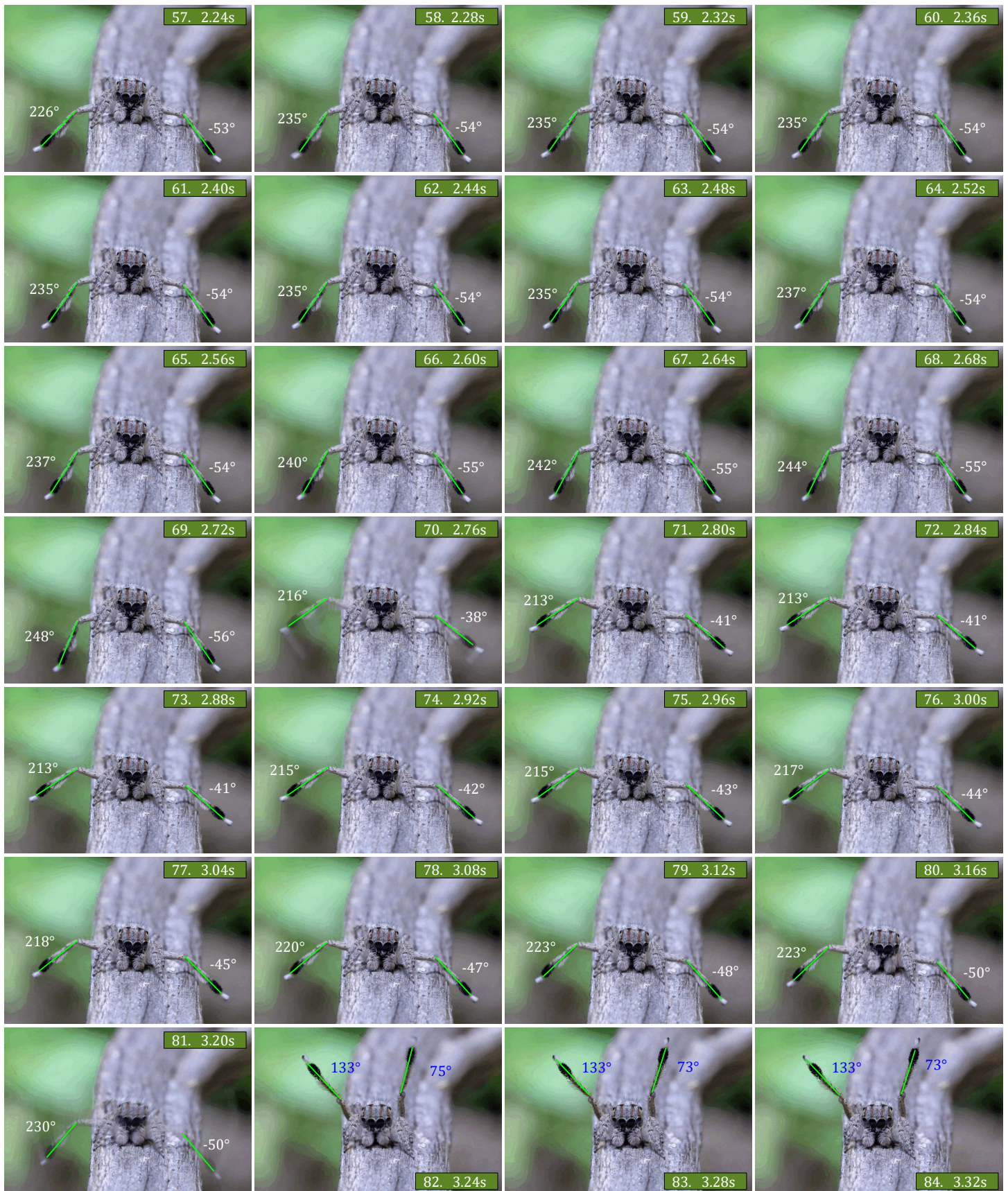


Figure 10 (continued from previous page). Sequential frames (25 fps) from a semaphore display. **Frame 82**, Note the sudden elevation of legs III.

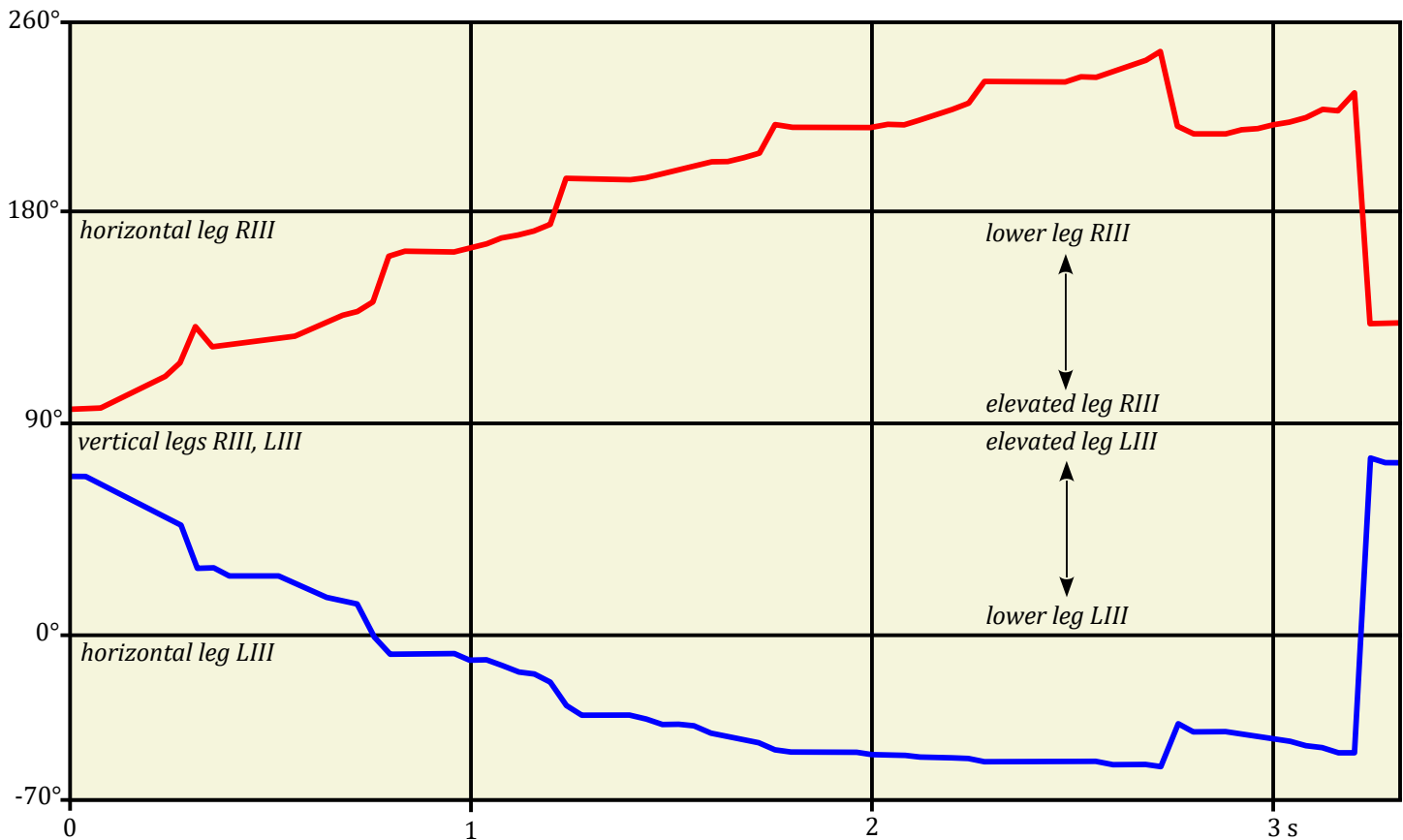


Figure 11. Charted elevation of legs III corresponding to frames shown in Figure 10. Note the symmetry of the discontinuous lowering of both legs over the first 3.2 s, followed by sudden elevation of both legs.

Courtship tactics. Our understanding of the *tactics* used by a male *Maratus constellatus* as he courts a female are limited by the fact that we have only observed a limited number of males and females, entirely in an artificial situation. Careful studies in the field might reveal many more details about this mating system, and it could reveal variation in the approach used by different males in a population. Field studies of behavior in the field are difficult, however, and they have their own limitations. In particular it is generally not possible to control complex events and situations in the field in order to determine that an individual behaves consistently.

From a study of extended interactions of males and females in the laboratory we can arrive at some preliminary conclusions about the male's use of his display repertoire. This requires the presence of a living, active female, as much of his behavior can only be interpreted with respect to the behavior of the female that he is courting. For many published studies of salticid courtship, only the displays of males in response to dead or immobilized females were studied (e.g., Elias et al. 2003, 2012, *Habronattus*; Girard et al. 2011, *Maratus volans*).

As shown in Figures 12-14, the fan dance appeared to be of more importance when the female was actively turning to follow the male. As in other salticids, side to side movement by the male probably allowed the male to determine when the female was no longer turning, a cue to advance. In this stage, the side-to-side fan dance could also alternate with semaphore display, at the end of each dance segment. In other cases, either close up as the male approached, or when the female turned away from the male, the semaphore display appeared to be more important. Finally the semaphore display continued as males attempted to mount females.



Figure 12 (continued on next page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. See also Figure 14 for interpretation of this sequence. **1-7**, Initially the male performed a fan dance, to either side of the female that turned to follow his movements. **8-16**, After the female stopped turning, the male transitioned to a semaphore display, initiated with legs III in a vertical position. During the transition to semaphore display (8) the fan and body of the male were lowered.

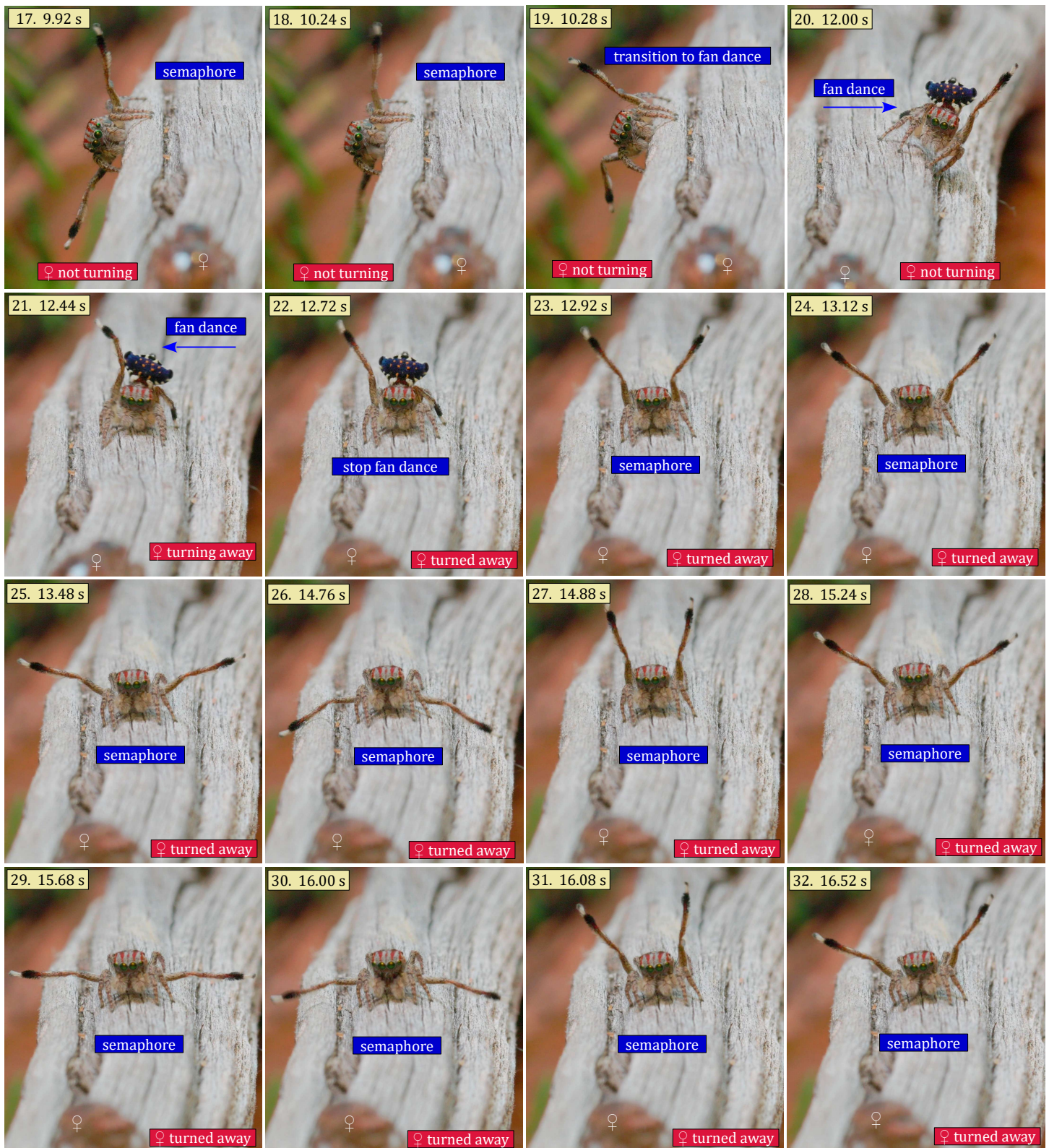


Figure 12 (continued from previous page, continued on next page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. **17-18**, Continuation of semaphore display (*semaphore signalling*). **19-21**, Perhaps in response to slight movement by the female, the male resumed the fan dance. **22-32**, After the female turned away, the male stopped the fan dance and began a semaphore display, still facing the female.

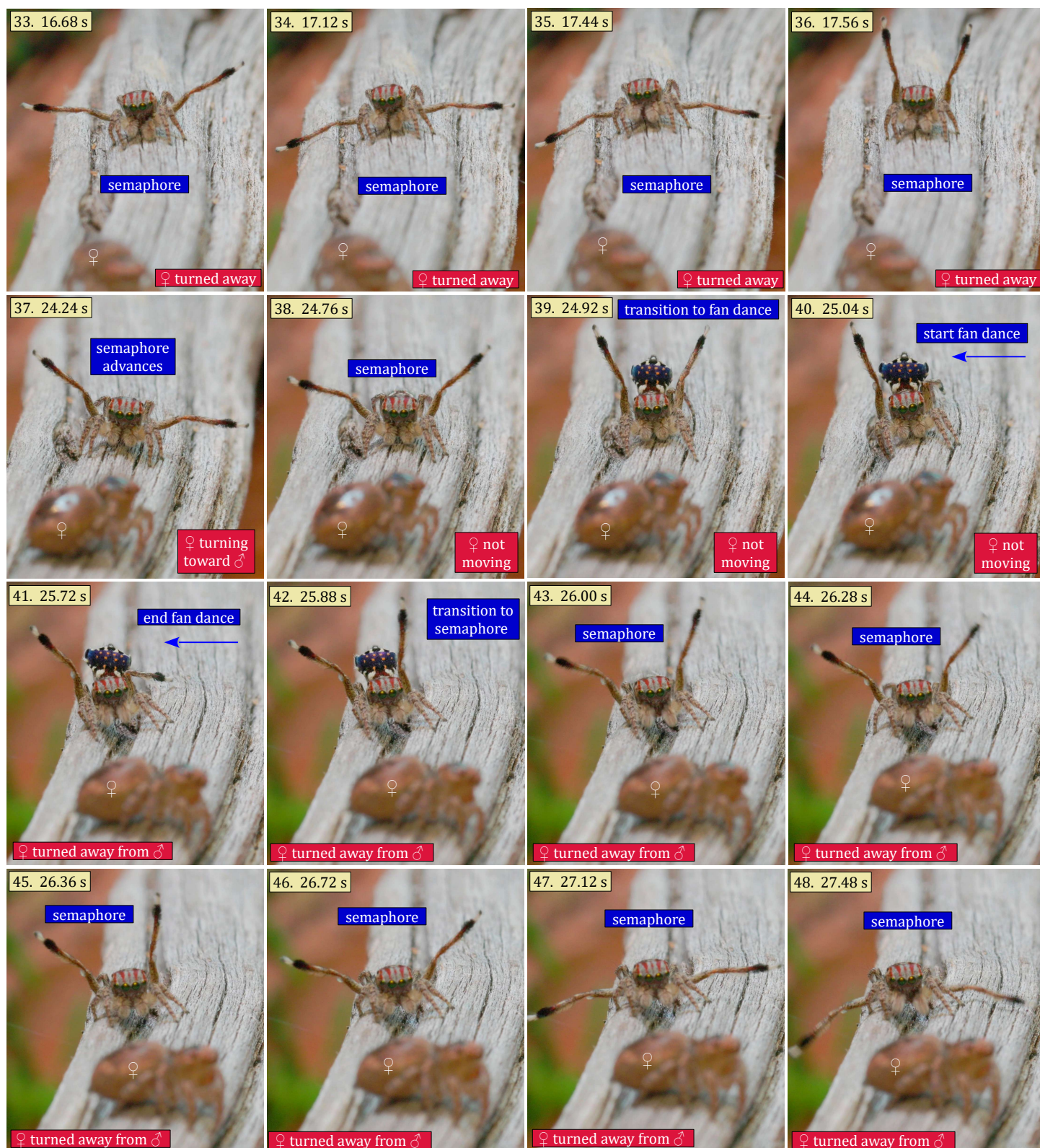


Figure 12 (continued from previous page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. **33-38**, Continuation of semaphore display. **39-41**, After the female turned back toward the male, the male resumed his fan dance. **41-48**, After the female turned further away from the male, the male once again began his semaphore display.

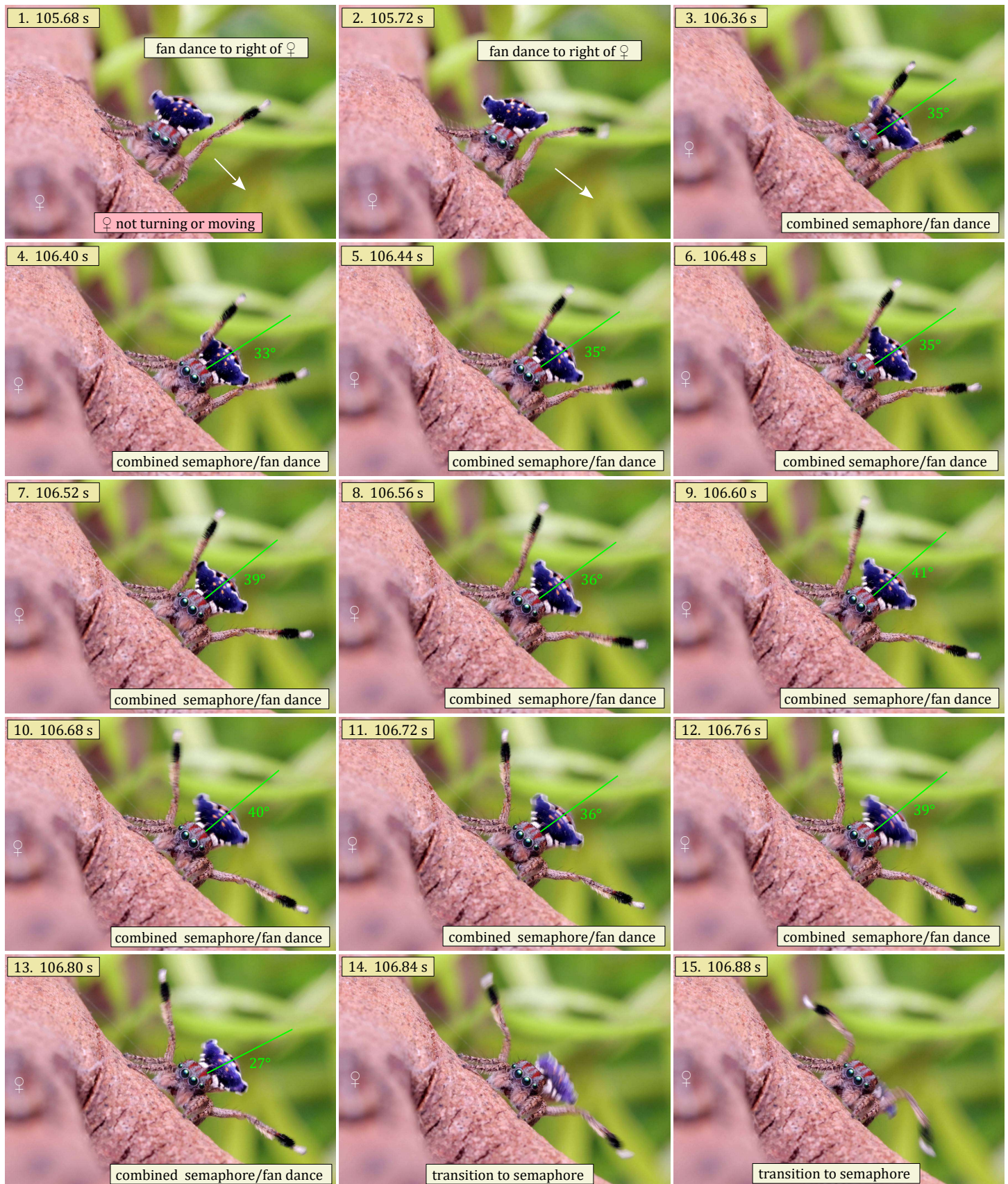


Figure 13 (continued on next page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. See Figure 15 for an interpretation of this sequence. **1-2**, Fan dance. Arrows show direction of movement. **3-13**, Semaphore display with components of the fan dance (body elevated, low amplitude waves of the elevated fan). During this display the pedipalps were also moved to expose the chelicerae. **14-15**, Transition to semaphore display (fan lowered).

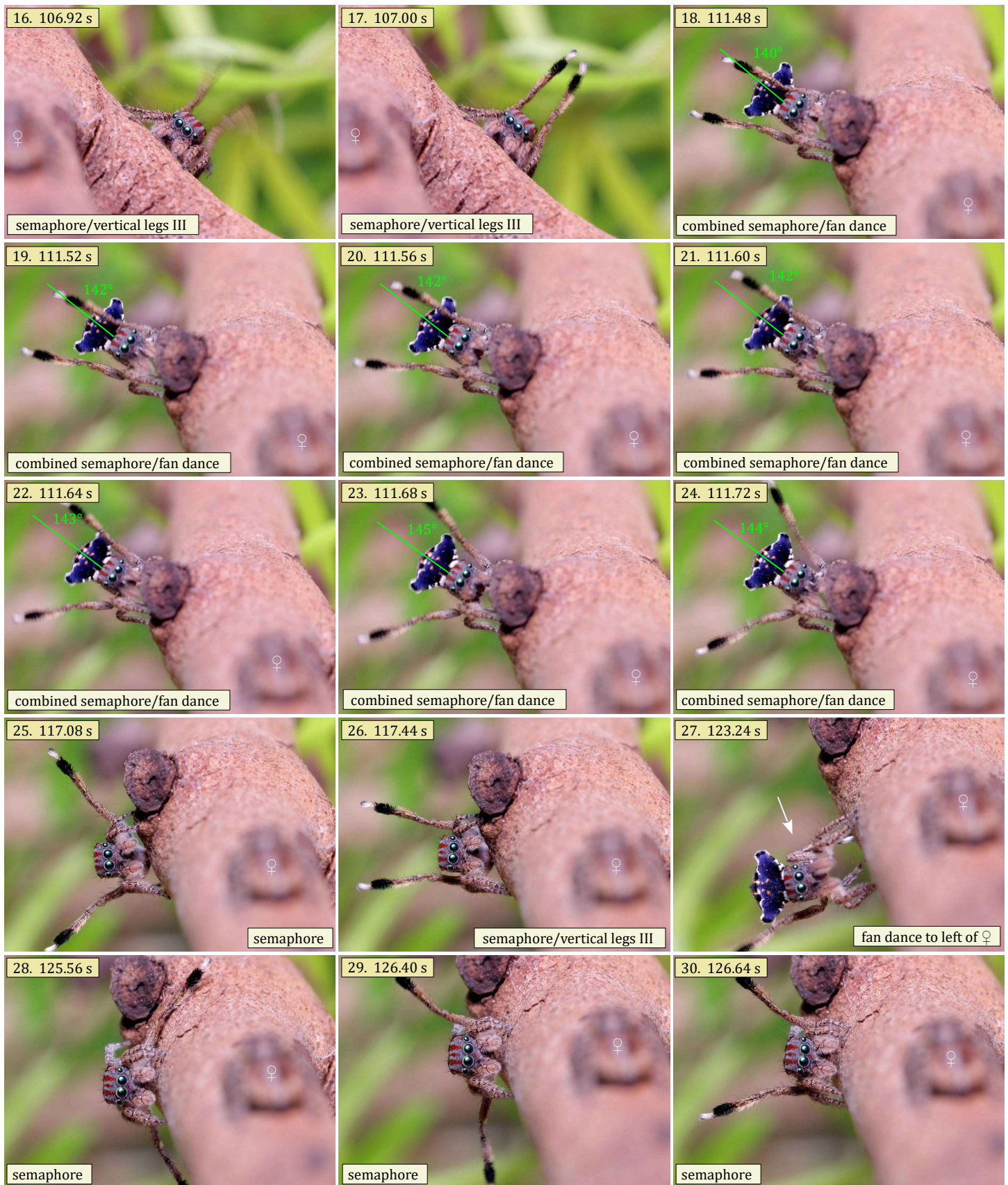


Figure 13 (continued from previous page, continued on next page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. **16-17**, Semaphore display. **18-24**, Semaphore display with fan dance components. **25-26**, Semaphore display. **27**, Fan dance in position below female. **28-30**, Semaphore display. Legs III were lowered as far as possible.

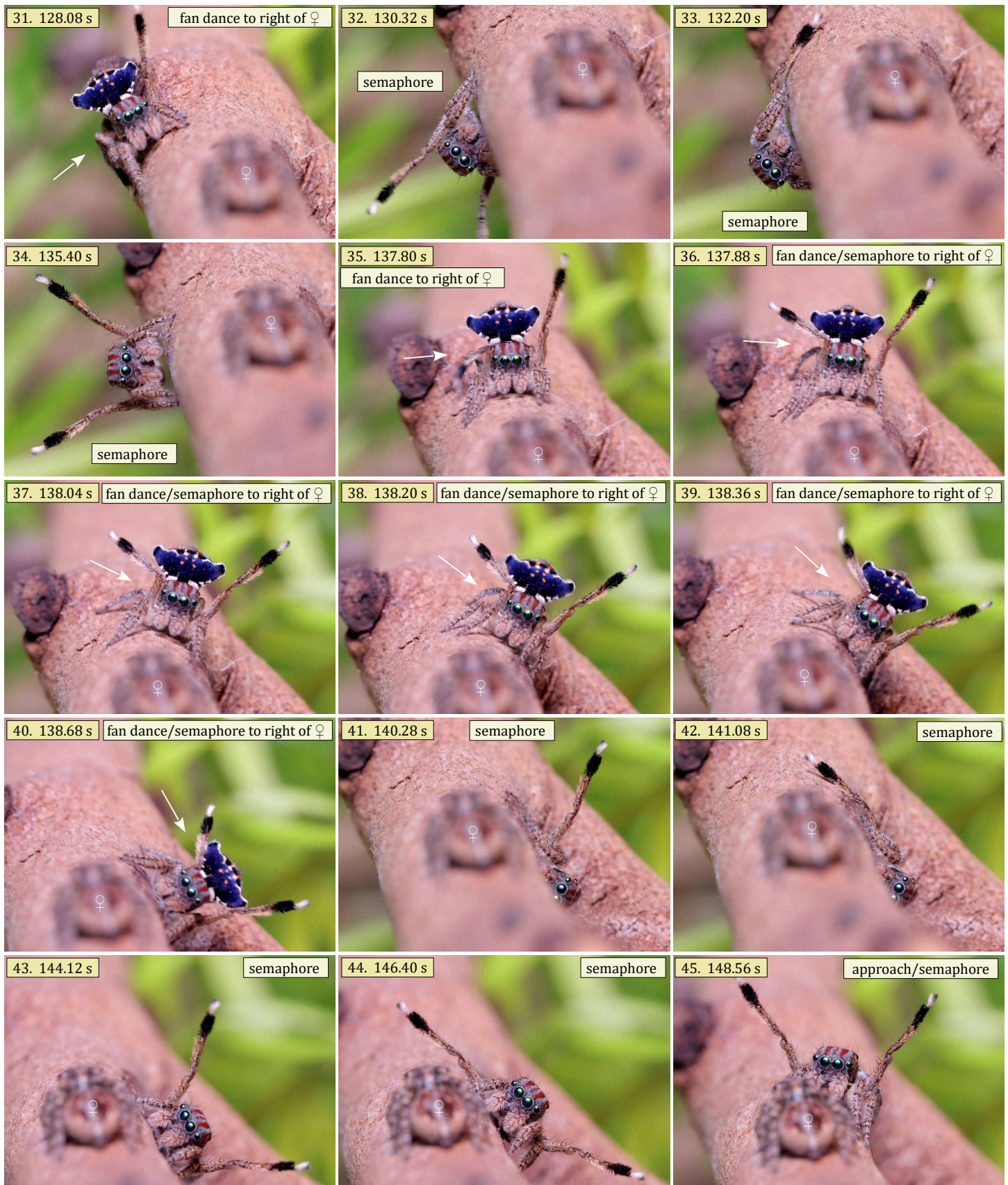


Figure 13 (continued from previous page, continued on next page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. **31**, Fan dance. **32-34**, Semaphore display. **35**, Fan dance. **36-40**, Fan dance with trailing leg partly extended. **41-42**, Semaphore display from position below the female. **43-45**, Semaphore display as the male approached the female from the right and began to align with her from the front.

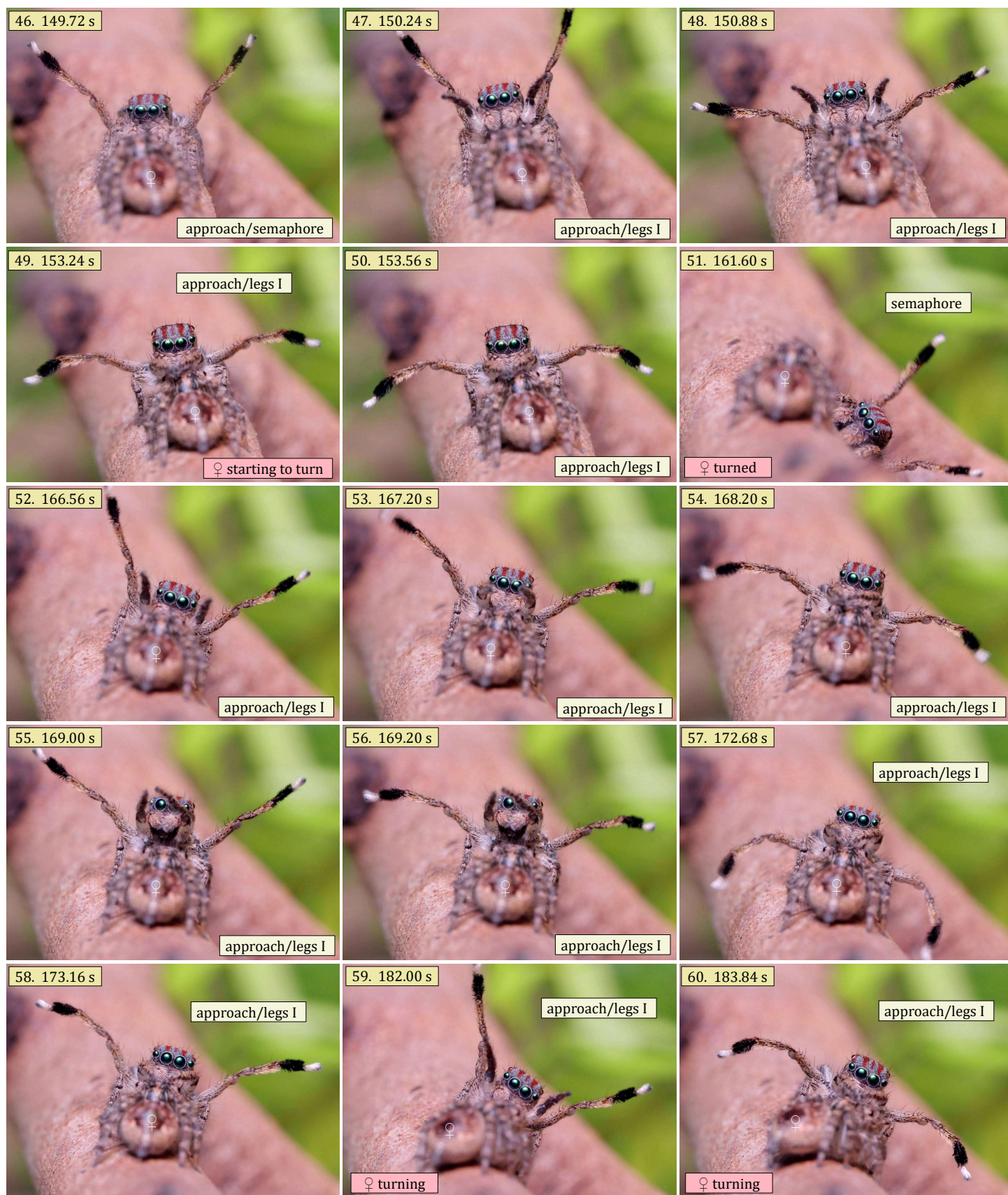


Figure 13 (continued from previous page). Selected, sequential frames from a 25 fps video of a male *Maratus constellatus* courting a female. **46**, Semaphore display while approaching female from the front. **47-50**, Continuing semaphore with legs III, legs I were elevated to position above the carapace of the female. **51**, Return to semaphore display after female moved. **52-60**, Subsequent approach with legs I elevated. Note flexion at the tibiometatarsal joint.

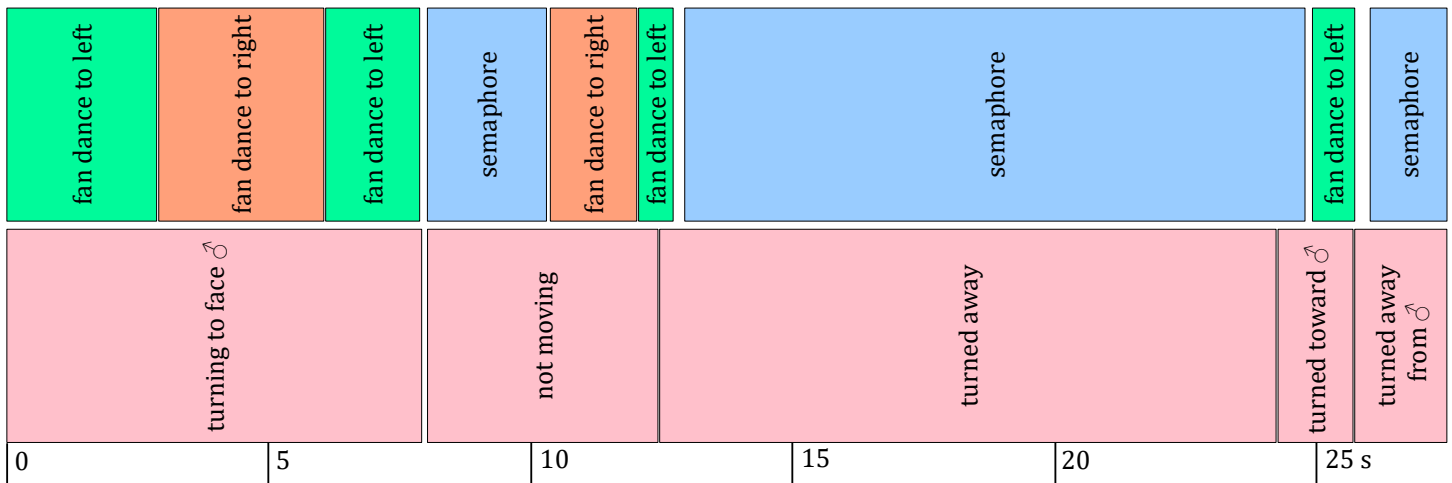


Figure 14. Timeline (~27 s) for courtship shown in Figure 12. The top half shows the male activity, the lower half the female activity. When the female was actively turning to face the male, the male danced from side to side. After the female stopped turning, and then turned away, the male pursued her with a semaphore display. This was briefly interrupted with a fan dance when the female turned toward the male (~25 s).

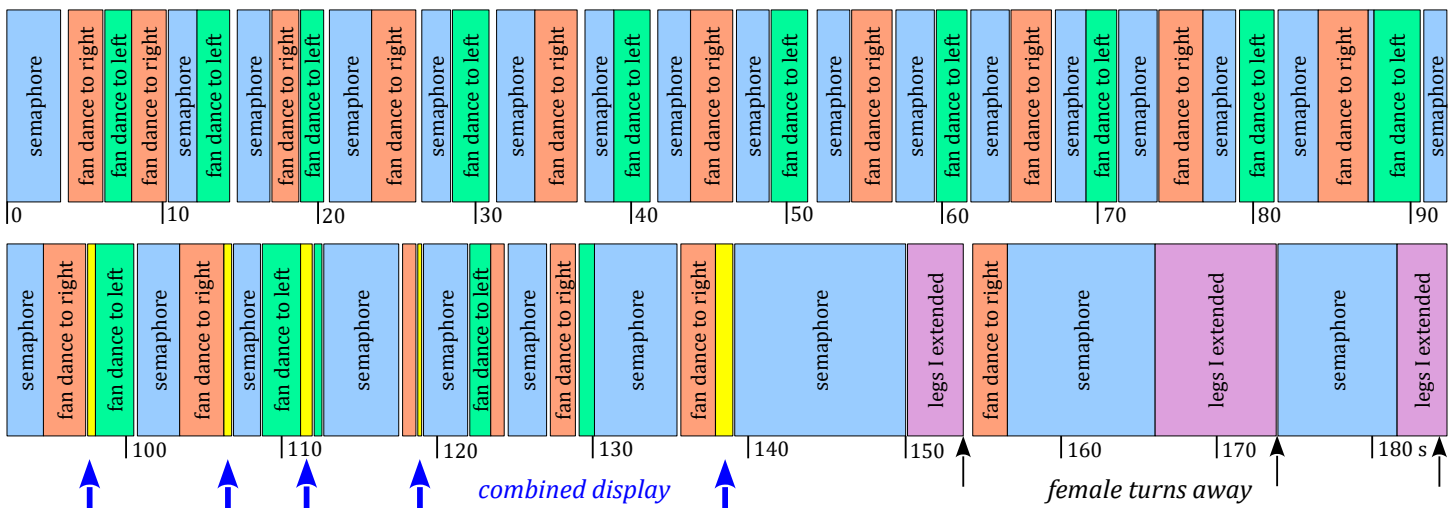


Figure 15. Timeline (~184 s) for the male courtship display shown in Figure 13. Until ~154 s the female was not moving, as the male displayed in front of her. After ~90 s the male moved closer (second row, ~1 cm), and continued his display with more emphasis on semaphore signalling, until moving into a mounting position with leg I extended over the carapace of the female (~150 s). Initially the male alternately fan-danced to one side of the female, performed a semaphore display on that side, then fan-danced to the other side, regularly alternating each fan dance with a semaphore display. Brief episodes of combined display (semaphore with elements of fan dance, or fan dance with both legs III elevated) are shown in yellow, identified by large blue arrows. Black arrows at right, bottom, show where the female made a turn away from the male, to interrupt what could have been a mating sequence. The mating approach (Figure 13) was similar to that of other *Maratus*.

Females. Living females, reared in the laboratory, are shown in Figures 16-17. Although we have not depicted the epigynum here, it is probably of little use with respect to identification of this species and almost certainly looks like the epigynum of other members of the *Maratus flavus* group. The dorsum of the female is darker brown, but the same can be said of the females of many other *Maratus* species. In general female *M. constellatus* resemble other *Maratus*, but they do have some of the scale tracts seen in the adult male (e.g., middorsal thoracic tract, striped eye region), in a much less distinct form.





Figure 16 (continued from previous page). Female *Maratus constellatus*.



Figure 17. Ventral views of four living female *Maratus constellatus*.

Immatures. Immature instars of one male (I1-I7) are shown in Figure 18.1-18.22. Two other penultimate males are shown in Figure 18.23-18.24, and one female (I1-I5) juvenile reared in the laboratory is shown in Figure 19. As they get older, males in particular appear to exhibit a transverse opisthosomal band corresponding to the rear of the dorsal opisthosomal plate of the adult male (Figures 18.17-18.24). Instar 7 of the male is the penultimate stage. The female (Figure 19) was only followed to the fifth instar (I5).



Figure 18 (continued on next page). Immature male *Maratus constellatus*, by instar (I-1 to I-7, instars 1-7). 1-22, A single male, followed to the penultimate stage (I-7). 23-24, Penultimate instar of two other males.



Figure 18 (continued from previous page). Immature male *Maratus constellatus*, by instar. **21-24**, Penultimate males (instar 7) have the dark chelicerae and carapace characteristic of adult males.

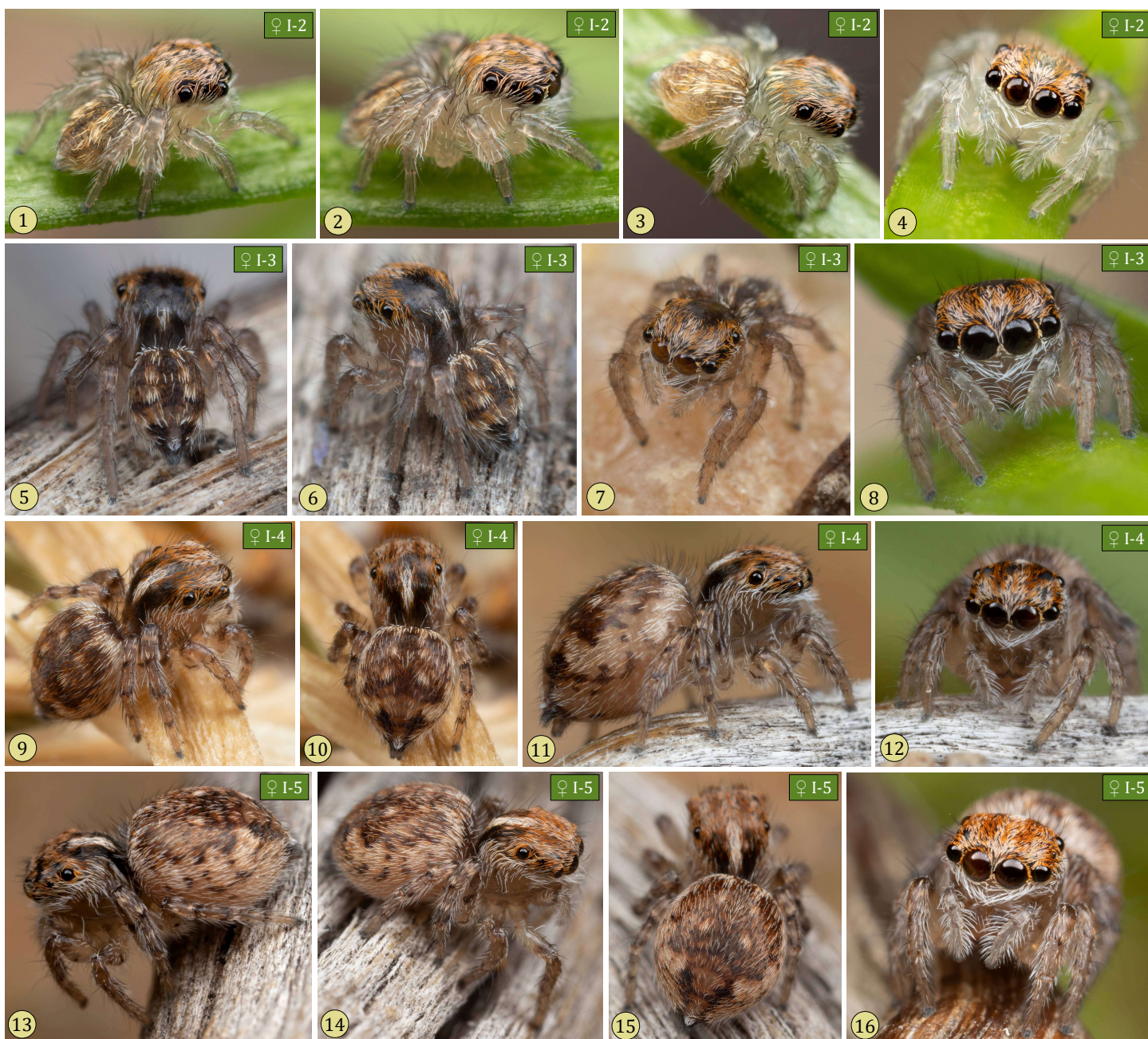


Figure 19. Immature female *Maratus constellatus*, by instar (I-1 to I-5, instars 1-5). All photographs represent a single individual, not tracked beyond the fifth instar (I-5).

Acknowledgements

We thank the Parks and Wildlife Service of Western Australia for permitting the collection of these spiders. All photographs are Copyright © Jürgen C. Otto.

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