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# Courtship display of the peacock spider *Maratus aquilus* (Araneae: Salticidae: Euophryini)

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**Abstract:** Seven stages of courtship display by the male and one display by the female *Maratus aquilus* are described based on video recordings in the laboratory. The roles of selection by the female and low dispersal in the evolution and speciation of isolated diverse and endemic populations in the *vespa* group are also discussed.

**Keywords:** dispersal, evolution, Fisher runaway selection, jumping spider, male success, *Maratus combustus*, *Maratus cristatus*, *Maratus icarus*, *Maratus tortus*, *Maratus unicup*, *Maratus vespa*, mating, sexual selection, Southwestern Australia Ecoregion, speciation, *vespa* group

*Maratus aquilus* Schubert 2019 is one of seven species presently assigned to the *vespa* group, a subclade of the genus *Maratus* Karsch 1878 (Otto & Hill 2019b). This recently discovered group of peacock spiders is endemic to the southwestern corner of Western Australia (Figure 1).

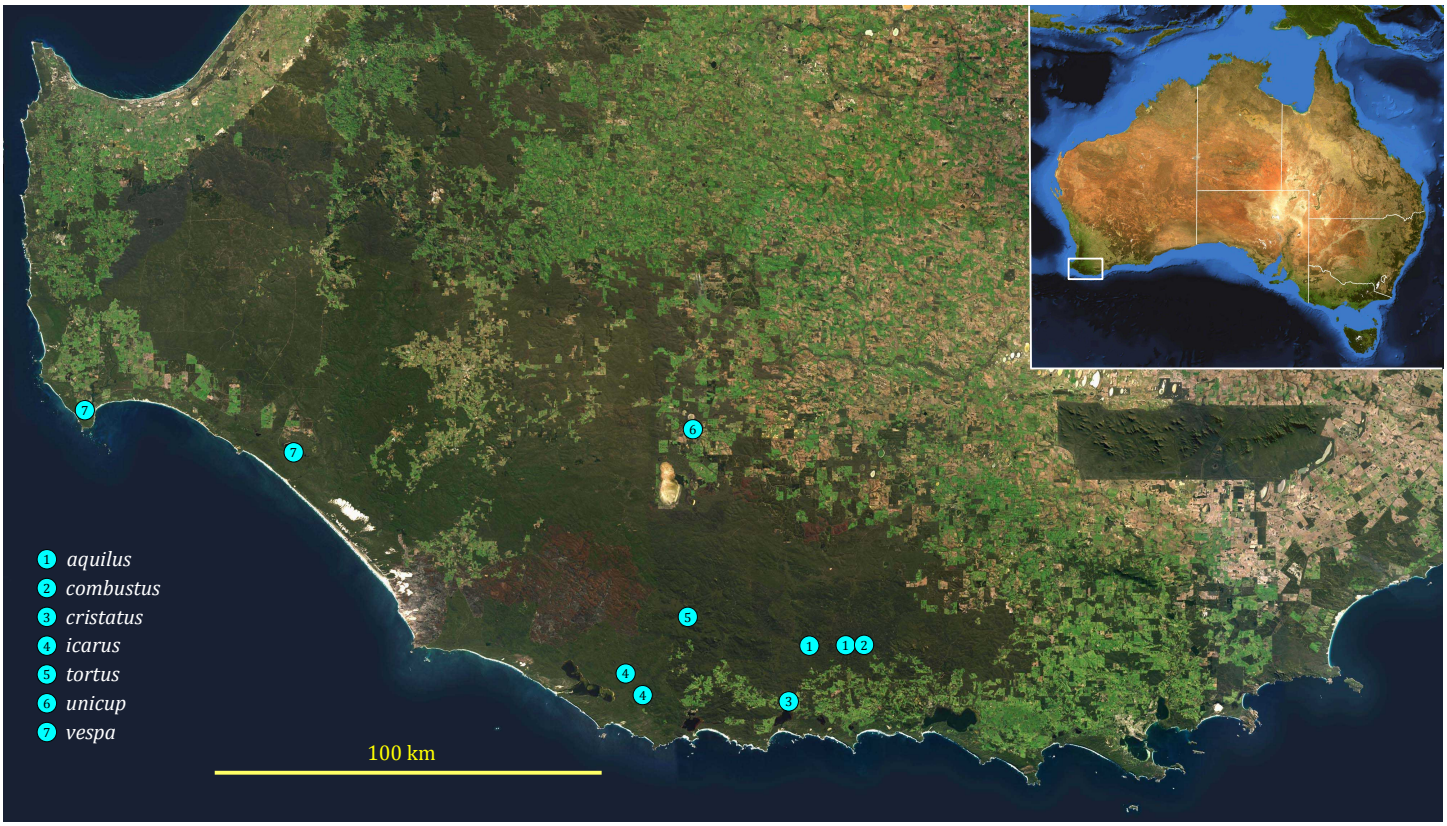


**Figure 1.** Known distribution for peacock spiders of the *Maratus vespa* group in Western Australia. At present each species appears to have a limited, parapatric distribution with respect to other members of the group. Future studies should reveal additional *vespa* group species in this coastal region, spanning little more than 200 km. Background courtesy USGS/Landsat.

Our current knowledge of courtship display by males in this group is reviewed in Table 1. All of these species engage in a *close fan dance* directly in front of an attending female at a distance of several mm. In this dance the female turns to follow each movement of the fan as it is moved rapidly from side to side. In all of these species except *Maratus tortus* this includes display of the middorsal features of the fan at the center, just behind the elevated legs III. In *M. tortus* the fan is twisted so that only one of the flaps is visible when it is held at a center position.

**Table 1.** General features of courtship display by members of the *Maratus vespa* group.

| species | known features of male courtship display | references |
|---|---|---|
| *aquilus* Schubert 2019 | low amplitude *unilateral* and *bilateral semaphore* signals with legs III; *elevated fan wave*; *active fan dance* with side-stepping, including large amplitude bilateral leg III waving and fan waving; *close fan dance* with side to side rotation of fan behind elevated legs just in front of following female | Schubert 2019; this paper |
| *combustus* Schubert 2019 | *close fan dance*; resembles *cristatus* and *icarus* | Schubert 2019 |
| *cristatus* Otto & Hill 2017 | *partly elevated fan wave* with flaps extended, *close fan dance* at low (~2°) or higher (~20°) amplitude of fan rotation | Otto & Hill 2017 |
| *icarus* Otto & Hill 2019 | *elevated fan wave* (~20° amplitude); *partly elevated fan wave* (~2° amplitude) with flaps retracted and side-stepping; *active fan dance* with bilateral calipers movement of legs III, fan waving and pedipalp flicker; *close fan dance* with only fan movement from side to side | Otto & Hill 2019a |
| *tortus* Otto & Hill 2018 | *unilateral semaphore* with one leg III; rapid *bilateral semaphore*; unusual *close fan dance* involving display of lateral flaps in the center position, with a second mode that includes waving the fan from side to side behind legs III | Otto & Hill 2018 |
| *unicup* Otto & Hill 2018 | wide and tall *bilateral semaphore* positions with extended legs III; *elevated fan wave* behind legs III; *close fan* dance moving fan to display flaps on either side | Otto & Hill 2018 |
| *vespa* Otto & Hill 2016 | *active fan dance* with bilateral calipers movement of legs III and low amplitude fan waving; *close fan dance* to alternately display flap at either side. | Otto & Hill 2016 |

The species name *aquilus* is based on the resemblance of the scale pattern on the dorsal opisthosomal plate (fan) of the adult male to the face of an eagle (Figures 2-3; Schubert 2019). During a *close fan dance* the posterior part of this fan is partly elevated (Figure 23:1) to display an iridescent posteromedial *ornament* between and behind the raised legs III (Figure 3:11). On the distal margin of each lateral flap of the fan a tuft of bright white setae is present in front of a larger fringe of black setae (Figure 3:1). This ornamentation of each flap contributes to its visibility when it is waved to the side during a *close fan dance*. The brighter red-orange markings of the anterodorsal fan, on a background of iridescent blue-green scales, appear to play no role in a *close fan dance*, but are prominently displayed during an *active fan dance*.

This study is based on still photographs and a series of 25 fps video recordings obtained in semi-natural conditions and captive animals in the laboratory. These animals were captured NOV 2018 west of Mount Romance (S34.843064°, E117.039091°). Stages of display observed for the male *Maratus aquilus* from this locality are listed in Table 2.

**Table 2.** Stages of display by the male *Maratus aquilus*. Interpretations for the *stimulus* that elicits each stage of display and the *positive female response* to each display are hypothetical, suggested by the video recordings that have been examined to date.

| stage | description of display | stimulus for male | positive female response | Figures |
|---|---|---|---|---|
| unilateral semaphore | no movement, or low amplitude movement of one extended leg III | possible female sighting, or possibility of female in area (?) | female turns to face or approaches male | 4, 6:1, 7:1-2 |
| bilateral semaphore | no movement, or low amplitude movement of both extended legs III with or without elevation of the fan | sighting of likely female, position may be maintained if female is still | | 5, 6:2-5, 7:3-14 |
| elevated fan wave | side to side rotation or waving of the elevated fan with or without bilateral leg III extension, includes variable use of fan and may include side to side display of flaps | sighting of likely female nearby | | 8-12 |
| active fan dance | stepping from side to side with waving of bilaterally extended legs III (not centered) and waving of the elevated fan | female identified nearby and may turn but does not approach and attend to male | | 13-19 |
| close fan dance | with extended legs III touching or nearly touching at the center, display of the posterior ornament of the partly elevated fan alternates with lateral display of each flap | female turns to face nearby male | female approaches and turns to follow each movement of the male | 20-28 |
| mounting | with legs III extended to the sides the male moves | female stops turning from side | female moves little but allows | 31:1 |


**Figure 2.** Nine different living adult male *Maratus aquilus*. **2,** The posterior part of the fan can be elevated when the fan is partly elevated as shown here. This makes the iridescent green posterodorsal ornament of the fan (Figure 3:11) visible from the front.


**Figure 3.** Detailed views of the fan of living adult male *Maratus aquilus*. **1-3, 5,** Elevated fan with flaps extended during display. The iridescent green colour of the posterodorsal ornament of the fan is scarcely visible in this orthogonal view. **4, 6-9,** In this perspective the folded fan resembles the head of an eagle (*aquilus*). **10,** Lateral view of opisthosoma showing folded fan of a mating male. **11,** View of the iridescent green ornament (inset at upper left) through legs III as seen by a female attending to the *close fan dance* of a male. With the posterior fan only partly elevated, the fan presents at an angle that appears to increase the intensity of light reflected from this ornament. To the rear, or just above the iridescent green scales of this ornament, lies a small patch of brighter, light blue iridescent scales. In this position the fan is also waved and moved up and down through a low amplitude. **12-14,** Ventral views showing flexible articulation of the pedicel and the opisthosoma.

*Unilateral semaphore display* (Figures 4, 6:1, 7:1-2). This display, involving slow or low amplitude movement of a single extended leg III, appears to represent a form of advertisement by the male at a greater distance, intended to solicit the response of a female that may be in the area. The orientation of the extended leg wave varies, from near-horizontal to near-vertical.

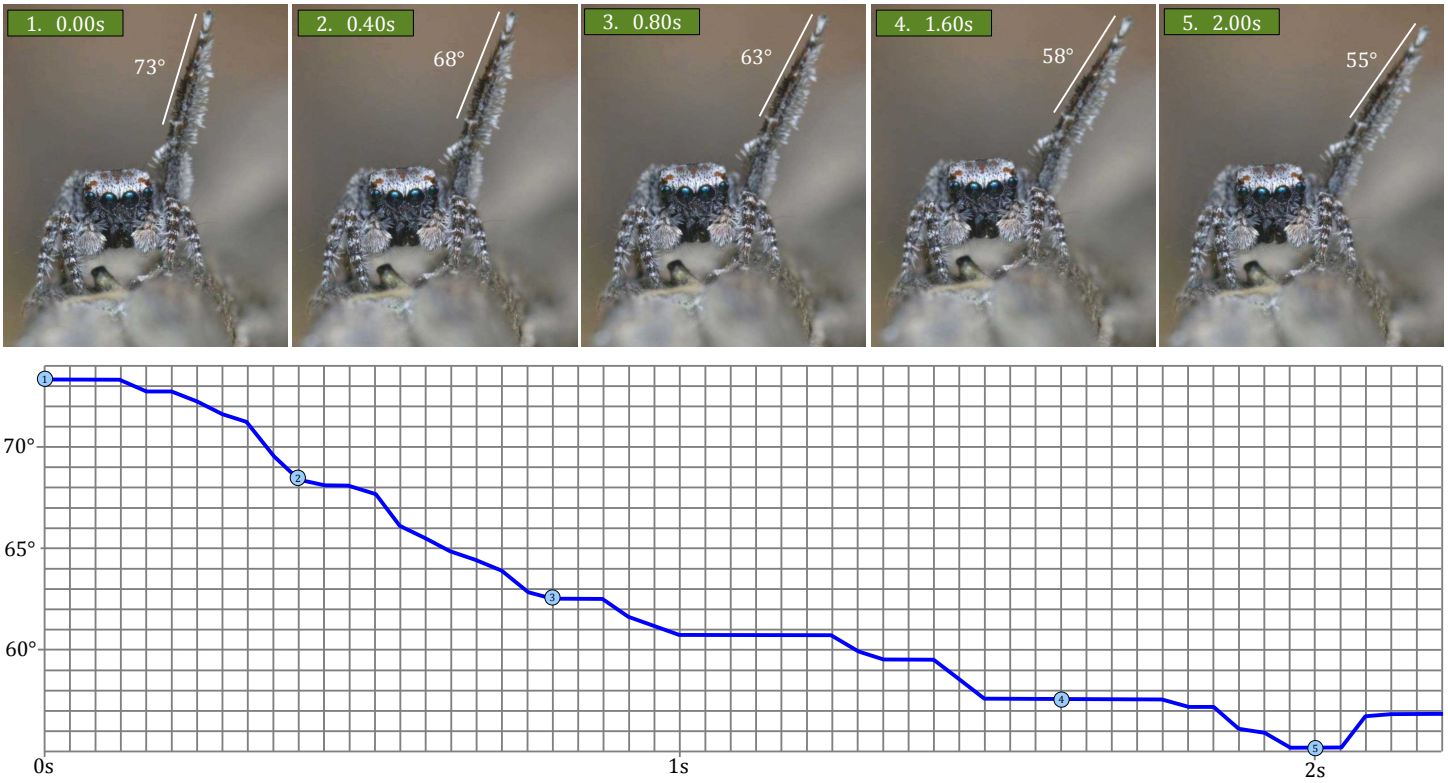


**Figure 4.** Selected frames (1-5) from a 25 fps video showing unilateral semaphore display by a male *Maratus aquilus*. Below, the orientation of the extended left leg III during each frame of this display is charted over the course of more than 2 seconds.

*Bilateral semaphore display* (Figures 5, 6:2-5, 7:3-14). Often a unilateral semaphore transitioned to a bilateral semaphore display with both legs III extended and held in a similar orientation. Like the unilateral semaphore, this display often included slow or low amplitude movement of both legs in a loosely synchronous manner. As a possible transition to more active forms of display, this display might also include elevation of the fan and extension of the flaps without side-to-side waving or stepping.

*Elevated fan wave* (Figures 8-12). In this display the male remained in place facing a female prospect and waved (rotated from side to side) the fan without moving the extended legs III, which were held in a symmetrical V-shaped orientation. Three variations on this display are shown here. In the first (Figure 8) the partly elevated fan was rotated over a larger amplitude to display the flap on either side, much as in the close fan dance display but with legs III separated. In the second (Figure 9) the fully elevated and extended fan was rotated over a small amplitude and legs III were not extended. In the third (Figures 10-12) the fully elevated and extended fan was rotated over a small to moderate amplitude with legs II fully extended in a symmetrical V-shaped orientation.

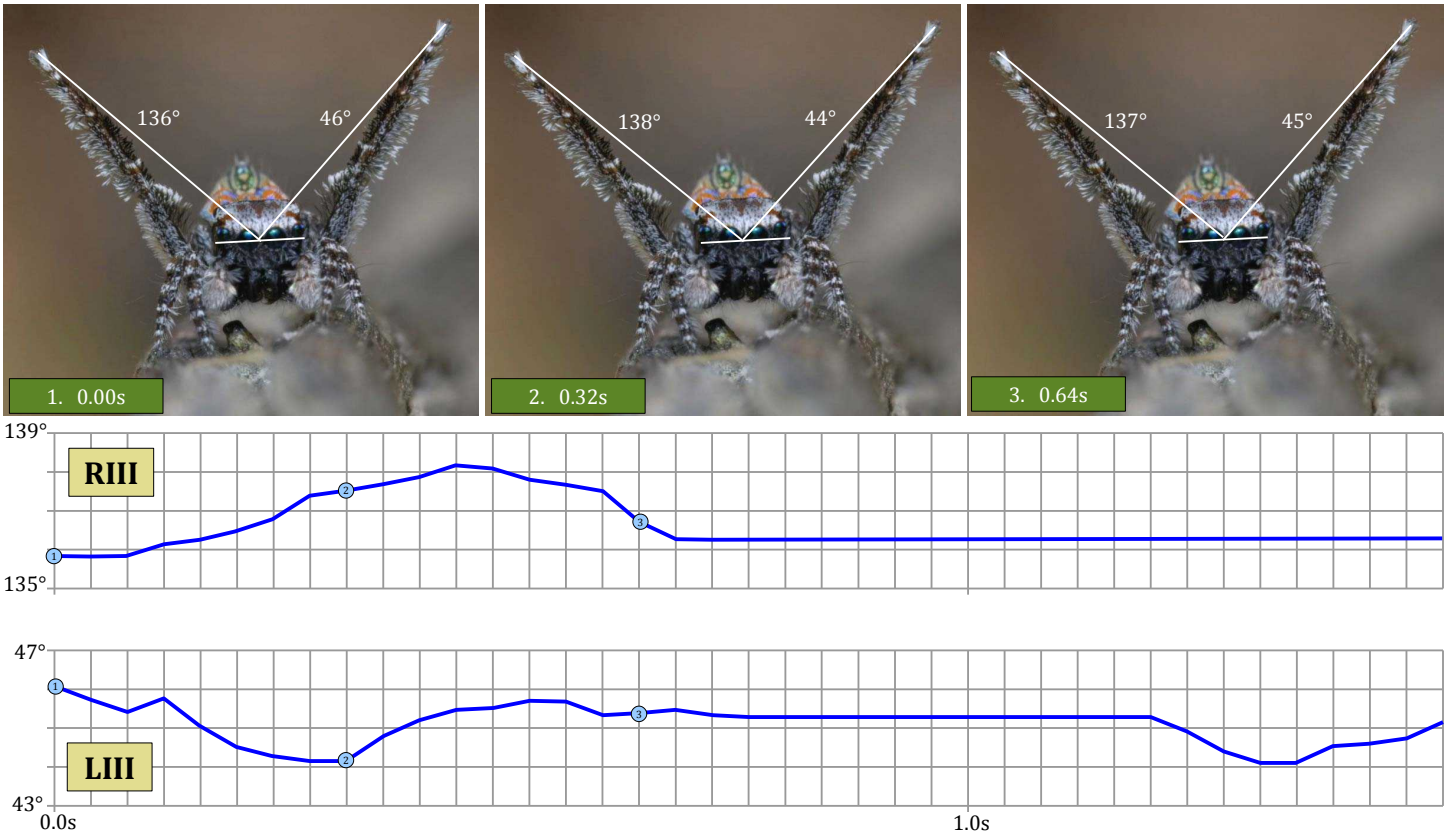


**Figure 5.** Selected frames (1-3, 25 fps) showing bilateral semaphore with slow or low amplitude movement of the extended legs III by a male *Maratus aquilus*. Below, the orientation of each extended leg III during each frame of this display is charted.

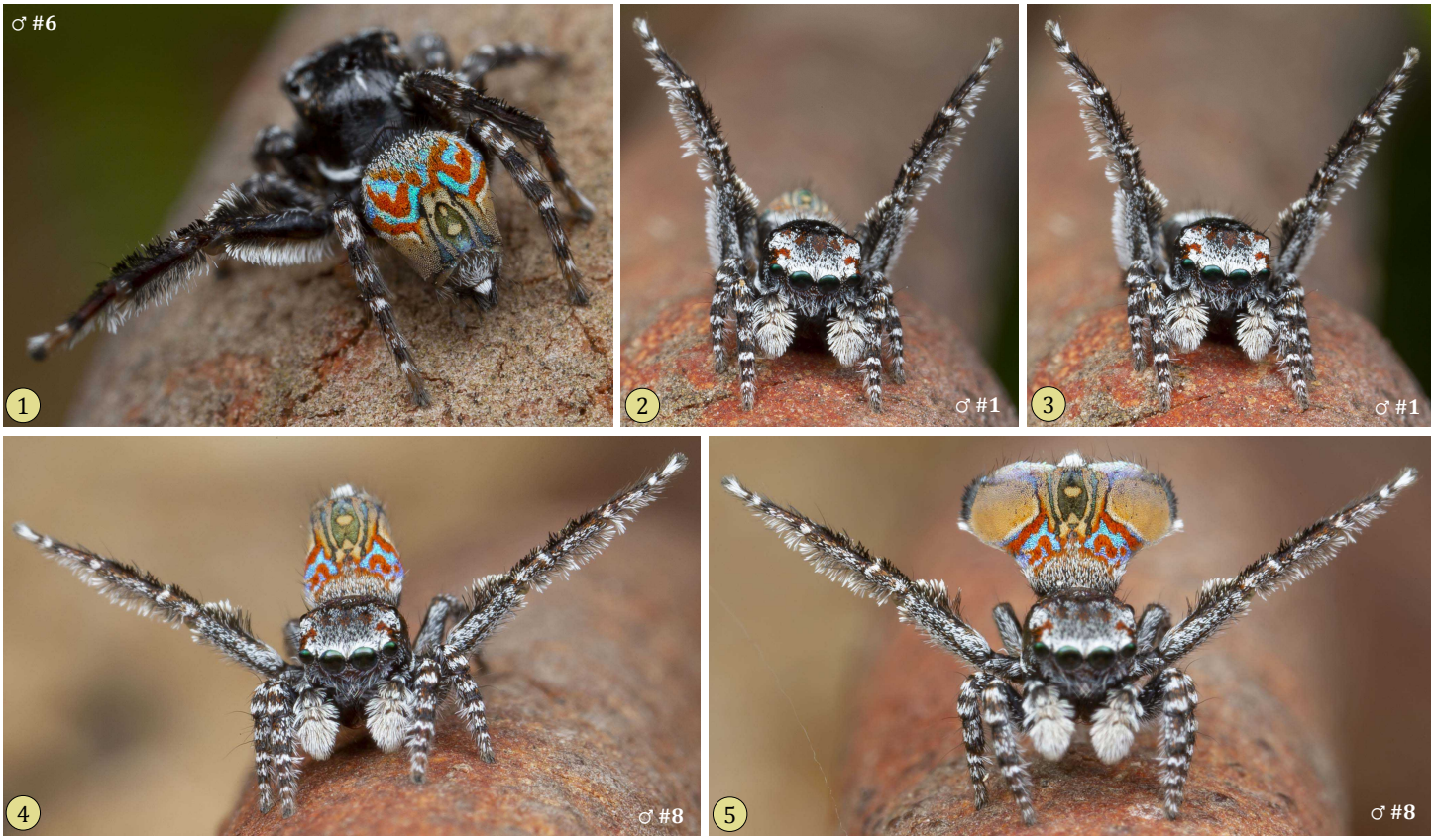


**Figure 6.** Unilateral (1) and bilateral (2-5) semaphore displays by male *Maratus aquilus*. Note variation in extension of flaps and elevation of the fan during bilateral display.


**Figure 7.** Selected frames (25 fps video) showing unilateral (1-2) or bilateral (3-14) semaphore displays by male *Maratus aquilus*.

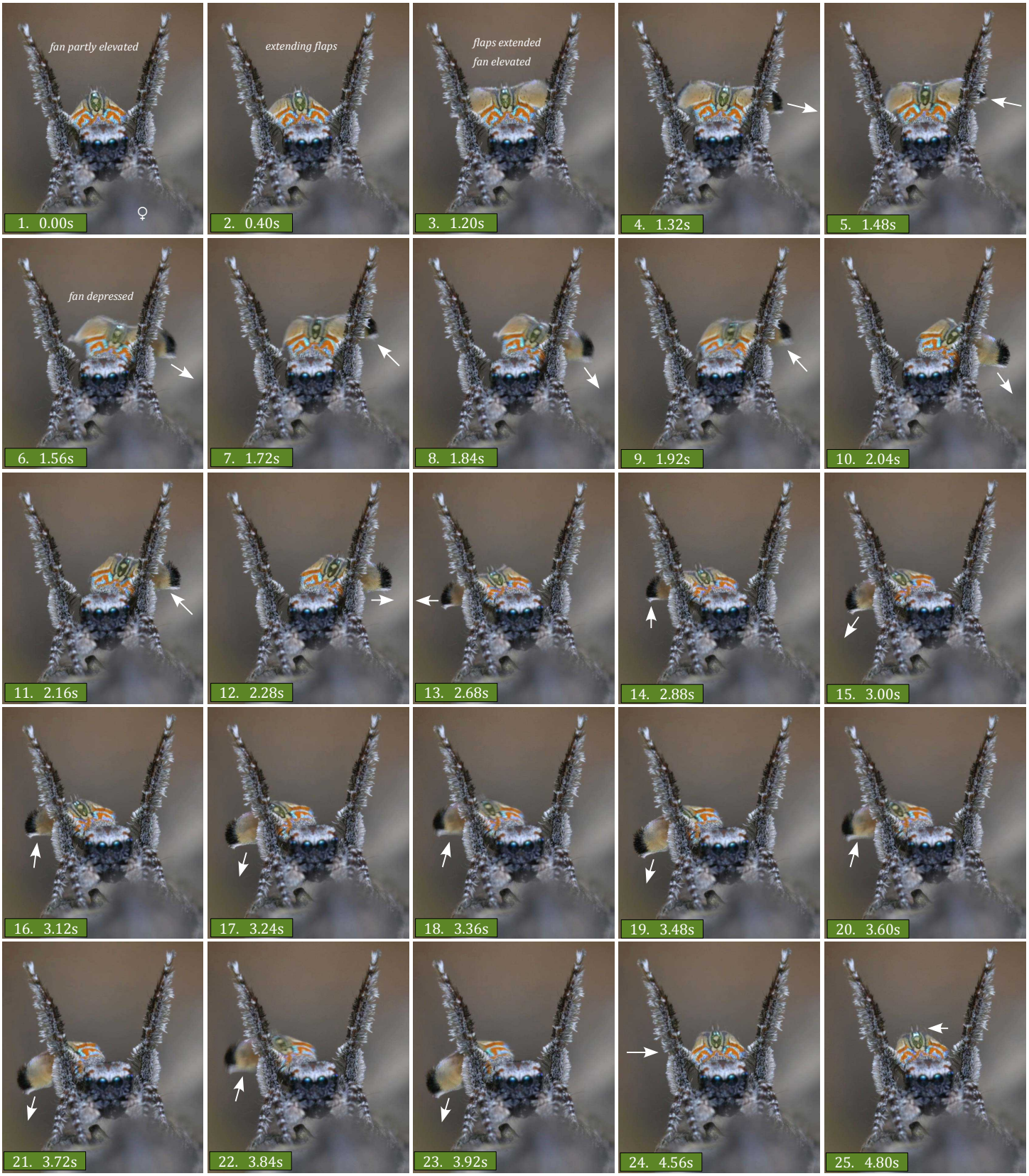


**Figure 8.** Selected frames (1-25, 25 fps video) showing an *elevated fan wave* display by a male *Maratus aquilus*. With legs III extended in an upright position, the flaps of the fan were displayed alternately on either side in a manner similar to that seen in the *close fan dance* (~3.5 lateral wave cycles/s). The female, facing the male, is visible as a blurred figure in the foreground (lower right) of each frame. Here as in subsequent figures movement of the fan or legs relative to the preceding frame is identified by an arrow. **4-11,** (1.20-2.16s), 4 *wave cycles* to the left over ~1s. **13-24,** (2.68-4.56s) 6 *wave cycles* to the right over ~2s.


**Figure 9.** Consecutive frames (1-25, 25 fps video) showing an *elevated fan wave* display without extension of legs III by a male *Maratus aquilus* directly in front of a female. The female, facing the male, is visible as a blurred figure in the foreground (lower left) of each frame. Each left/right wave was relatively slow (~2/s, amplitude ~22°).

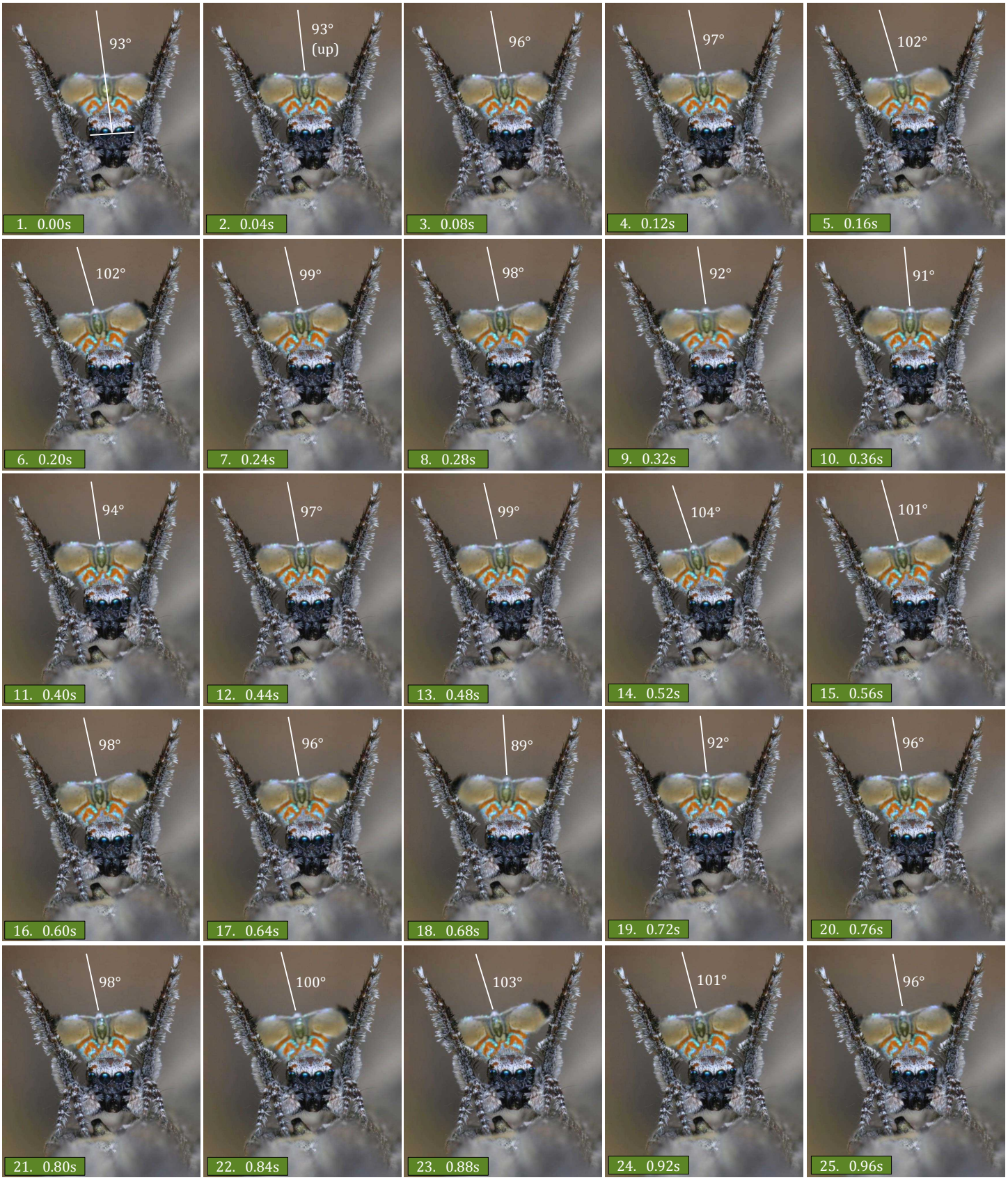


**Figure 10.** Consecutive frames (1-25, 25 fps video) showing an *elevated fan wave* display with legs III extended by a male *Maratus aquilus*. In this example the fan was fully elevated with extended flaps and waved continuously at a relatively low to moderate amplitude (2.8 left/right cycles/s, amplitude 10-15°). Chelicerae were exposed but the pedipalps were not moved.

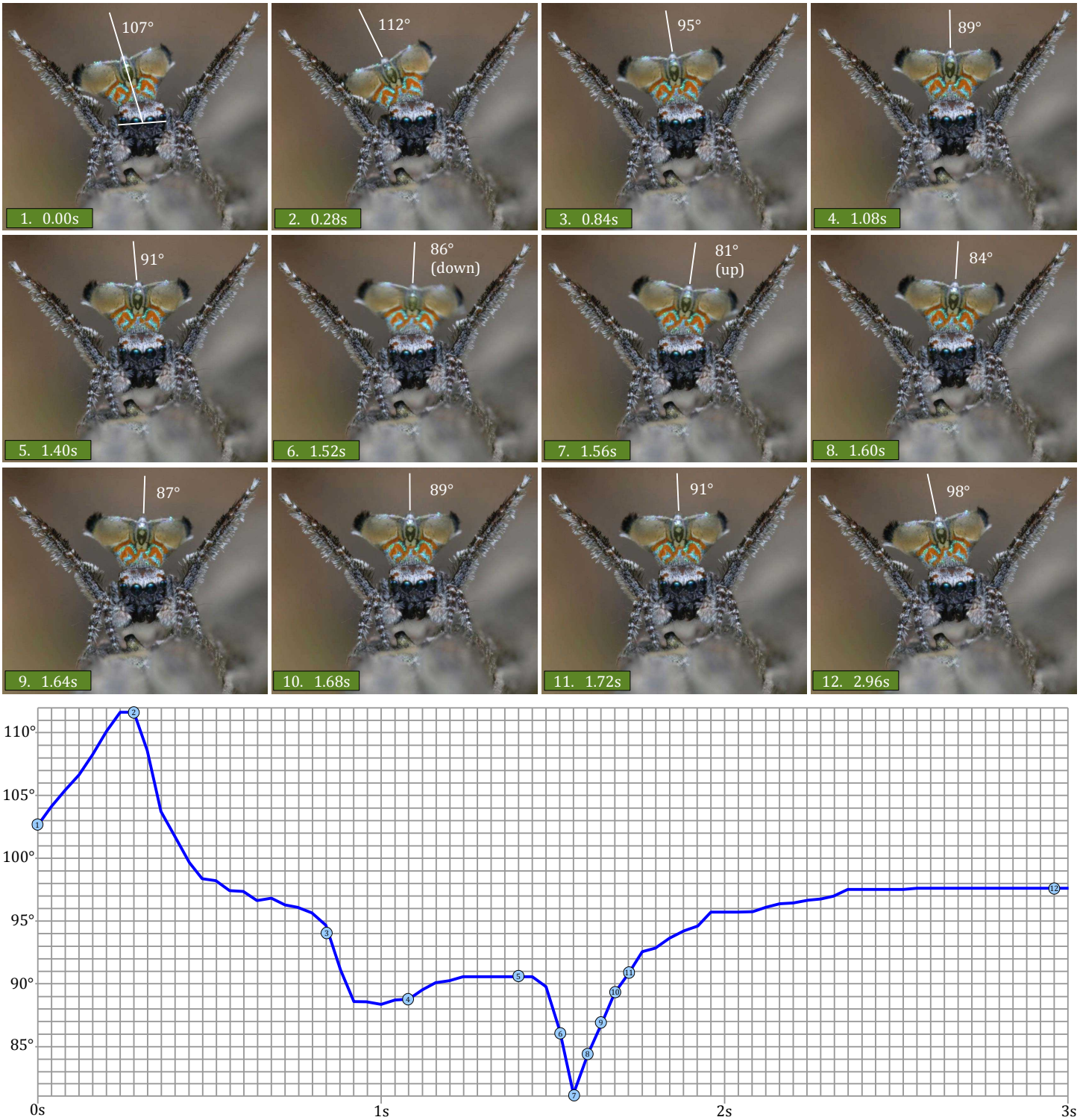


**Figure 11.** Selected frames (1-12, 25 fps video) showing an *elevated fan wave* display with legs III extended by a male *Maratus aquilus*. The fan was fully elevated and extended during this display, and the pedipalps were held in place to the sides to expose the shiny, black chelicerae. The chart shows rotation of the fan over the course of 3 seconds during this display.

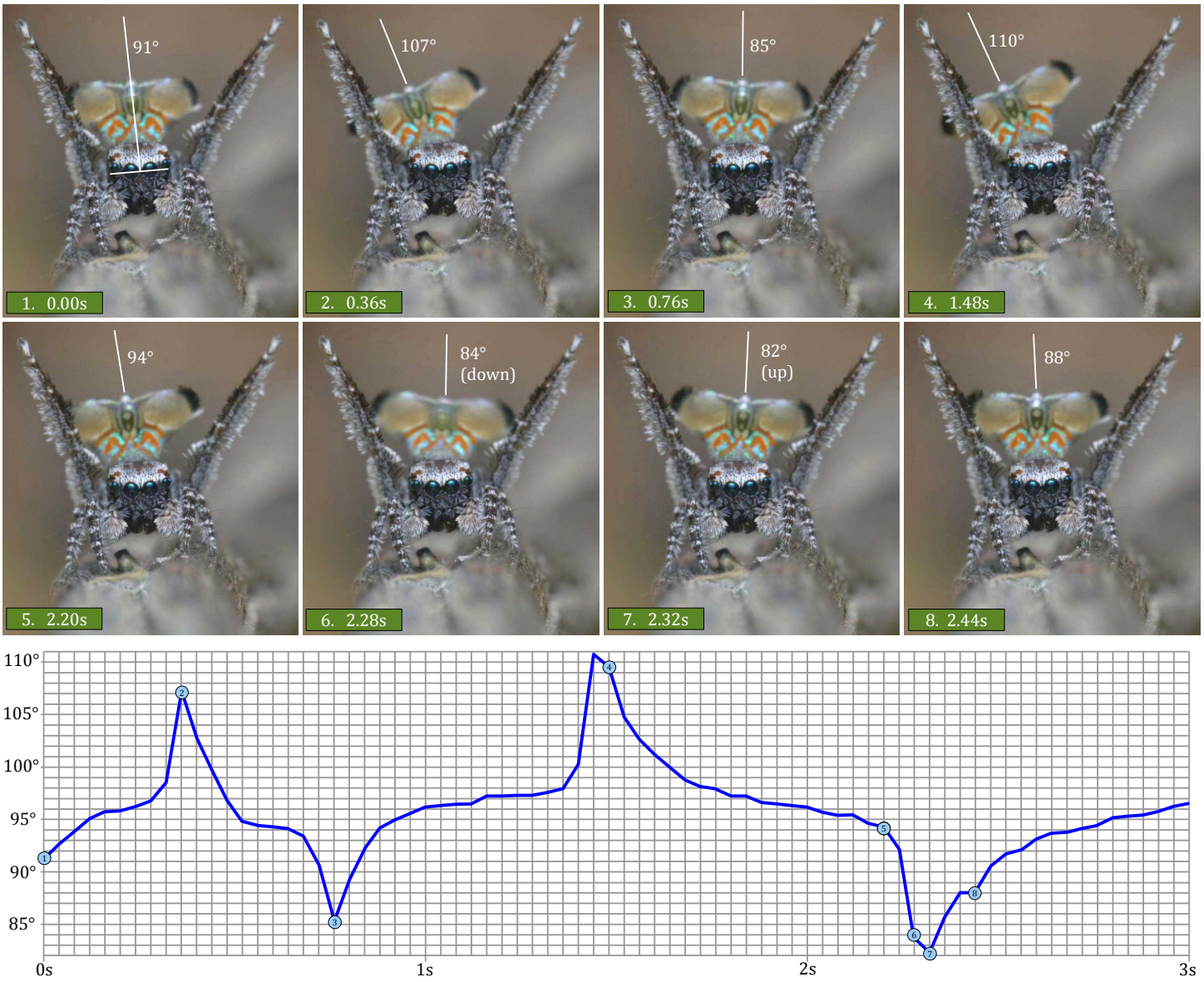


**Figure 12.** Selected frames (1-8, 25 fps video) showing an *elevated fan wave* display with legs III extended by a male *Maratus aquilus*. **6-7,** The fan was slightly depressed and then elevated in this position. The chart shows regular alternation between right and left positions of the fan during 3 seconds of this display (~0.7 left/right cycles/s, ~25° amplitude).

*Active fan dance* (Figures 13-19). The *active fan dance* involves rapid bilateral movement of the extended legs III, waving the fan from side to side or raising and lowering it, side-stepping and even (in some cases) up-and-down flickering of the pedipalps. In this display lowering of the opisthosoma is typically associated with side-stepping and/or raising one or both legs III to a vertical position. This contrasts greatly with the controlled performance of the *close fan dance* and appears to represent generation of the maximum degree of activity or movement possible to secure the attention of a nearby female that is not turning to face or attend to a courting male. When a female does provide this attention, the male may transition (Figure 17) to a *close fan dance*, moving legs III to an upright position.

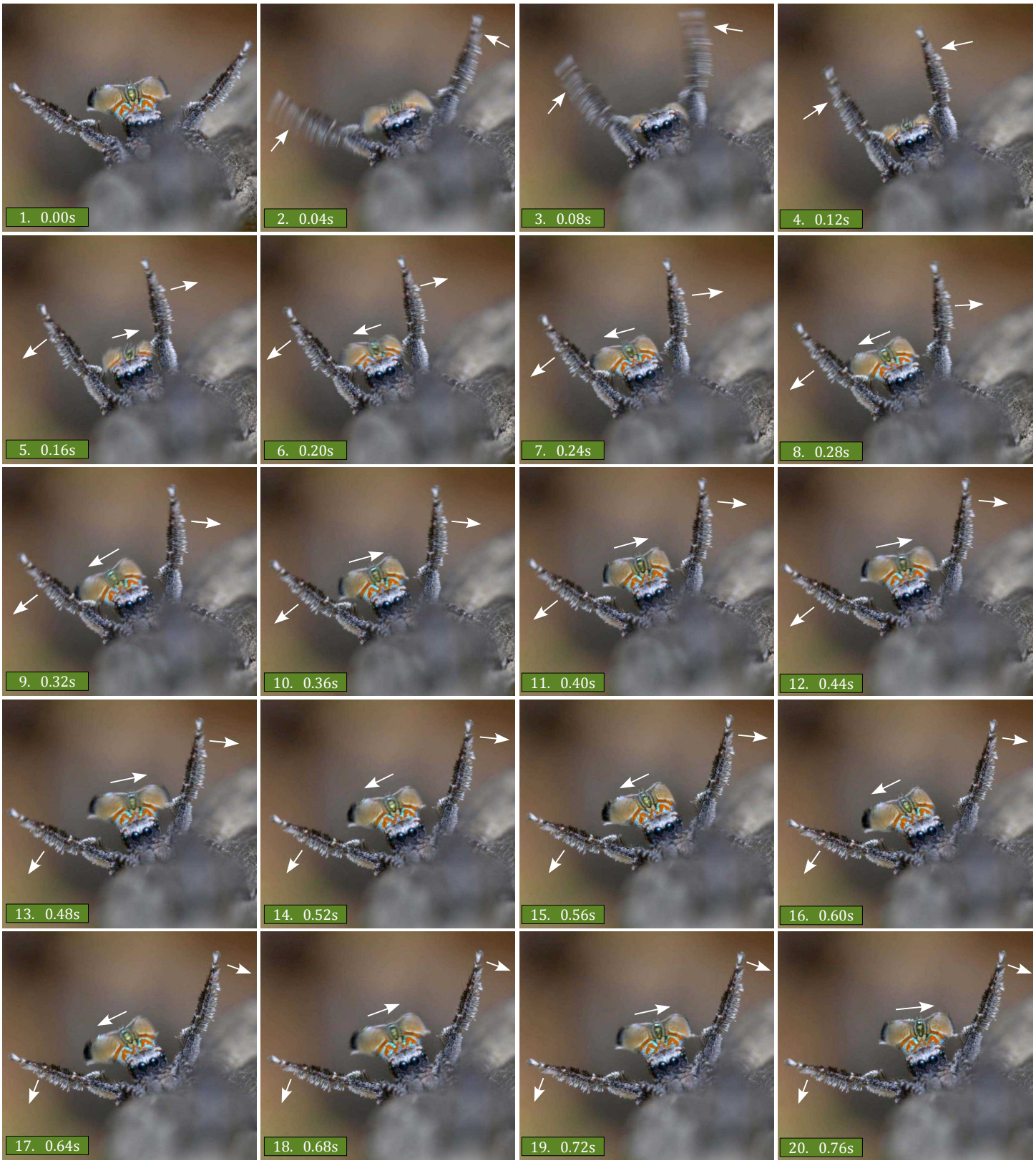


**Figure 13.** Consecutive frames (25 fps video) showing continuous movement of the fan and extended legs III during the *active fan dance* of a male *Maratus aquilus*. The female (blurred image at lower right) was in front of, but not facing, this male. **1-4,** Fan lowered as legs III moved to a vertical orientation over 0.12s. **4-20,** Slow lowering of legs III as fan was waved over the next 0.64s (fan rotated at a rate of ~3 left-right cycles/s). Note the position of the pedipalps in front of the chelicerae.

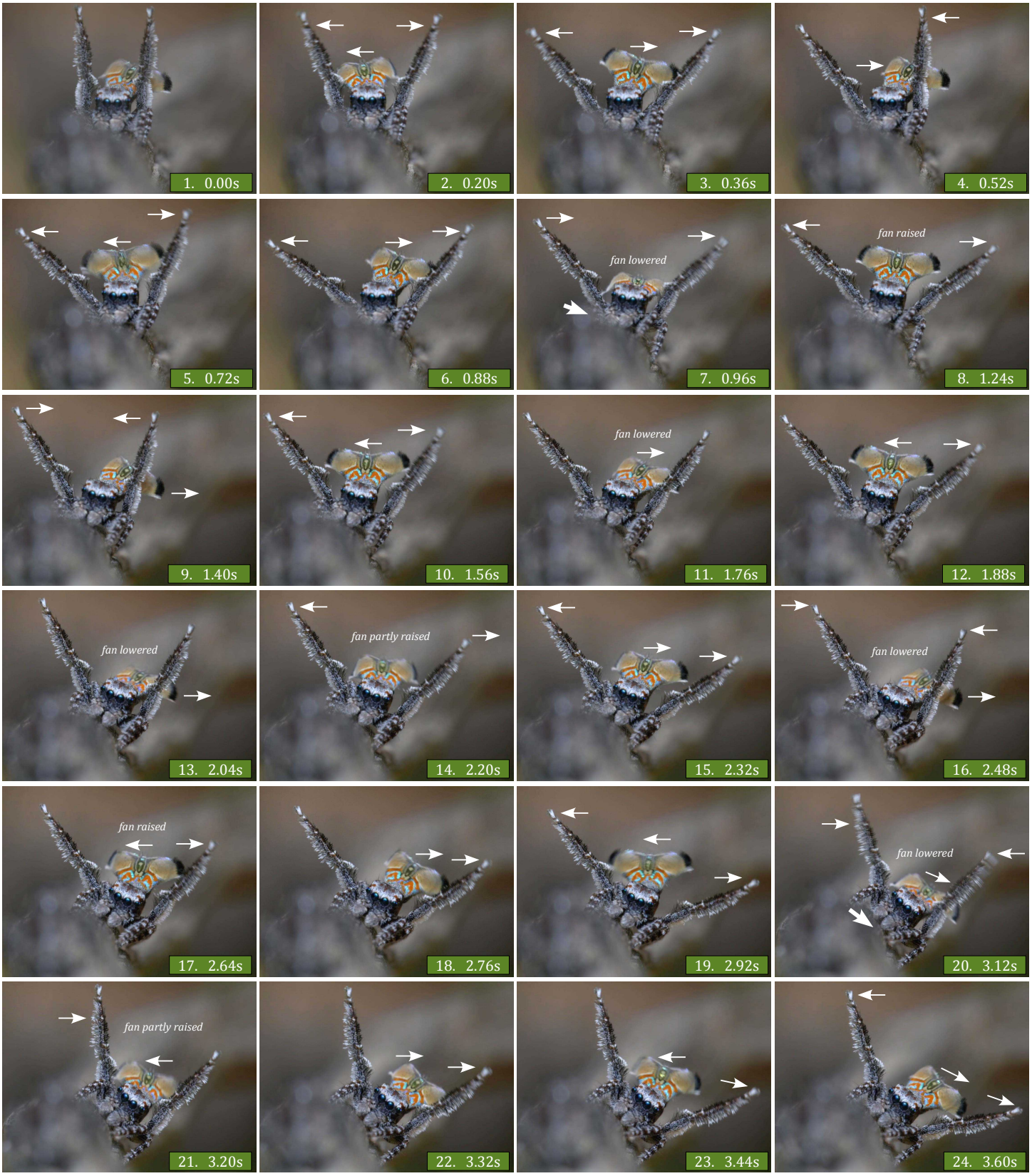


**Figure 14 (continued on next page).** Selected sequential frames (25 fps video) showing continuous movement of the fan and extended legs III during the *active fan dance* of a male *Maratus aquilus*. The female (blurred image at lower left) was directly in front of this male. **7, 20,** Each larger arrow identifies a step to the spider's left side.

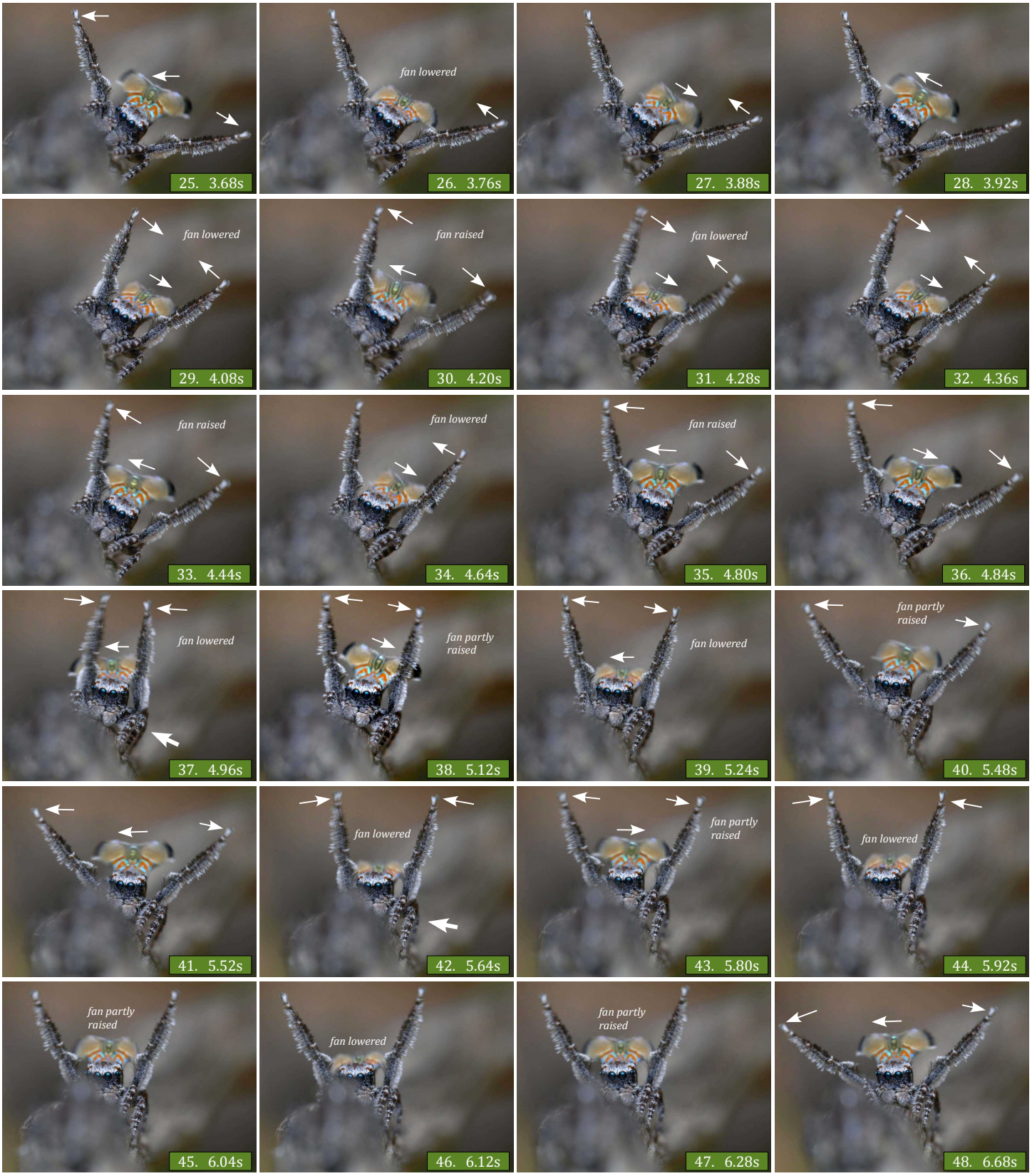


**Figure 14 (continued from previous page).** Selected sequential frames (25 fps video) showing continuous movement of the fan and extended legs III during the *active fan dance* of a male *Maratus aquilus*. **37, 42,** Each larger arrow identifies a step to the spider's right side.

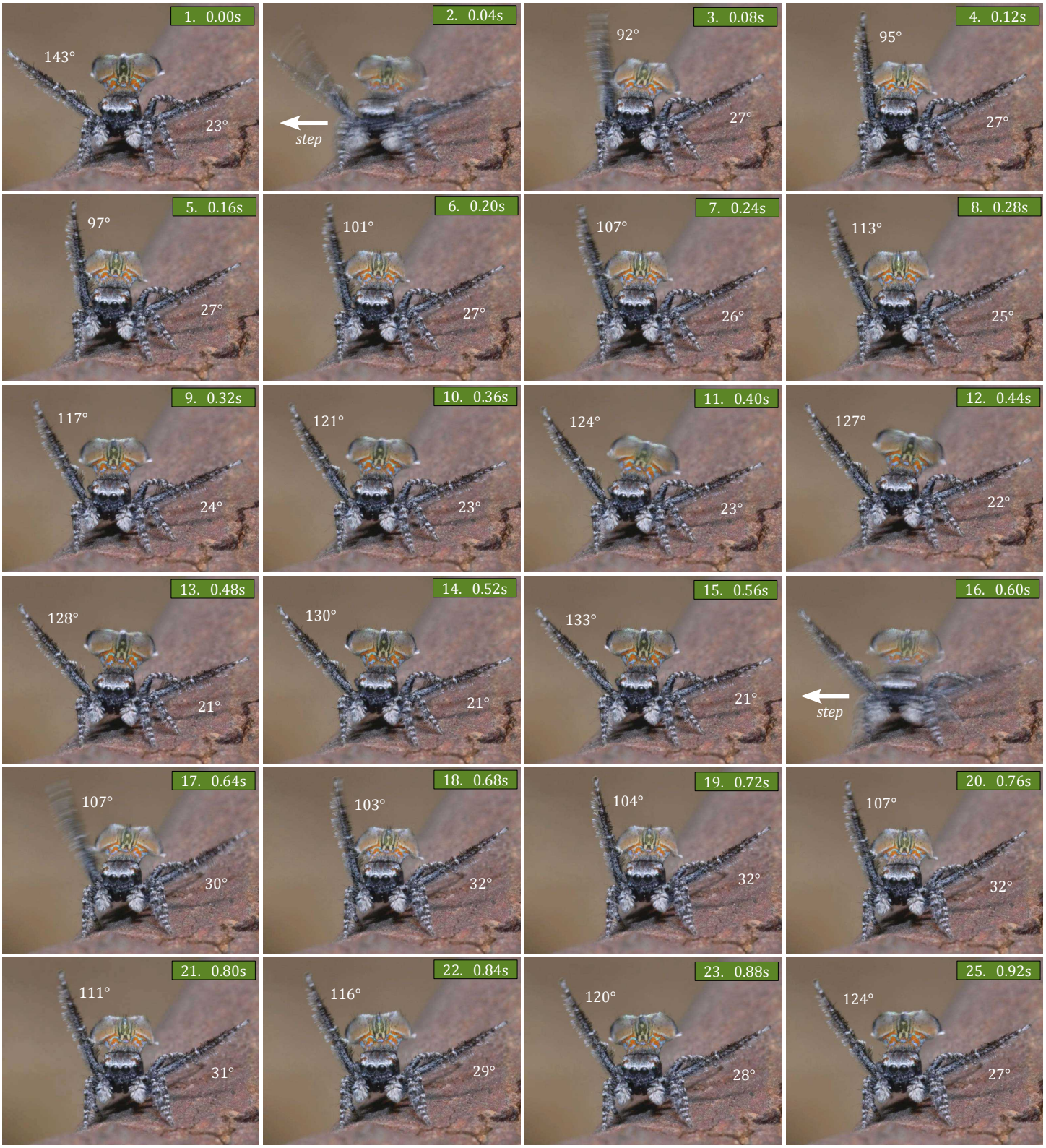


**Figure 15.** Consecutive frames (25 fps video) showing movement of the fan and extended legs III during the *active fan dance* of a male *Maratus aquilus*. **2, 16,** Each large arrow identifies a step to the spider's right side as the lead leg III was raised to a near-vertical position.

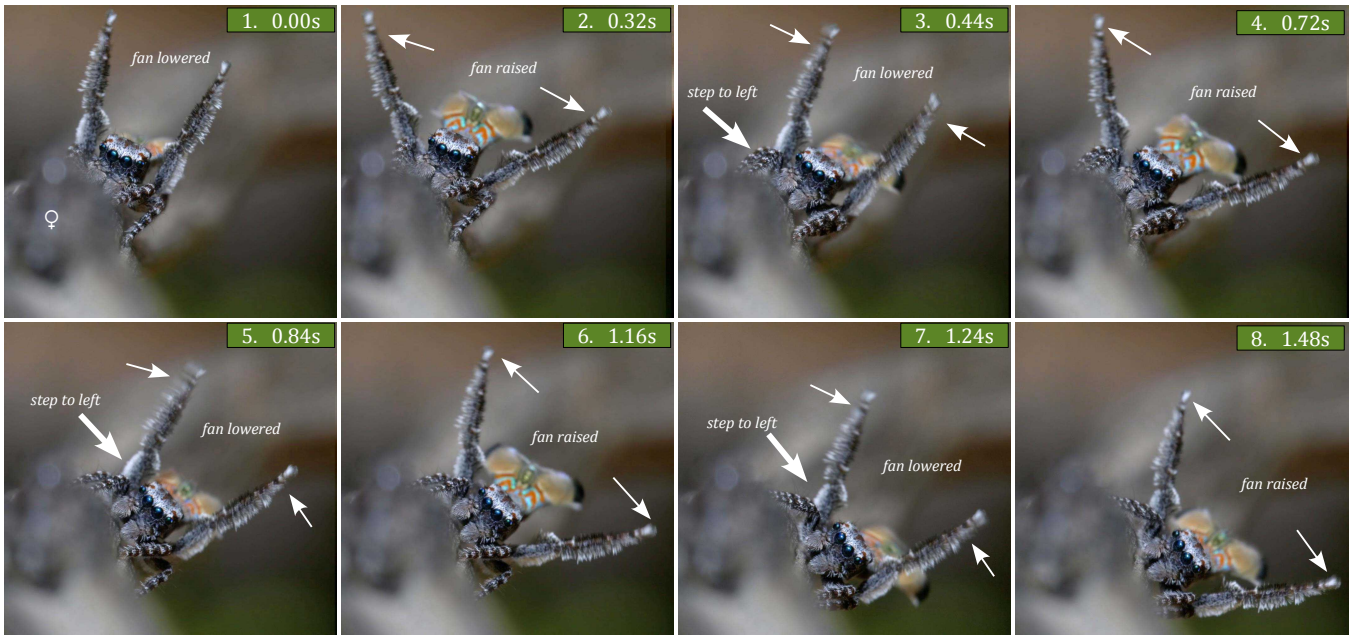


**Figure 16.** Selected frames (25 fps video) showing movement of the fan and extended legs III during the *active fan dance* of a male *Maratus aquilus*. The female (blurred image at lower left) was directly in front of this male. Each time that this spider stepped to one side (3, 5, 7) the fan was lowered and legs III were raised to a near-vertical orientation.


**Figure 17.** Sequential photographs showing transition to a *close fan dance* by male *Maratus aquilus* as a female approached (6-7, blurred image in foreground).


**Figure 18.** Photographs depicting typical positions associated with either an *elevated fan wave* or an *active fan dance* of a male *Maratus aquilus*.


**Figure 19.** Photographs depicting typical positions associated with the *active fan dance* of a male *Maratus aquilus*. **1-3,** Lateral rotation of the fan during an *active fan dance* can resemble its movement during the *close fan dance*, but legs III are not drawn together to a central position. **4-6, 8-9, 10-13,** Each of these sequences shows movement of the male toward a female (blurred image in foreground).

*Close fan dance* (Figures 20-28). The *close fan dance* of male members of the *vespa* group is unusual, even when compared to the elaborate courtship seen in other *Maratus* groups, in that it involves close scrutiny of a male by an attending female following each movement of that male at a distance of several millimeters. In the *vespa* group, this represents one last test for the male before female acceptance can be assured. Compared to the rigorous movement of an *active fan dance*, the *close fan dance* is very controlled, limited to movement of the partly elevated fan from side-to-side to alternately expose the flap on either side, all behind a visual barrier imposed by the elevation of legs III. Male *Maratus aquilus* bring their extended legs III close together in a vertical orientation during this display, often touching. This leaves only a small window at the center through which an iridescent green posterodorsal *ornament* can be displayed toward the front.

This display can include many *center-to-right-to-center-to-left-to-center* cycles (~6.2s/cycle) over several minutes and appears to last as long as the attending female turns to follow each movement of the male. Most of the time (~72%) the partly elevated fan was displayed at the center where it was rotated vertically and laterally through a small amplitude to display the iridescent green posterodorsal ornament, adorned at the rear with a small group of bright, light-blue iridescent scales. Each lateral rotation of the fan, to the left or right, involved 2-7 smaller *wave cycles* at a rate of ~0.193/s (Figures 25, 27). Movement of the fan to one side or the other and then back to the center is so fast that it is usually completed before the female can finish a turn to face it. In effect we observe the female turning rapidly from side to side to catch a glimpse of a rapidly moving but elusive target.


**Figure 20.** Sequential photographs (1-4) showing a female *Maratus aquilus* turning from side to side to follow the *close fan dance* of a male. As with other members of the *vespa* group, legs IV are extended far to the rear during this display, allowing for movement of the fan toward each side of the elevated legs III.


**Figure 21.** Selected sequential frames (1-10) showing a female *Maratus aquilus* turning from side to side to follow the *close fan dance* of a male.

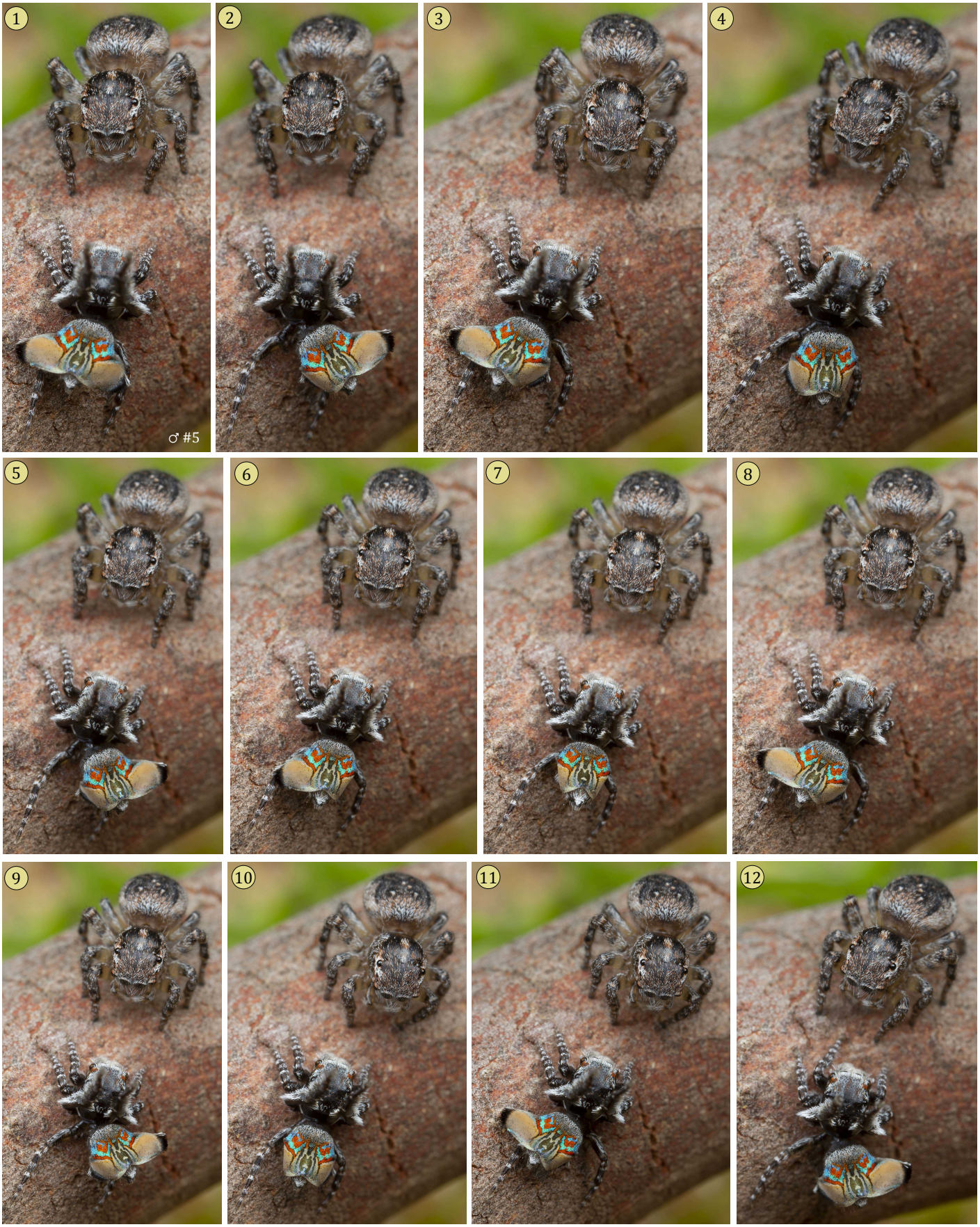


**Figure 22.** Sequential photographs (1-12) showing a female *Maratus aquilus* turning from side to side to follow the *close fan dance* of a male. Usually movement to display the lateral flap on one side is completed before the female can complete a turn to face the respective direction.


**Figure 23.** Photographs showing the close fan dance of a male *Maratus aquilus* in front of a female. **1-3,** Lateral views of this display. Note the elevation of the posterodorsal fan ornament when the partly elevated fan is held at the center position (1, 3). **4-10,** Sequential rear views of this display showing alternating extension of the lateral flap on either side.


**Figure 24 (continued on next page).** Sequential photographs showing the close fan dance of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image at lower left).


**Figure 24 (continued from previous page).** Sequential photographs showing the close fan dance of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image at lower left).

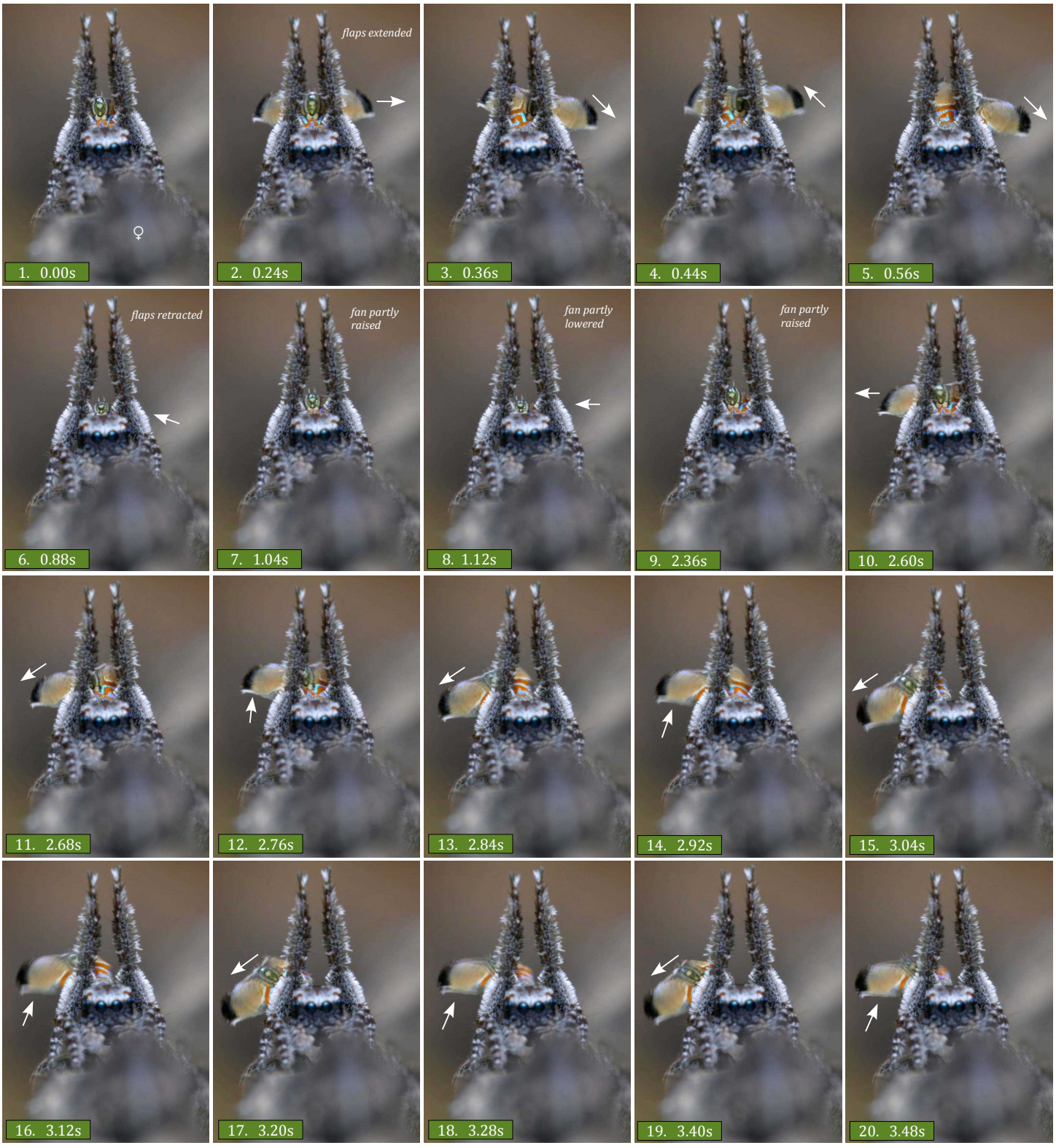


**Figure 25 (continued on next page).** Selected sequential frames (1-80, 25 fps video) showing the *close fan dance* of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image in foreground). Arrows indicate movement of the fan relative to its position in the preceding frame. The partly elevated fan was first waved for 2-7 cycles (3-4 represents one *wave cycle*) to one side, then centered, then waved for 2-7 cycles to the other side. The duration of each of these cycles averaged 0.193s. Most of the time (14.32s of 19.72s or 72%) the fan was moved up and down and from side to side through a low amplitude at the center, displaying the iridescent posterodorsal fan ornament through the window between legs III. **3-6,** 2 wave cycles to the left. **10-22,** 6 wave cycles to the right.

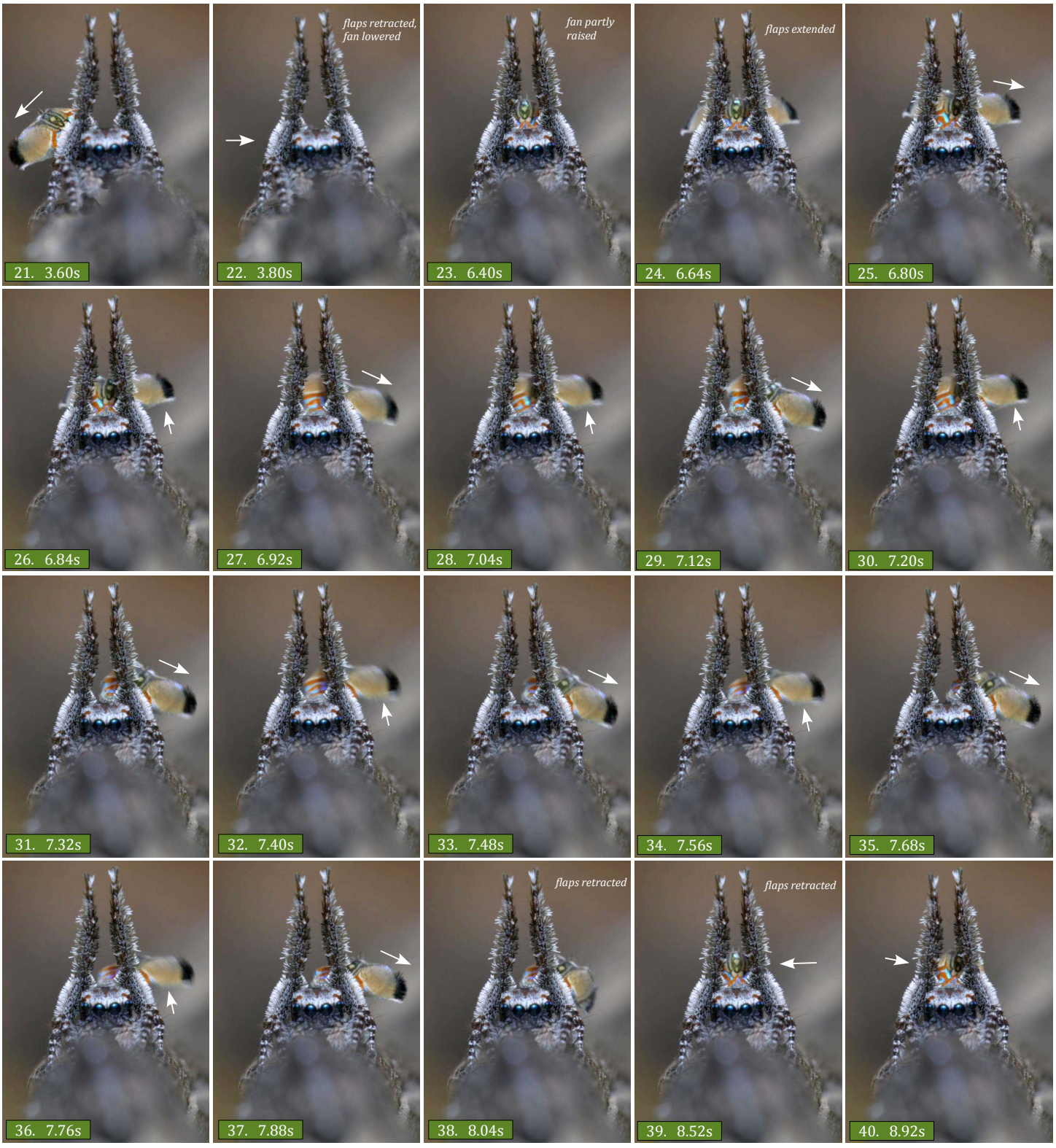


**Figure 25 (continued from previous page, continued on next page).** Selected sequential frames (1-80, 25 fps video) showing the *close fan dance* of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image in foreground). **25-37,** 6 wave cycles to the left.


**Figure 25 (continued from previous page, continued on next page).** Selected sequential frames (1-80, 25 fps video) showing the *close fan dance* of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image in foreground). **43-55,** 6.5 wave cycles to the right.

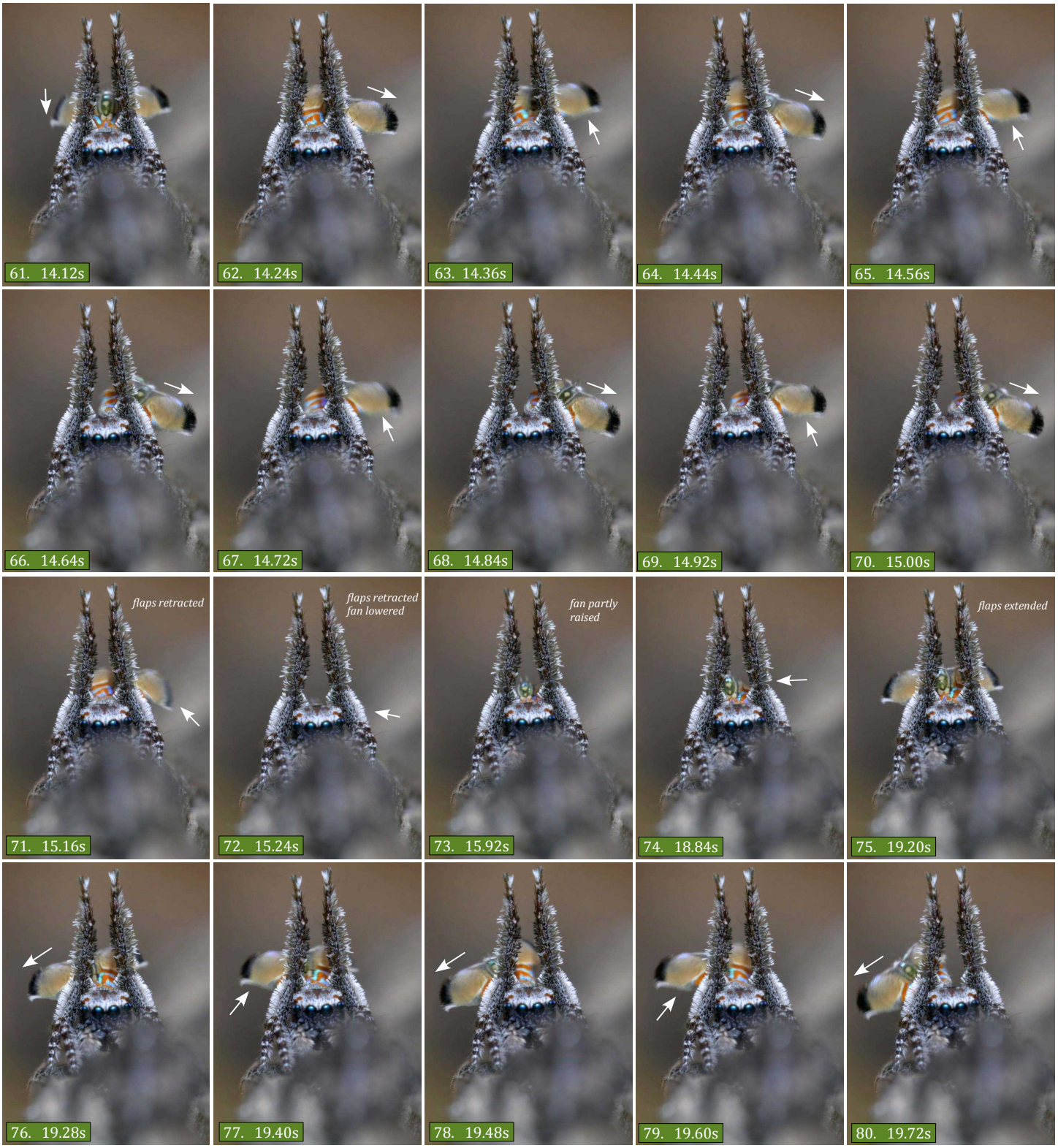


**Figure 25 (continued from previous page).** Selected sequential frames (1-80, 25 fps video) showing the *close fan dance* of a male *Maratus aquilus* from the perspective of a closely attending female (blurred image in foreground). **62-71,** 5 wave cycles to the left. **76-80,** 2.5 wave cycles to the right.

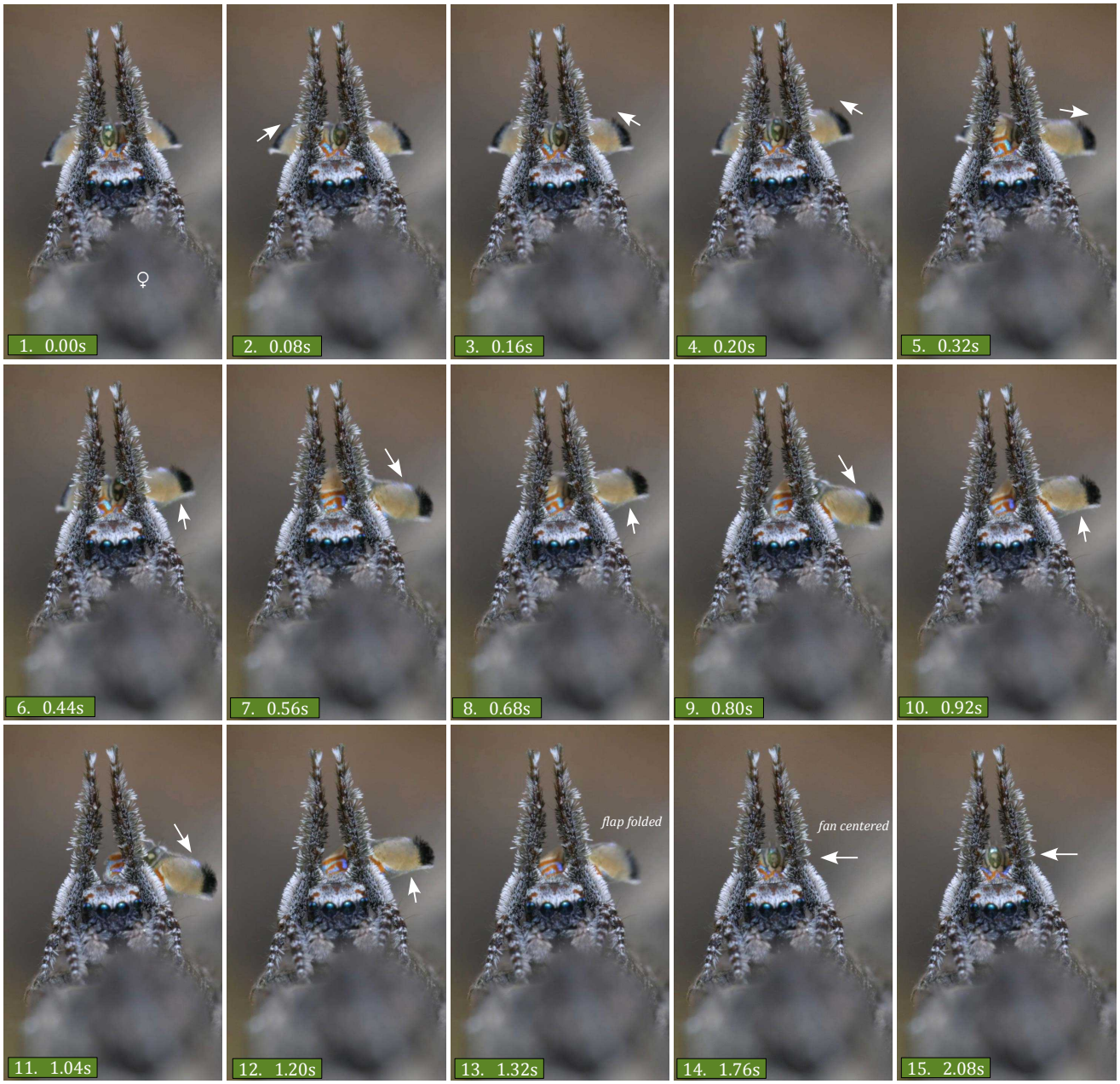


**Figure 26.** Sequential frames (1-15, 25 fps video) showing each step of the *close fan dance* of a male *Maratus aquilus* from the perspective of an attending female (blurred image at lower right). **5-12,** 4 wave cycles to the left. **1, 15,** Note the light blue iridescent flash at the top of the centered posterodorsal fan ornament.

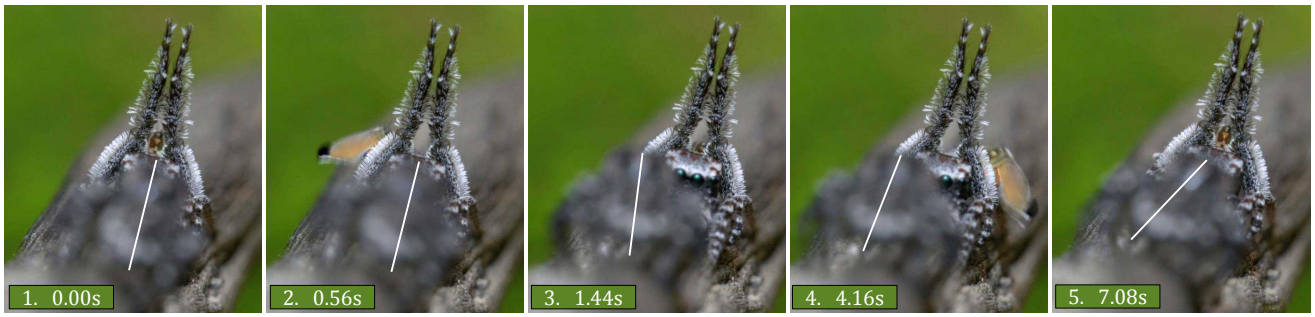


**Figure 27.** Sequential frames (1-15, 25 fps video) showing alignment of the midline of the turning female (white lines) attending to the *close fan dance* of a male *Maratus aquilus*. Frames are from an ~80s display sequence that included ~13 center-to-right-to-center-to-left-to-center cycles (~6.2s/cycle). Most of the time the fan was displayed in a center position (1, 3, 5) and moved up and down or sideways through a small amplitude.

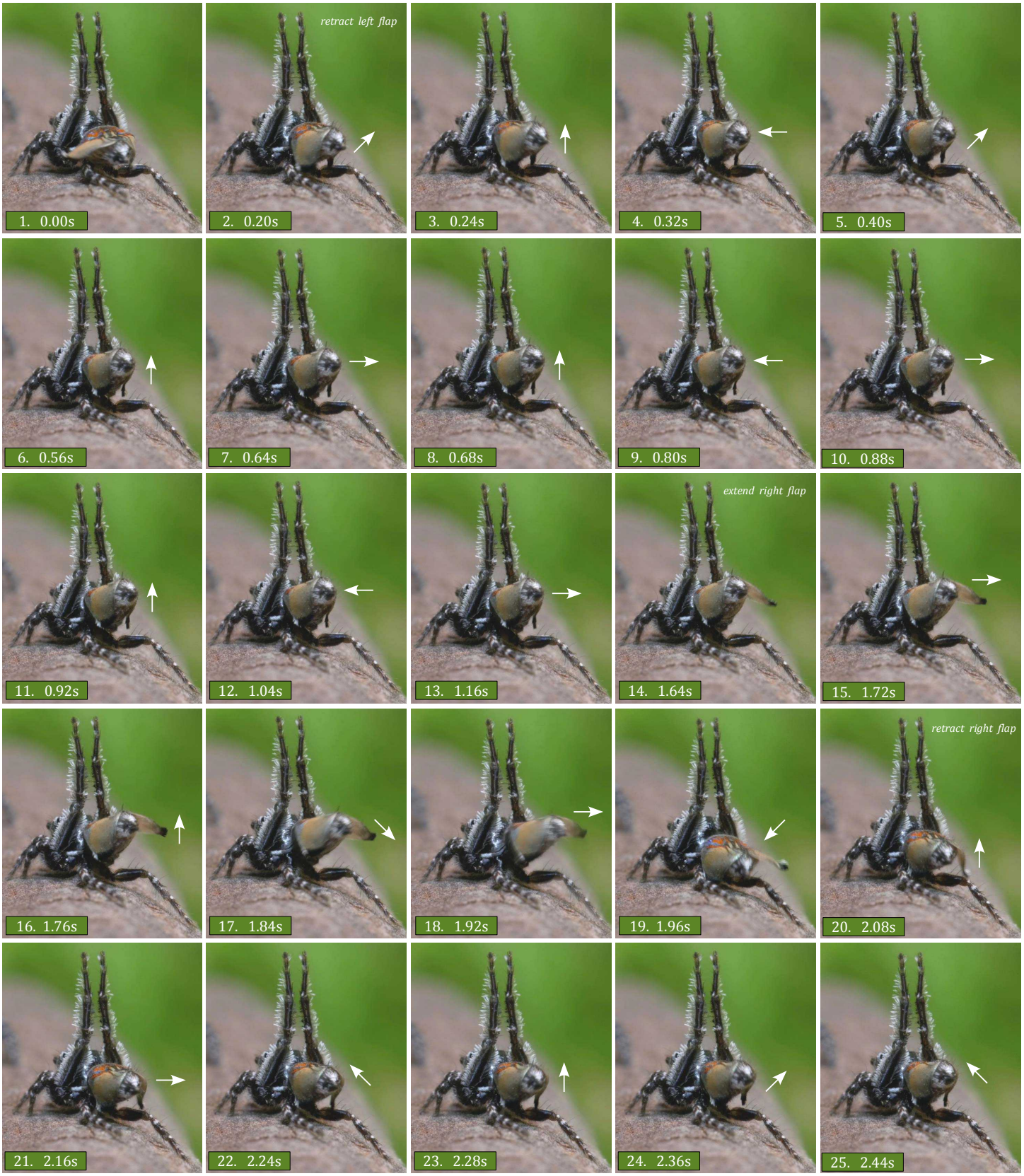


**Figure 28.** Sequential frames (1-25, 25 fps video) showing each position of the opisthosoma during the close fan dance of a male *Maratus aquilus* in front of a female, viewed from the rear. Each arrow indicates movement of the opisthosoma relative to the preceding frame. **3-13, 20-25,** Low amplitude movement of the partly elevated fan near the center position with flaps retracted. **15-18,** Two wave cycles to the right with the right flap extended.

*Female display* (Figures 29-30). As previously reported for other *Maratus* species, female *M. aquilus* appear to indicate rejection of a male in the vicinity by elevating their opisthosoma and slowly waving one or both legs III.

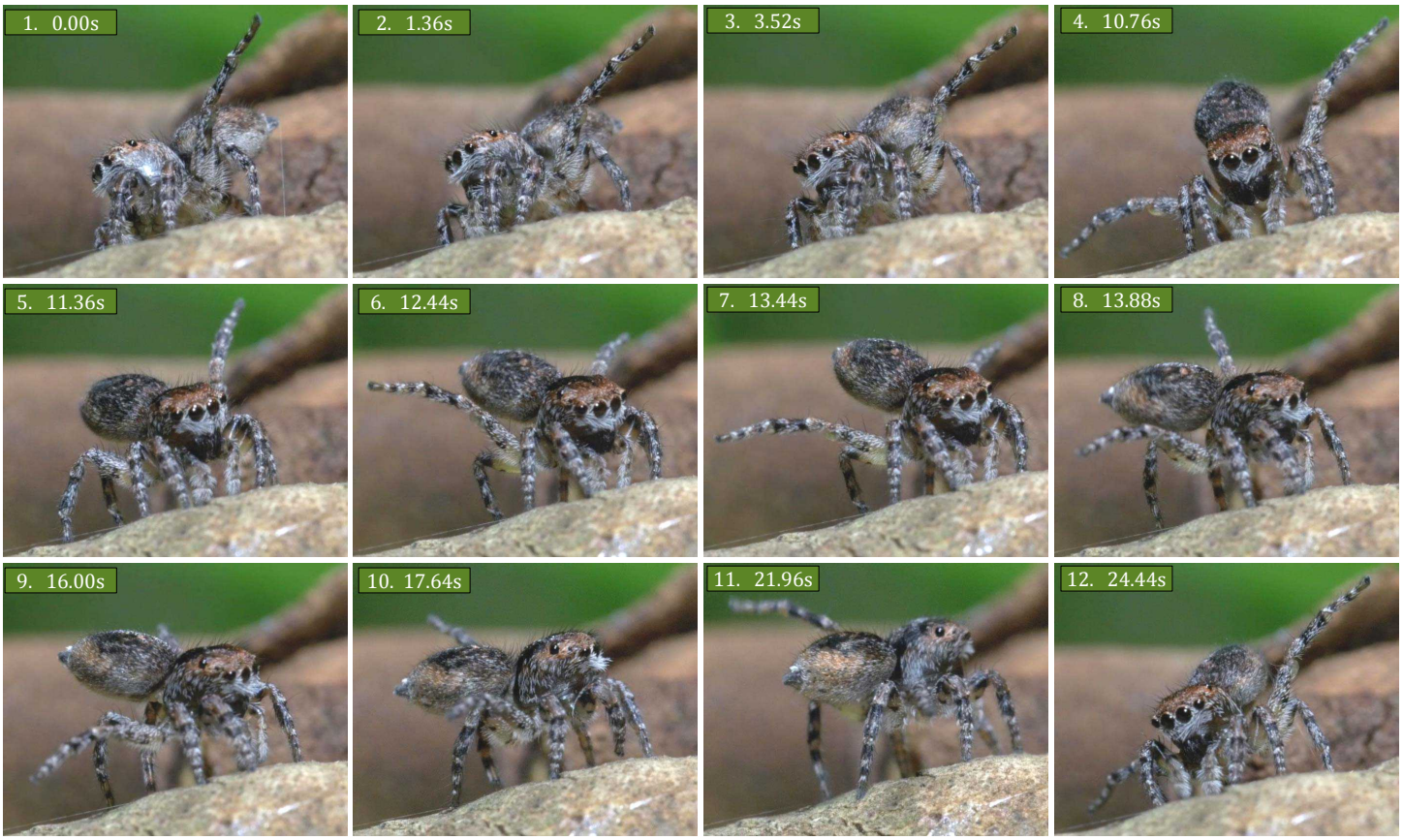


**Figure 29.** Sequential frames (1-12, 25 fps video) showing the display of a female *Maratus aquilus*.

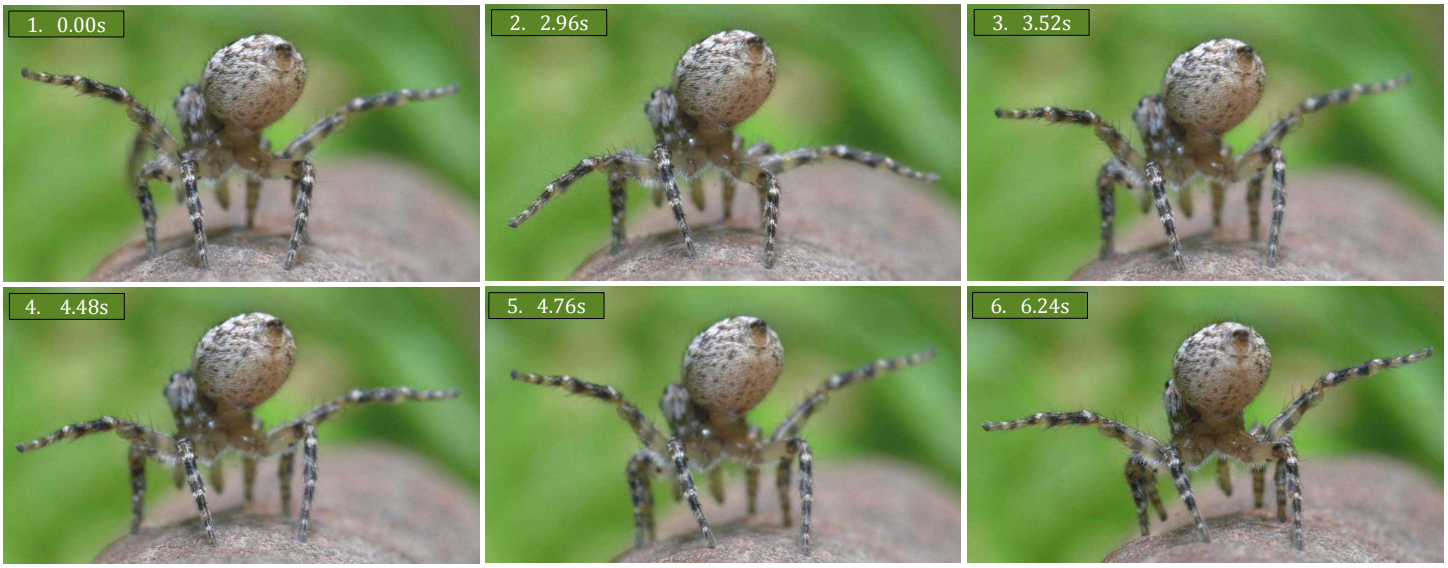


**Figure 30.** Sequential frames (1-6, 25 fps video) showing the display of a female *Maratus aquilus*.

*Final approach and mating*. Once a female stops turning from side to side the male *Maratus aquilus* will approach from the front with legs III extended laterally and tap the top of the female carapace with legs I before mounting (Figure 31:1). The same behaviour has been reported for other *Maratus* species. As in other *Maratus* species, the female opisthosoma can be rotated through a 180° angle to facilitate mating (Figure 31:2-7). The male opisthosoma is elevated with flaps folded when mating.

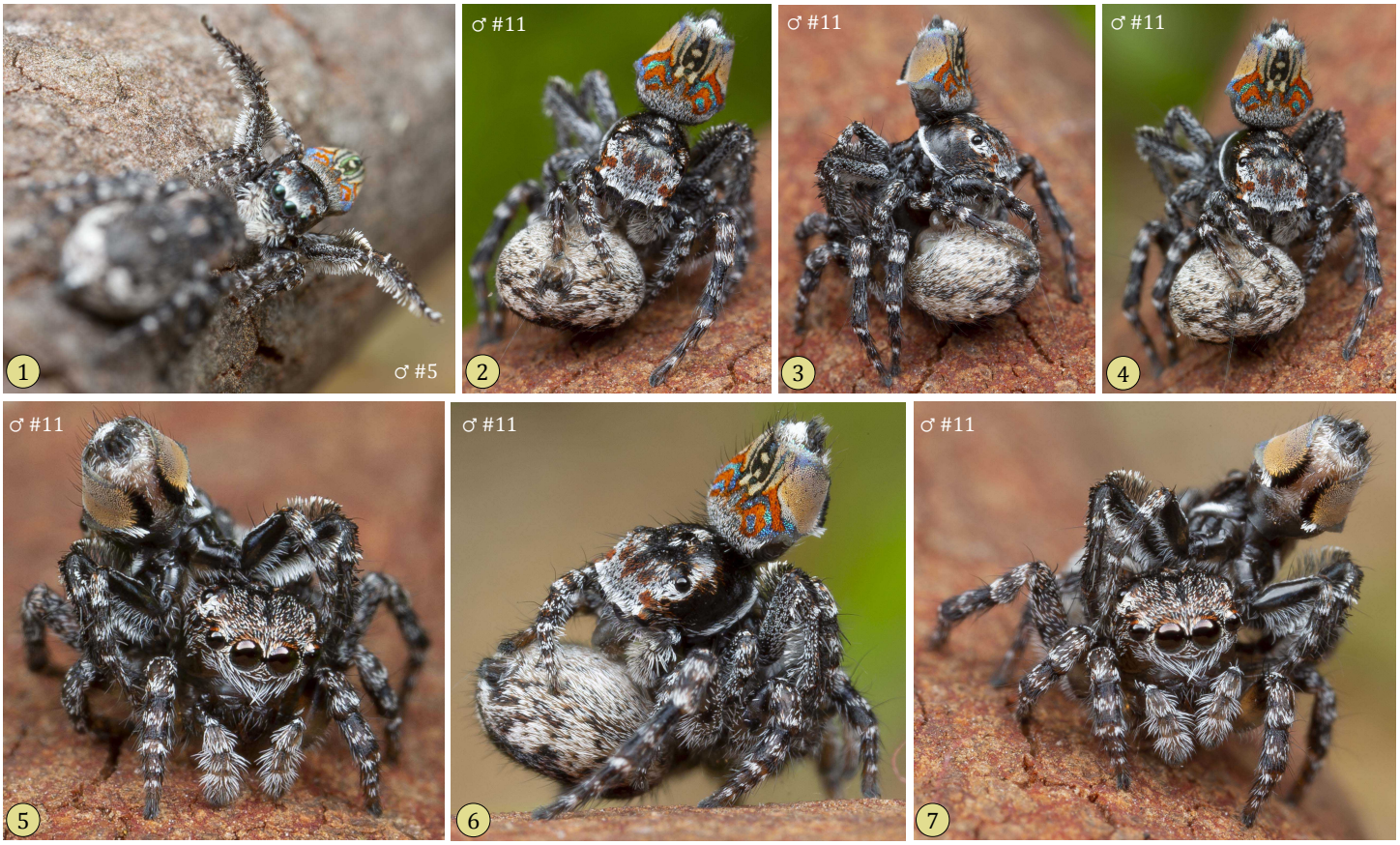


**Figure 31.** Final approach of a courting male (1), and mating by a *Maratus aquilus* pair (2-7).

*Discussion*. The *vespa* group of the genus *Maratus* is of particular interest because it includes a diverse set of related species, each endemic to a limited range in the southwestern corner of Australia. In addition the courtship display of species in this group includes performance of a highly interactive *close fan dance* with prolonged female inspection of the male at a very short distance. Earlier stages of courtship by these spiders, including the *active fan dance*, resemble those seen in other *Maratus* groups. But in the *vespa group* it appears that this display, as colourful and active as it may be, does not by itself lead to female acceptance. In this group it represents, rather, an invitation to participate in the next stage, a *close fan dance*.

Based in part on the focus on spider genitalia by taxonomists (Eberhard 2010), it is widely thought that speciation within the Araneae, like speciation in other arthropod groups, is closely tied to the coevolution of male and female genitalia, or *lock and key* coevolution (Sota & Kubota 1998; Huber et al. 2005; Eberhard & Huber 2010; Brennan & Prum 2015; Genevcius et al. 2016). This evolution may be driven by selection against hybridization, sexual antagonism (differing objectives of males and females), or by what is known as *cryptic female choice* (female control of the fate of sperm secured from a male). Models suggest that both male and female genitalia can evolve rapidly to support divergence of isolated populations (Simmons & Fitzpatrick 2019).

But in many salticid genera, including *Maratus*, there is little variation in the structure of the male pedipalp and the female epigynum. Indeed, the genitalia of all species placed in the *vespa* group are nearly identical, and very similar to the genitalia of several other *Maratus* groups endemic to southwestern Australia (Otto & Hill 2016, 2017, 2018, 2019a; Schubert 2019).

From the great diversity of form, colouration and display it seems evident that sexual selection in the genus *Maratus* is associated not with structural modification of the genitalia, but with ornamentation of males, and related behaviour of both males and females. Rapid coevolution of these characters may be driven by a low *cost of choice* or a relatively small penalty associated with rejection of some suitors (Pomiankowsi & Iwasa 1993, 1998; Mead & Arnold 2004; Seddon et al. 2013; Harrison et al. 2015). *Fisher runaway selection* is a proposed mechanism for the rapid coevolution of these secondary sexual characteristics that contribute to mating success, even at the cost of reduced survival, and models indicate that this can readily account for the presence of *multiple* male ornaments and related male and female behaviours (Fisher 1930; Harvey & Arnold 1982; Pomiankowsi & Iwasa 1993; Kuijper et al. 2012). *Fisher runaway selection* may also support associative mating (mating restricted to a subpopulation) and sympatric speciation (Payne & Krakauer 1997), although this subject is controversial and needs real-world demonstration.

Even with the possibility of reproductive isolation and sympatric speciation, studies of other animal groups (e.g. Worsham et al. 2017) suggest that speciation within the *vespa* group may be primarily *allopatric*, driven by a combination of rapid *Fisher runaway selection* and some degree of geographic isolation related to a low dispersal rate. Dispersal behaviour may represent a flexible response at the individual level (e.g., a spider may move if prey is locally scarce) but there may also be alleles that favor low-dispersal and high-dispersal in the same population (McPeek & Holt 1992; Lowe & McPeek 2014). If a species becomes established in an area, or the degree of isolation of that area (*landscape connectivity*) changes, the relative frequency of alleles or genes related to dispersal may change in a local breeding population or *deme* (Olivieri et al. 1995; Henriques-Silva et al. 2014). The low fertility rate (offspring per female) of *Maratus* species must certainly limit their dispersal. Although physical barriers to dispersal clearly have an impact on speciation, models suggest that genetic isolation of local demes (*stochastic phylogeographic discontinuities*) can develop in the absence of these barriers (Kuo & Avise 2005).

Subtle differences in ecology or microhabitat may also be at play here, selecting for divergent and adaptive characters in separate demes, then driving an increased level of sexual selection to reduce the possibility of deleterious hybridization between demes (van Doorn et al. 2004). Southwestern Australia represents a Mediterranean (dry summer and wet winter) ecosystem that has high rainfall reliability (particularly during the dry season when drought is moderate), low soil fertility, and selection by fire under a 3-20 year interval; the reliability or stability of this climate appears to have supported a higher level of speciation and a lower level of extinction during the Pleistocene (Cowling et al. 2004). This Mediterranean ecosystem is still incredibly diverse with respect to both species and microhabitats, and the greatest biodiversity can be found toward the southwestern corner (Judd et al. 2008). The *flavus*, *linnaei* and *vespa* groups of the genus *Maratus* are all endemic to this corner of Australia (Otto & Hill 2019b).

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