

Courtship display by the peacock spider *Maratus robinsoni* (Araneae: Salticidae: Euophryini: Australphryni): use of flashing light reflected from the surface of nanoscale diffraction gratings

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Summary. A 29.97 fps video record of the courtship display of a male *Maratus robinsoni*, recorded in the field, was used to measure the positions and movement of this spider as it courted a female. During this display the male makes short steps from side to side in front of the female, with the fan fully erected and expanded to display tracts of iridescent scales. At the same time the fan is also rotated from side to side, the pedipalps are moved up and down, and sometimes a leading leg III is extended and then flexed to the side in which the spider is moving. The structural features contributing to the rainbow colours of these scales, as well as their function under natural lighting, are reviewed.

Keywords. Australia, grating formula, iridescence, microhabitat, reflective diffraction grating, spectral interference

The remarkable iridescent scales of the small (♂ ~2.3-2.9 mm) Australian peacock spider *Maratus robinsoni* Otto & Hill 2012 (Otto & Hill 2012a, 2012b) have been the subject of several studies in recent years (Hsiung et al. 2017; Wilts et al. 2020; Hill 2022). These scales are noteworthy because each has two regular, reflective diffraction gratings on its surface, one on either side. Each field of iridescent scales on the fan is surrounded by velvet black scales that absorb light (see McCoy et al. 2019). In addition, they can reflect (or diffract) light that spans the entire visible spectrum (Figures 1-2). Hsiung et al. (2017) reported that the surface of these gratings was convex, but only one of their figures (fig. 2i; see Figure 12.4) supports this; in their other figures (figs. 2e, 2g; see Figures 12.2-12.3) they are flat. A later study by Wilts et al. (2020) included SEM images of only flat gratings. The iridescent scales of several other peacock spiders (*M. chrysomelas*, Hsiung et al. 2017; *M. nigromaculatus*, Wilts et al. 2020) have less regular gratings on convex surfaces.

Originally found at Newcastle near the coast of New South Wales, *Maratus robinsoni* have now been found at a number of different locations in southeastern Australia, from the Sunshine Coast of Queensland to the border of South Australia and Victoria (Figure 3). These spiders appear to shelter in the ground, possibly between sand grains on beaches or in sandy soils. They are generally observed on or near the ground (Otto & Hill 2012a, 2012b). Adult females, not previously figured or formally described, are shown in Figure 4. Their light colours apparently provide camouflage on a sandy soil.

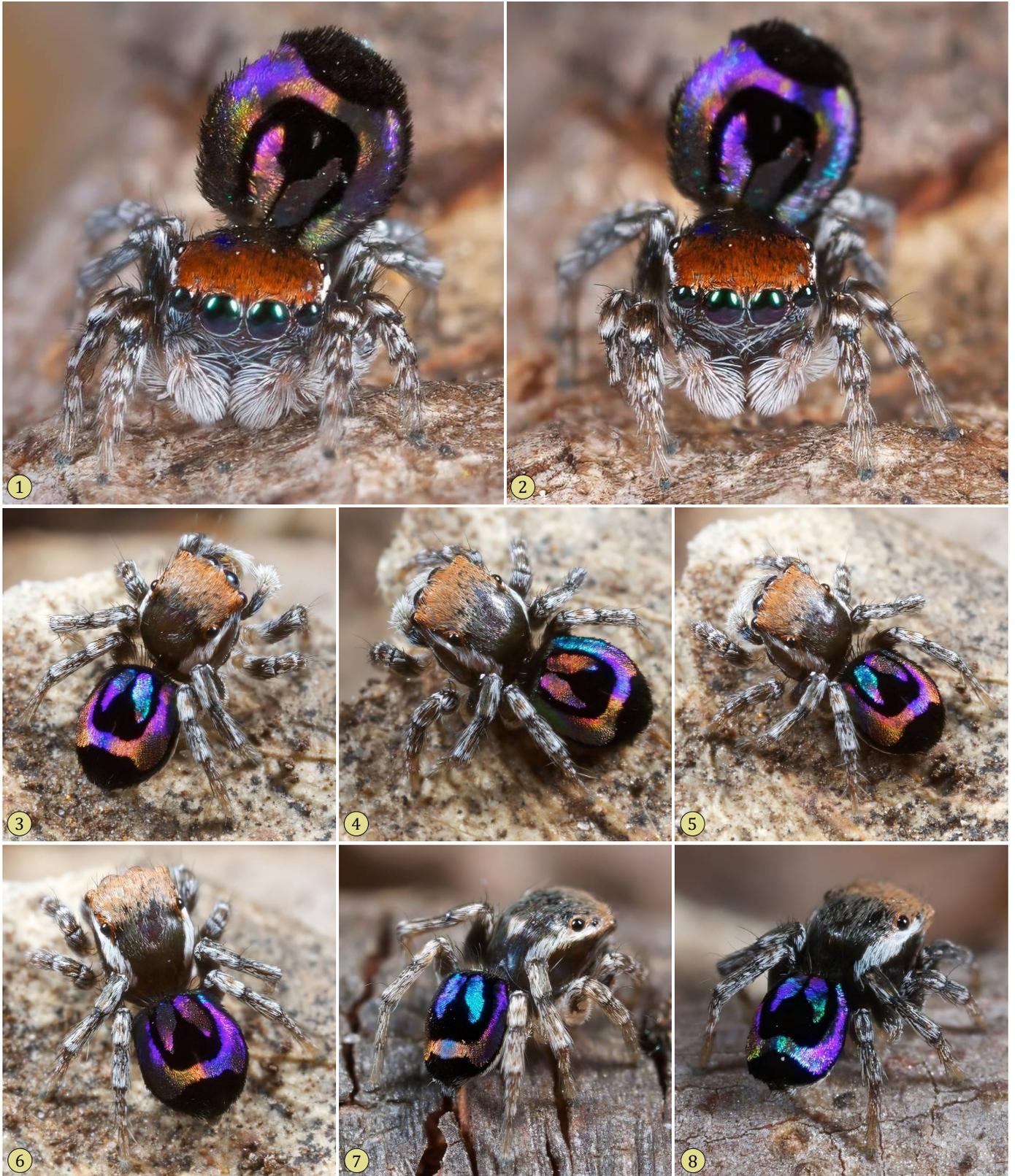


Figure 1. Adult ♂ *Maratus robinsoni*, photographed indoors in a natural setting. **1-2**, Front view of courtship display. Based on reflections from the eyes, you can determine that these photos were taken with two light sources. The tracts of iridescent scales are surrounded by jet-black scales that prevent reflection of light. The many colours of these iridescent scales span the entire visible spectrum, and the colour that is observed depends on the direction of incident light, the spectrum of incident light, and the direction of the observer. In photographs, this colour also depends on the spectral sensitivity and image processing software of the camera.

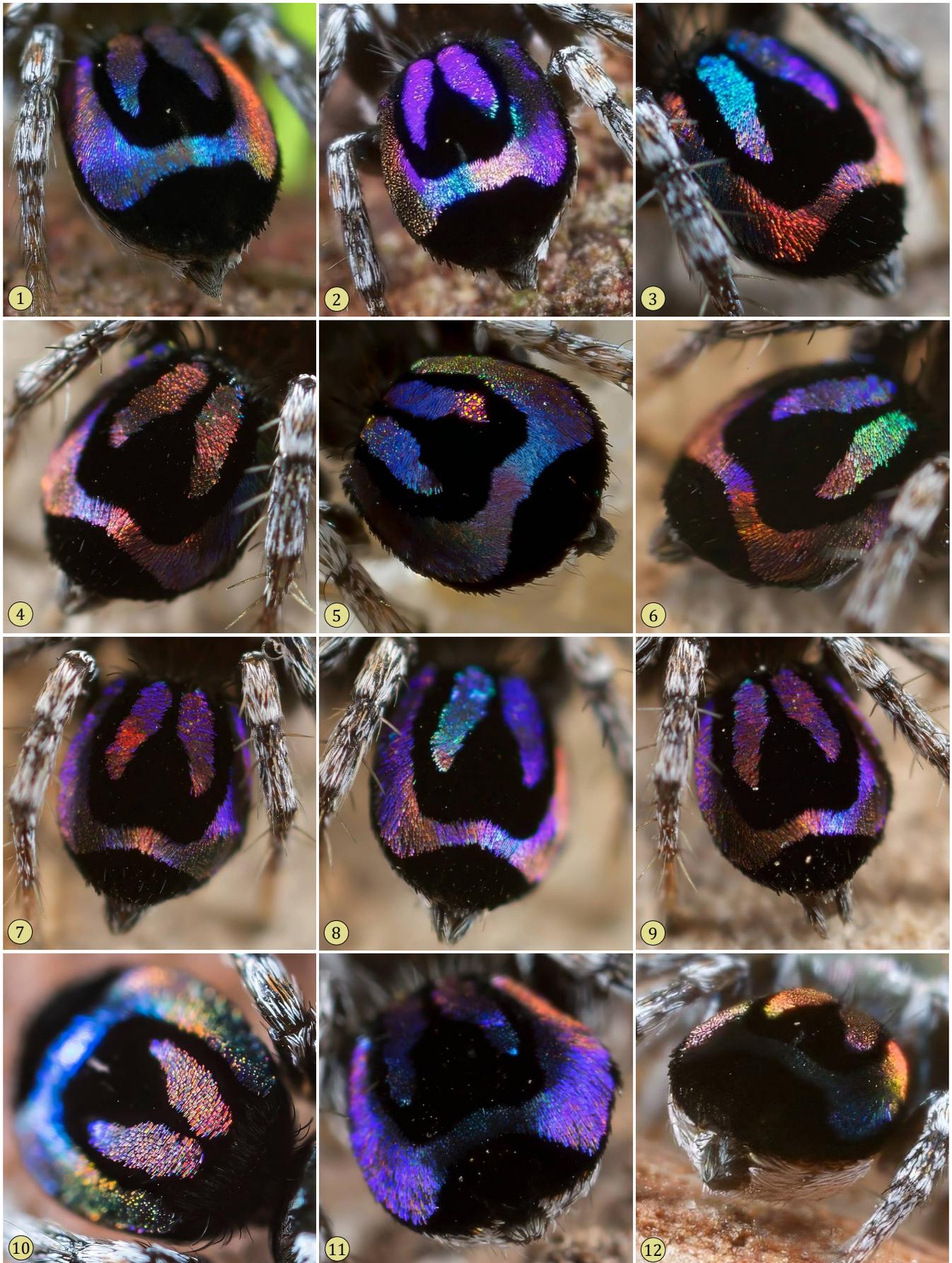


Figure 2. Dorsal opisthosoma (or fan) of adult ♂ *Maratus robinsoni*, photographed indoors in a natural setting.

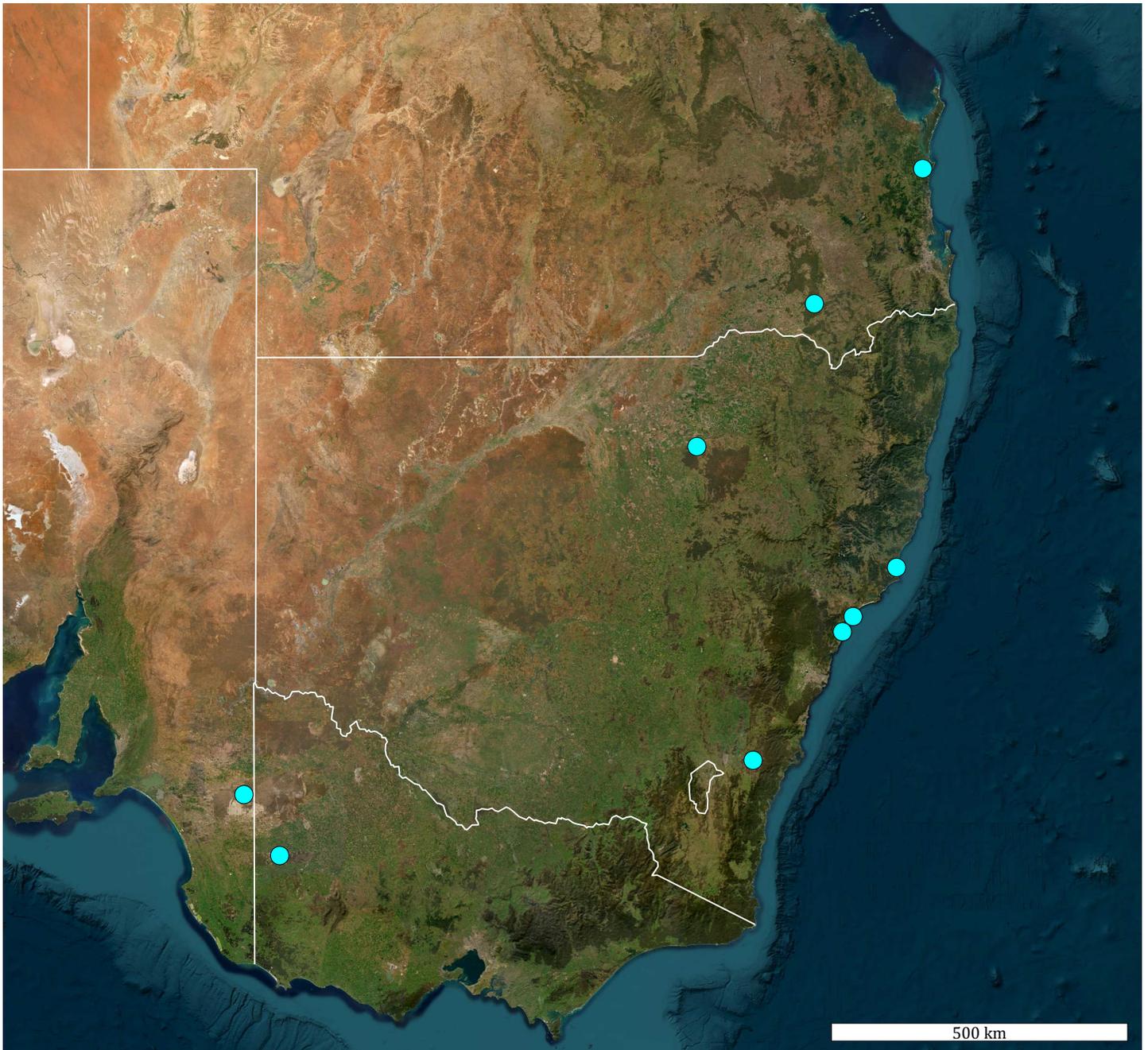


Figure 3. Known distribution of *Maratus robinsoni* in southeastern Australia (based on Otto & Hill 2012b, 2021; Schubert 2020; Atlas of Living Australia (ALA) records; iNaturalist records). Relative to many *Maratus*, these have a wide distribution, and should be found at many other locations in the future. However, they are very small. Base map © OpenStreetMap.



Figure 4. Adult ♀ *Maratus robinsoni*.

Courtship display. Courtship by the male *Maratus robinsoni* is relatively simple. The basic dance, as we described previously, includes lateral movement from side to side by the male, facing a courted female. This includes lateral waving of the elevated and expanded fan (Otto & Hill 2012b). Flynn Prall recently recorded this display with 29.97 fps video in the field, at the edge of Wondul Range National Park. Frame by frame analysis of this video record now allows us to provide a more detailed description of this display (Figures 5-11).

Each sequence of this display was brief, usually ~2 s or less in duration, beginning with elevation and expansion of the fan, and ending when the fan is lowered (Figures 5-6). As the fan was moved (by rotating or waving, and by side-stepping) during this display, the spectral hue of light diffracted from its fields of iridescent scales varied considerably, as a result of changes in the direction of incident light. Stepping to one side and then to the other (step rate 6-12 Hz) coincided with waving of the fan (variable, 2-6 Hz per left-then-right cycle, over a large amplitude that may exceed 90°). At the same time the pedipalps were moved quickly (6-10 Hz up-down cycles, almost entirely synchronous; *pedipalp flicker*). In some displays (Figures 9, 11) a leading leg III was also elevated and extended, then flexed and lowered over a brief (~0.2 - 0.7 s) interval.

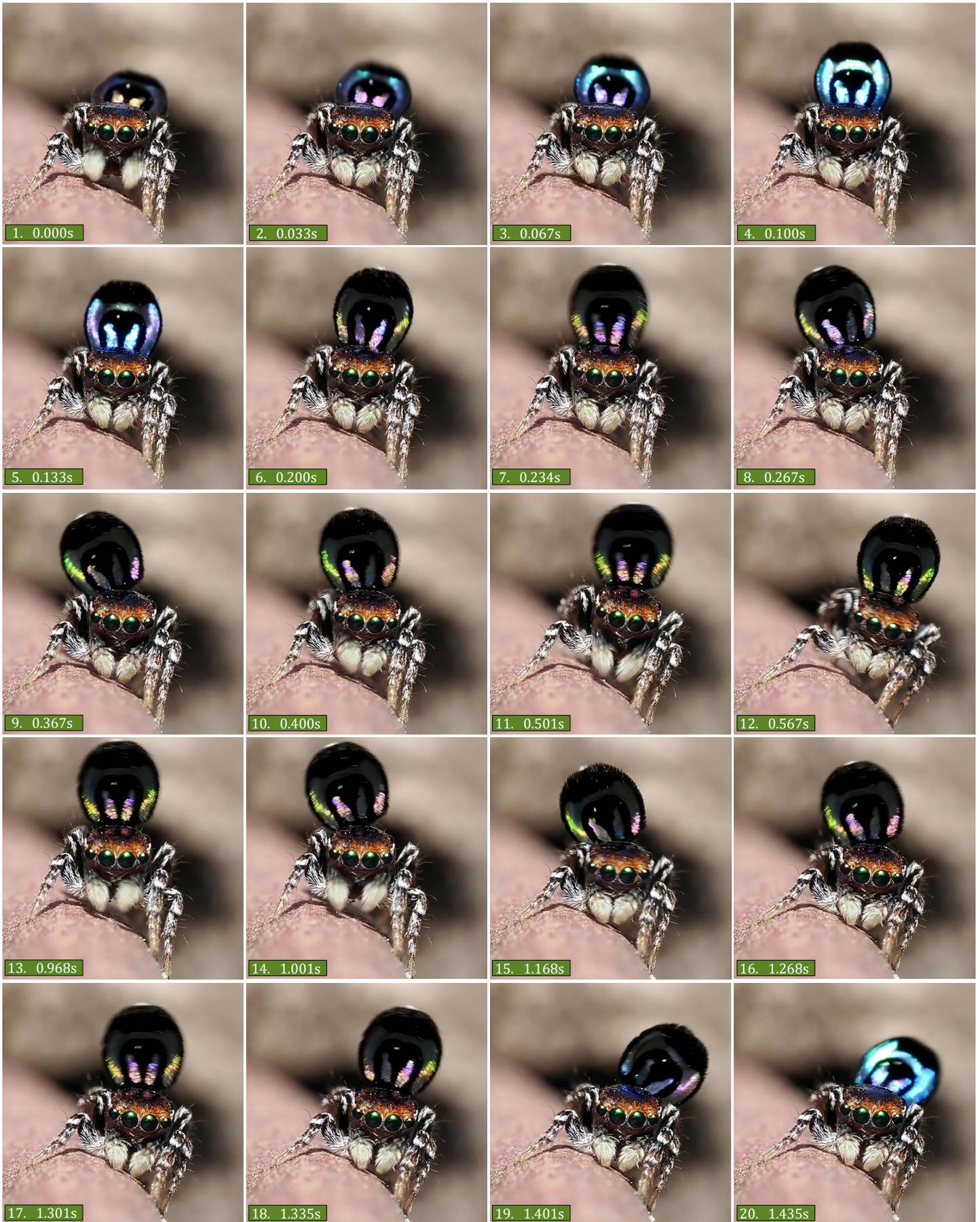


Figure 5. Selected frames from a 29.97 fps record of a display by a ♂ *Maratus robinsoni* that lasted for less than 1.5 s.

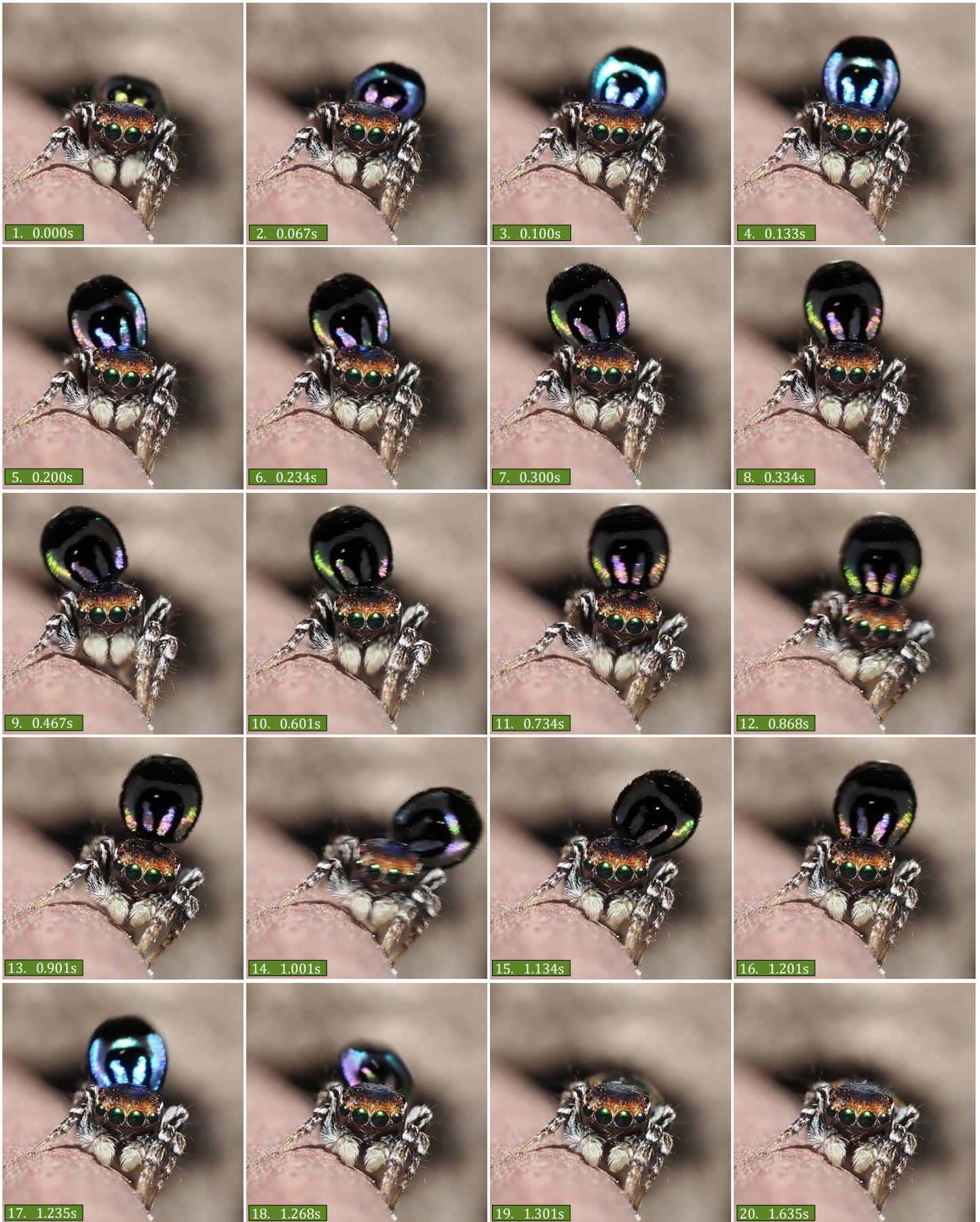


Figure 6. Selected frames from a different 29.97 fps record of a display by a ♂ *Maratus robinsoni* that lasted for less than 1.5 s.

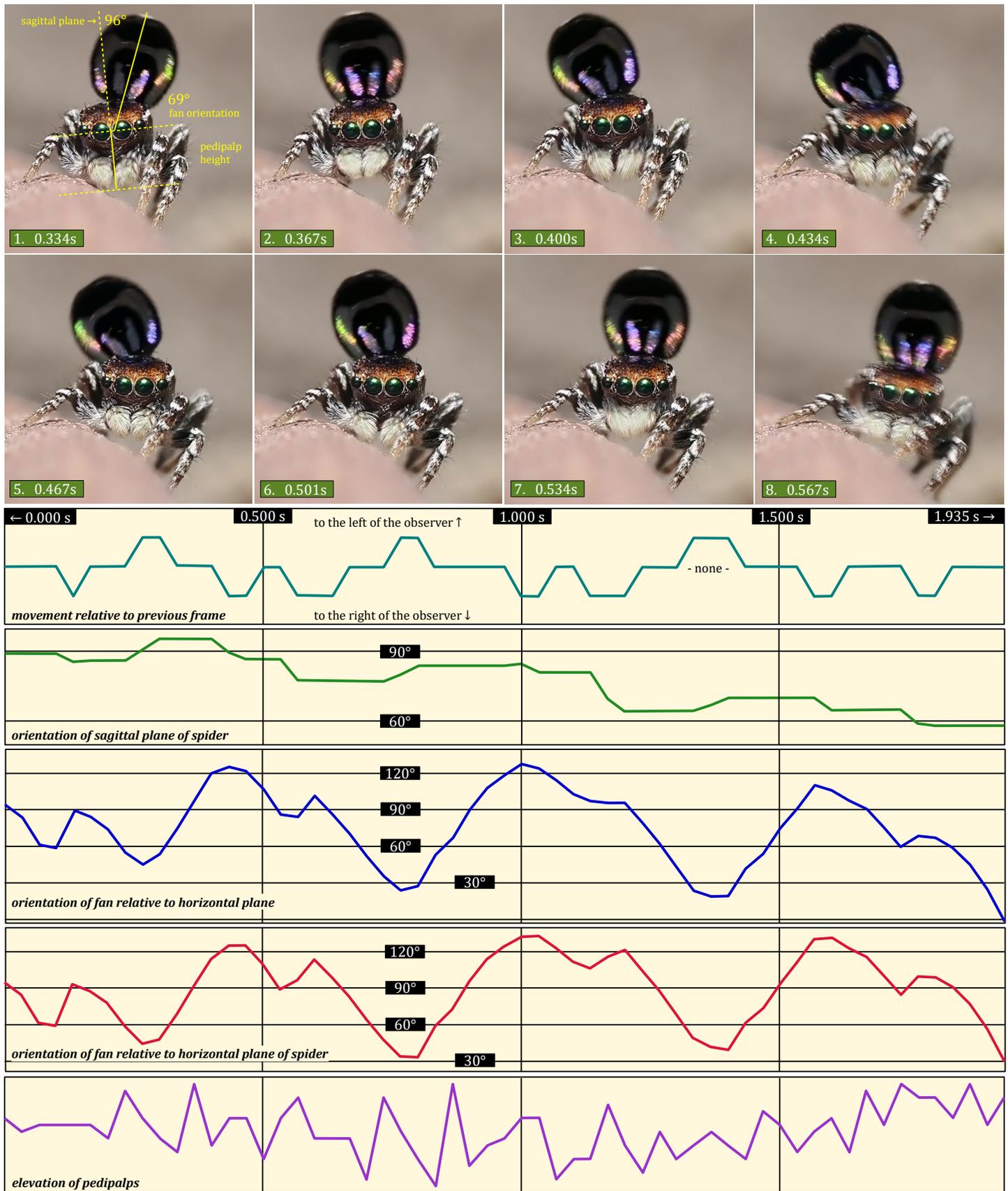


Figure 7. Frame by frame analysis of movement during courtship display by a ♂ *Maratus robinsoni*, based on a 29.97 fps video record. This included a series of small steps in alternating directions at a rate of 7-8 Hz, waving of the fan over an amplitude of ~90° at ~2 Hz (or at a lower amplitude over ~4 Hz), and up-down pedipalp flicker (both pedipalps, nearly synchronous) at a faster rate (~8-10 Hz).

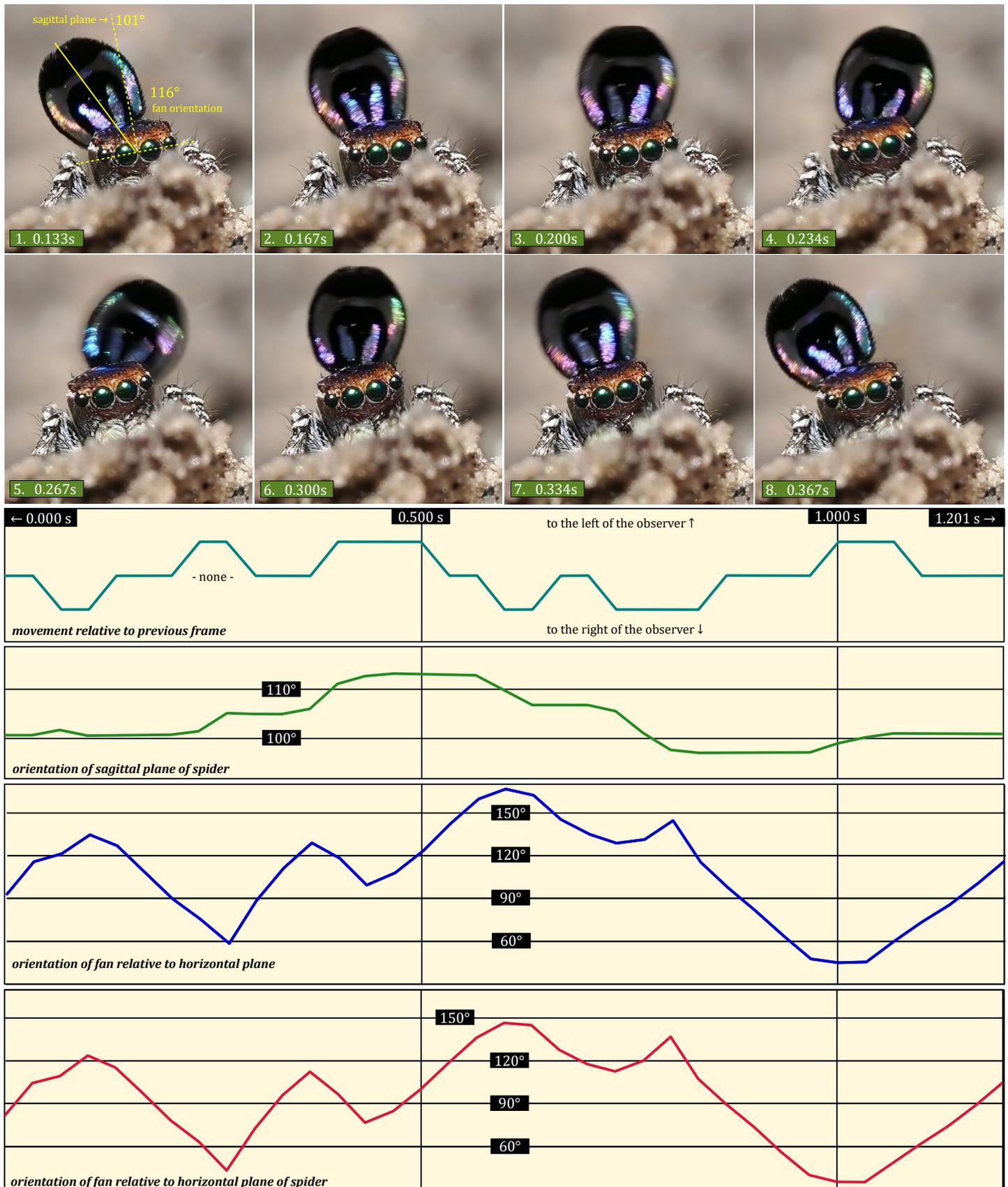


Figure 8. Frame by frame analysis of movement during courtship display by a ♂ *Maratus robinsoni*, based on a 29.97 fps video record. This included a series of small steps in alternating directions at a rate of ~ 8 Hz and waving of the fan over an amplitude of $\sim 90^\circ$ at ~ 2 Hz (or at a lower amplitude over ~ 4 Hz). Pedipalp flicker could not be measured in this sequence.

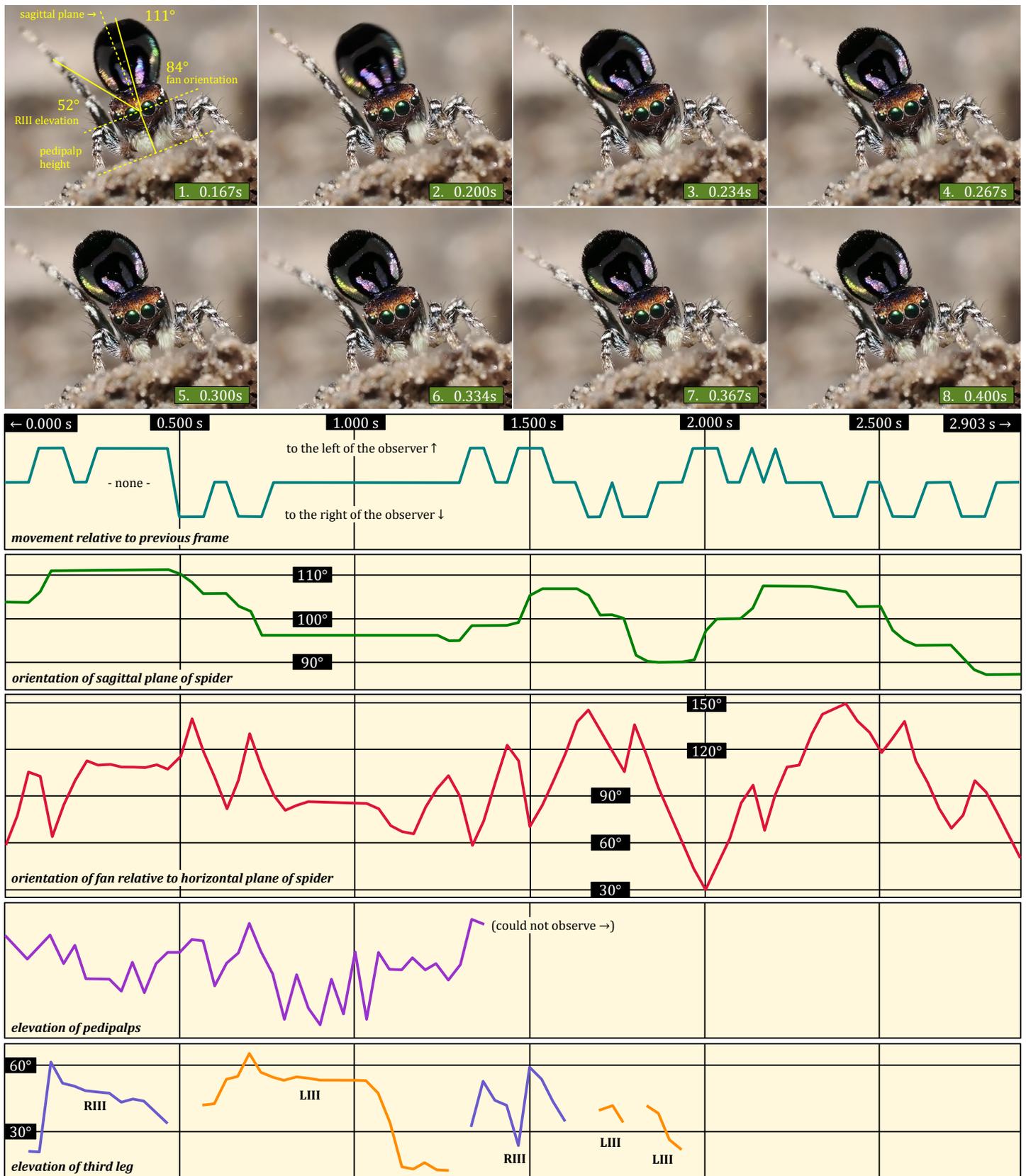


Figure 9. Frame by frame analysis of movement during courtship display by a ♂ *Maratus robinsoni*, based on a 29.97 fps video record. This included a series of small steps in alternating directions at a rate of 7-8 Hz, waving of the fan over an amplitude of as much as 110° at ~2-4 Hz, and up-down pedipalp flicker (both pedipalps, nearly synchronous) at ~8 Hz. The lower chart shows extension, followed by flexion, of leading legs III during this display, measured as shown in (1).

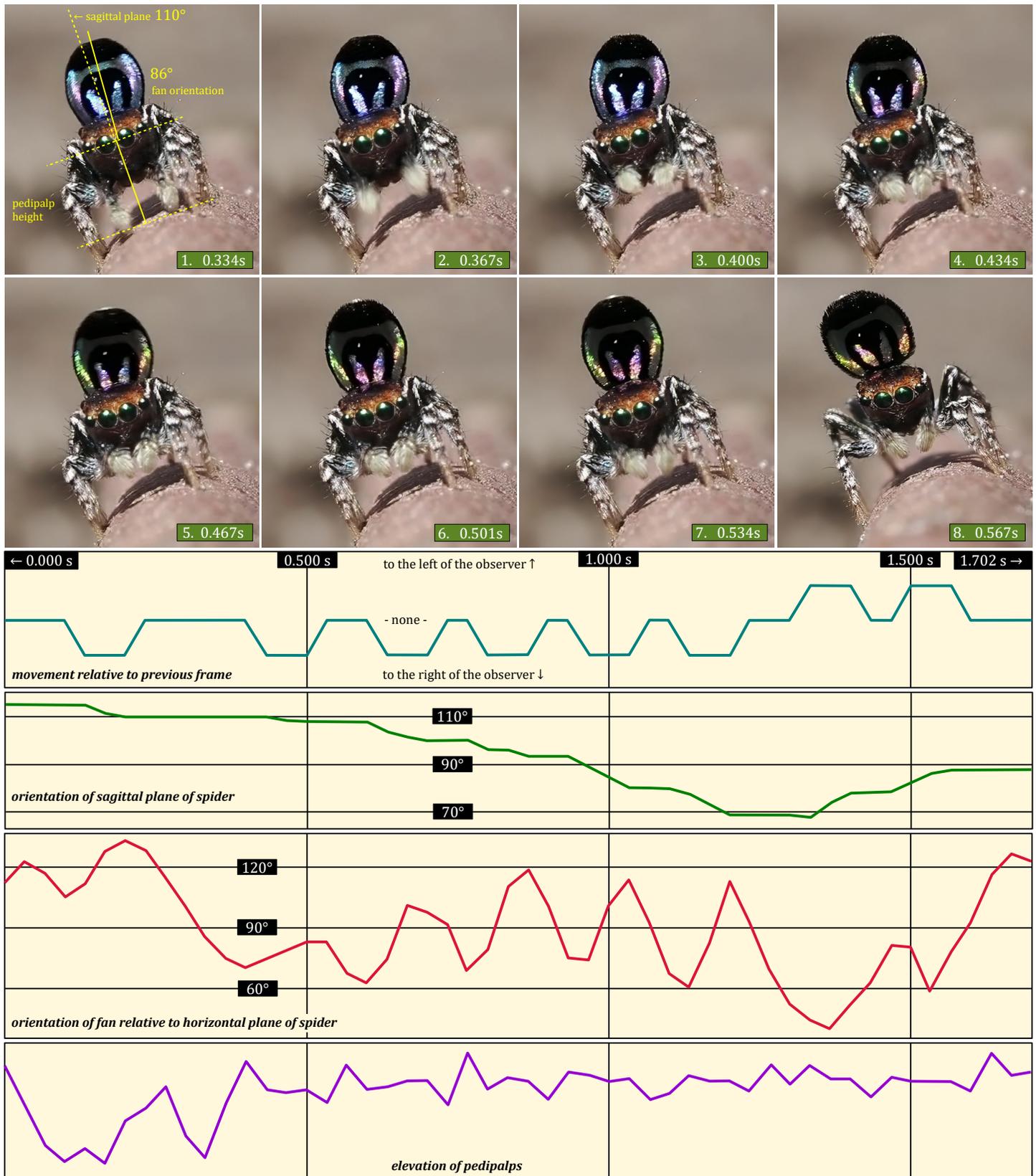


Figure 10. Frame by frame analysis of movement during courtship display by a ♂ *Maratus robinsoni*, based on a 29.97 fps video record. This included a series of small steps in alternating directions at a rate of 8-12 Hz, waving of the fan over an amplitude of as much as 90° at ~4-6 Hz, and up-down pedipalp flicker (both pedipalps, nearly synchronous) at ~8 Hz.

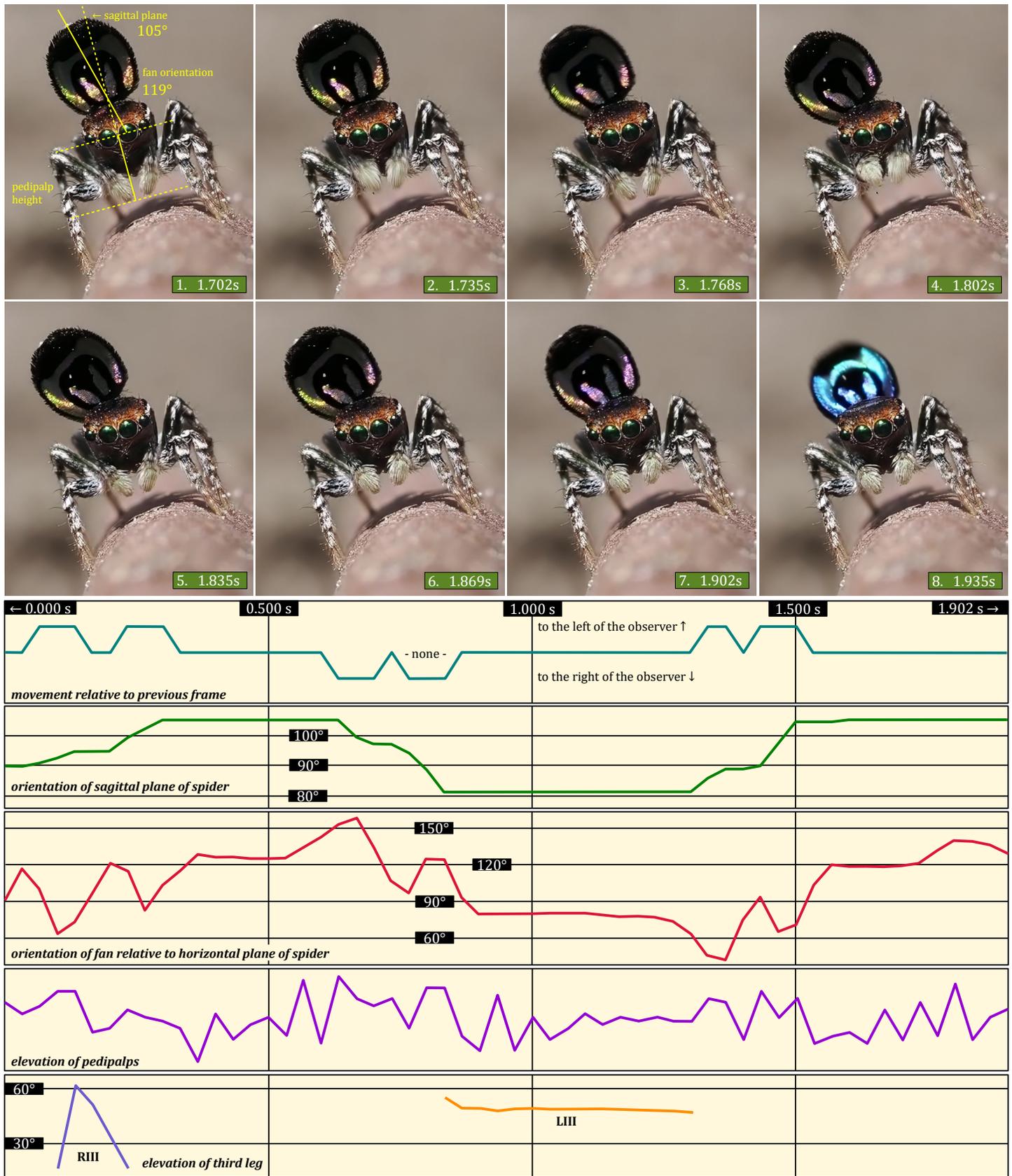


Figure 11. Frame by frame analysis of movement during courtship display by a ♂ *Maratus robinsoni*, based on a 29.97 fps video record. This included intermittent small steps in alternating directions at a rate of ~8 Hz, waving of the fan over an amplitude of more than 100° at ~4-6 Hz, and up-down pedipalp flicker (both pedipalps, nearly synchronous) at ~10 Hz. The lower chart shows extension, followed by flexion, of leading legs III during this display, measured as shown in (1).

Iridescent light and communication. There are many examples of iridescence in spiders, particularly in jumping spiders (Foelix et al. 2013; Hill 2022). In most cases this is the result of reflection through multiple layers of cuticle, but in *Maratus* we have several remarkable species, like *M. robinsoni*, where brilliant colours are produced by reflecting diffraction grids on the surface of scales (Hsiung et al. 2014, 2017; Wilts et al. 2020; Hill 2022). For most *Maratus*, iridescent scales are located only on the fan of the male, but one species, *M. plumosus*, displays brilliant blue iridescent scales on the femur of each leg III when it is elevated and kicked to the side (Otto & Hill 2013). Since groups of these scales are often separated by high contrast tracts of jet-black (super black) scales that emit almost no light (McCoy et al. 2019), the visual effect is even more remarkable.

The use of iridescent colours, which are direction-specific and can be quite variable, to communicate with potential mates is problematic, as one might expect constancy to be a more important characteristic of signalling with colour (Stuart-Fox et al. 2021). However, the sheer brilliance or intensity associated with a beam of iridescent light, in contrast with a dark surround, represents a powerful signal by itself. In addition, the directional aspect of iridescence contributes to the flashing (or flickering) of this beam, and, this flashing must play an important role in communication by a courting male *Maratus*. Even without iridescent scales, male peacock spiders often wave their elevated fan from side to side.

Digital photographs of *Maratus robinsoni* illuminated with artificial light (Figures 1-2) reveal a wide spectrum of brilliant colours that span our visible spectrum. Although these give a good indication of the capabilities of the iridescent scales of these spiders, real-world lighting in the microhabitat of these spiders is quite different, and it changes rapidly with changes in cloud cover, the elevation of the sun, or simply the direction faced by the spider. Even when these spiders are photographed with natural lighting, the sensors and image processing software of digital cameras do not record colours with great precision, and they use a form of "trichromatic" (RGB) vision to collect colour into three wider categories. The capture of directional, narrow-spectrum iridescent colour with conventional photography is a particular challenge with respect to contrast, as diffracted colours are often several orders of magnitude brighter than other colours in an image.

Two recent studies looked more closely at the structure and function of the iridescent scales of *Maratus robinsoni* (Figure 12). Both studies (Hsiung et al. 2017; Wilts et al. 2020) include SEM images of a *flat* reflective grating, with grating lines (separated by ~330 nm) parallel to the axis, on either side of each scale.

To understand the ability of a diffraction grating to separate and to redirect light according to frequency, we need to first review the *standard grating equation* (Figure 13). Although by itself this does not explain the true nature of diffraction, it allows us to predict this with great precision. The principle is simple: for a given direction of incidence, incoming light is preferentially diffracted in the direction that produces constructive interference. As shown in Figure 14, the direction of diffraction is very sensitive to the separation of grid lines (d). Calculations based on the geometry of the iridescent scales of *Maratus robinsoni* (Figure 15) are in agreement with the earlier studies. These show that longer wavelengths tend to be diffracted toward the top of each scale (away from the surface of the fan), and shorter wavelengths tend to be scattered toward the side of each scale. However, at lower angles of incidence, these scales are much better at collecting and diffracting light of shorter wavelength (blue), i.e. blue light that comes from the side of the spider. This agrees with our observation that these scales appear to be more dark blue or blue-violet when viewed from the front of the courting male (the female's perspective) when illuminated at a lower angle under natural conditions. Based on the position of the fan during courtship, the top-down illumination of scales (Figures 12.1-12.2, 15.1-15.2) could only occur if all light came from the direction of the courted female.

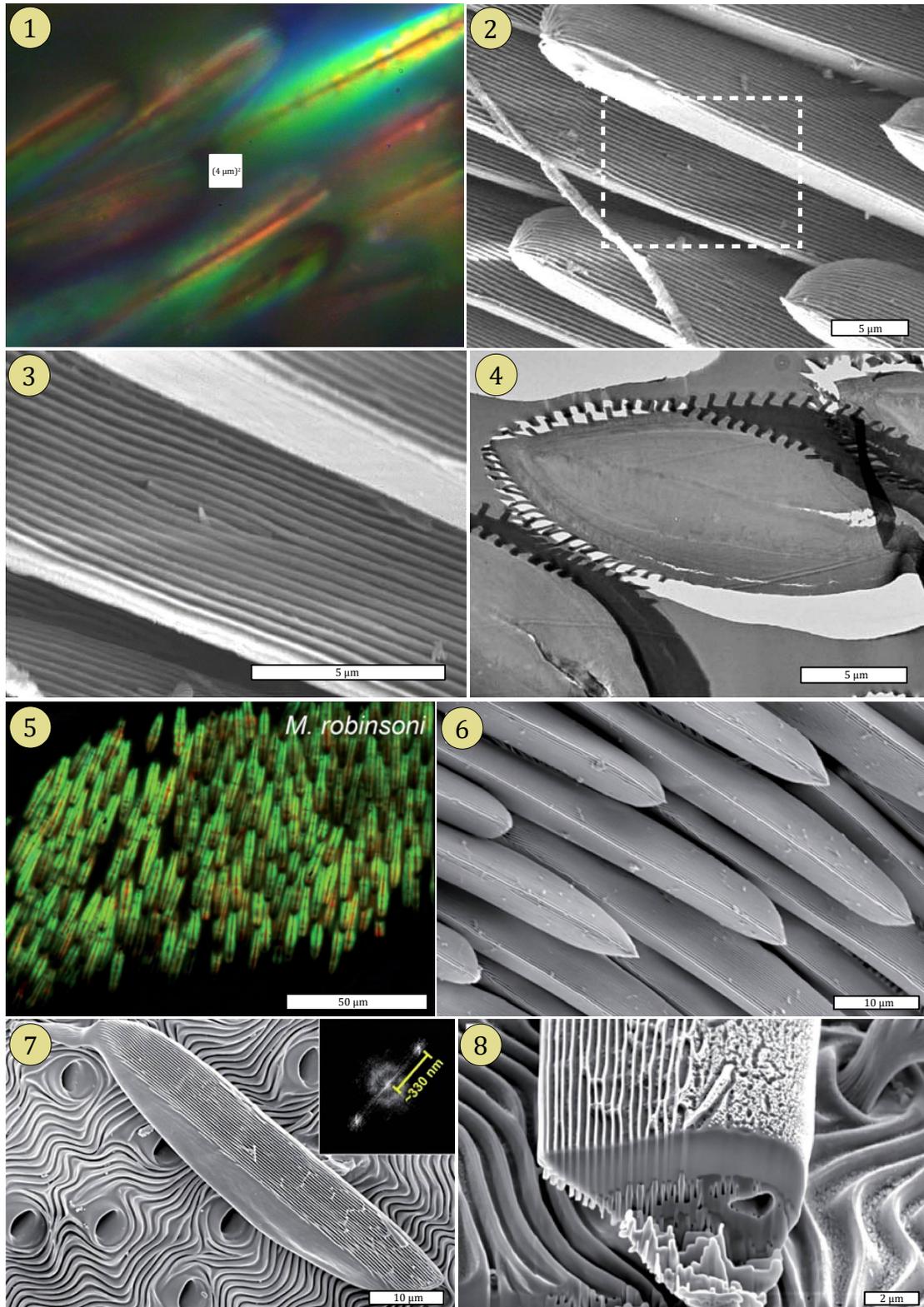


Figure 12. Iridescent scales of *Maratus robinsoni*. **1, 5,** Light micrographs of multiple scales, viewed from above under artificial lighting. Note the parallel alignment of the scales. **2-3, 6,** Detailed SEM views showing diffraction grating on two sides of each scale. **4,** This was described as a cross section of a single scale of *M. robinsoni*, with a convex diffraction grid on either side. But based on the scale bar, the spacing of grid lines (~ 1000 nm) is wrong. **7,** Side view (SEM) of a single scale surrounded by sockets of other detached scales. Grid line spacing is shown in the inset. **8,** View (SEM) of break across a single detached scale, showing internal structure. The acute upper edge of this scale is at the left side. Photo credits: 1-4, Hsiung et al. 2017; 5-8, Wilts et al. 2020.

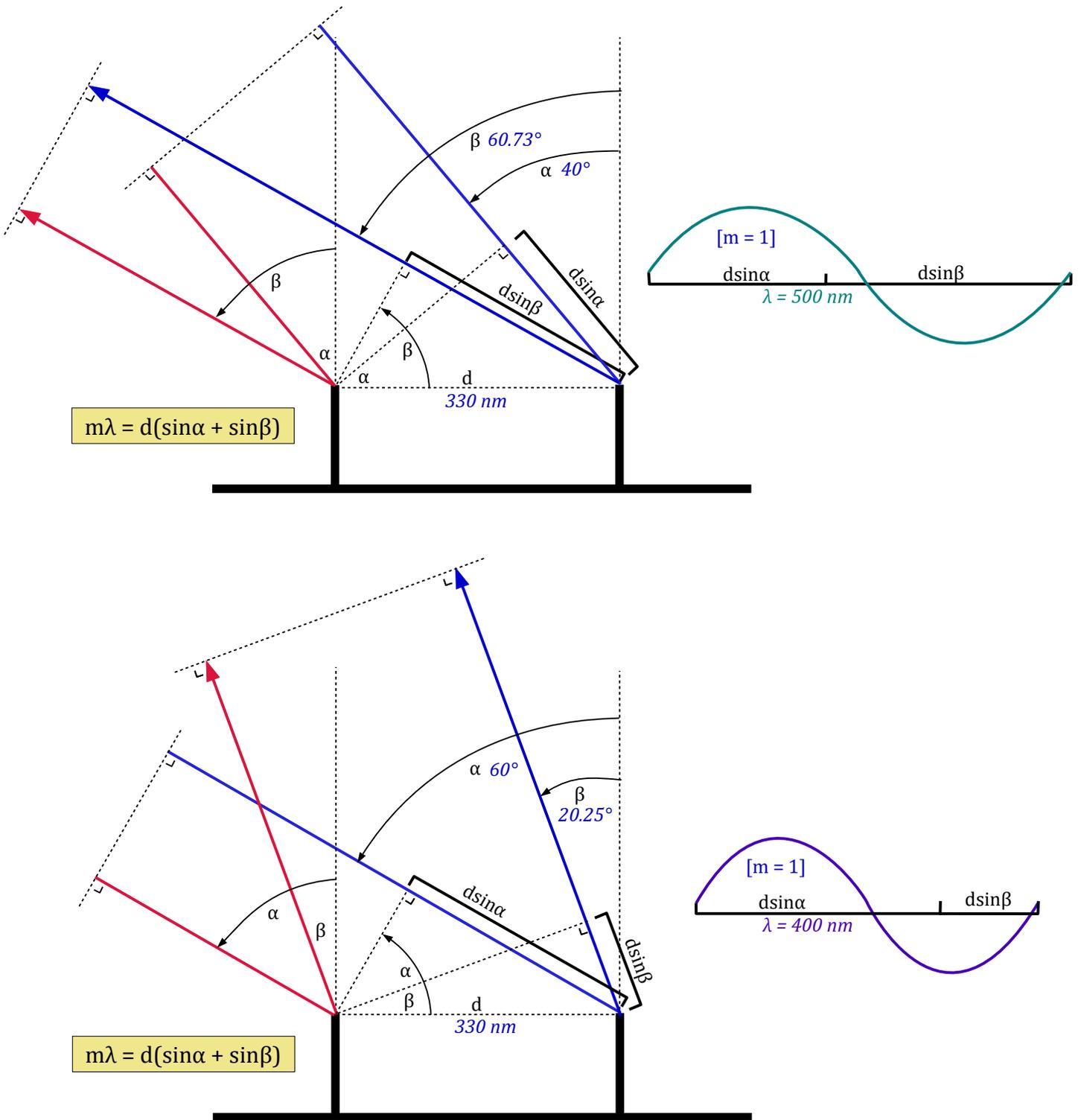


Figure 13. Derivation of the standard grating equation (in box at lower left) from diagrams (drawn to scale) representing diffraction of two wavelengths (top: $\lambda = 500 \text{ nm}$, bottom: $\lambda = 400 \text{ nm}$) by the scales of *Maratus robinsoni*. In each case the wavelength (λ) is an integer multiple (m) of the difference in distance ($d\sin\alpha + d\sin\beta$) between the two light pathways (shown in red and blue, respectively). That multiple (m), also known as the *order* of diffraction, is equal to 1 in these examples. This is the only nonzero value that works for this grid, for the visible spectrum. If $m = 0$, we have simple reflection. In interpreting related presentations, it is important to understand the convention used to determine whether an angle of incidence or reflection (diffraction) is positive or negative, and this can be very confusing. Here we follow the convention that angles measured to the left of the grid normal (line perpendicular to the plane of the grid) are positive, and those measured to the right are negative. For *M. robinsoni* grids, which have a smaller line spacing (d) than the wavelengths of visible light, the diffraction angle (β) for light with a positive angle of incidence (α) is also positive (both angles carry the same sign).

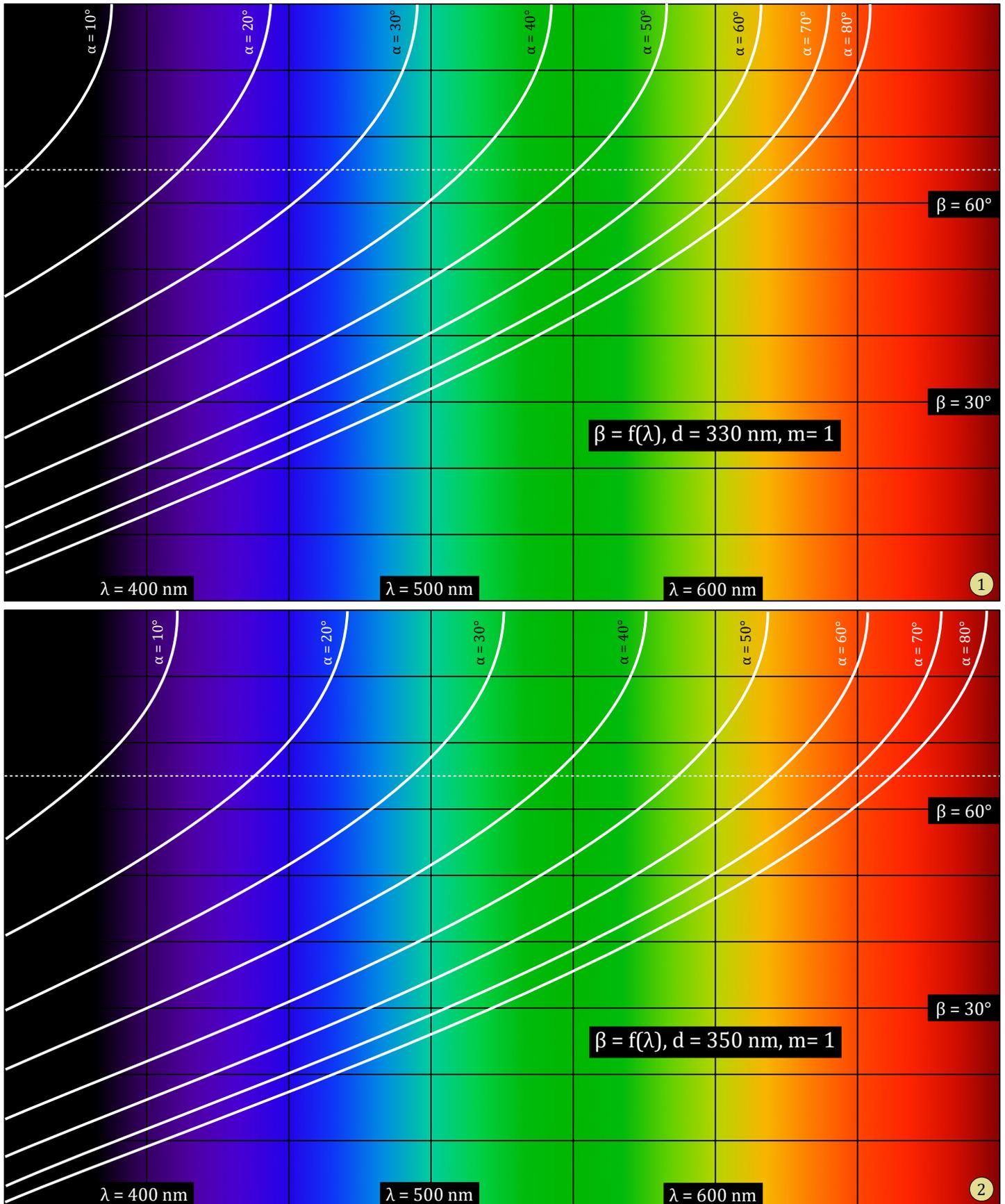


Figure 14. Angle of diffraction (β) as a function of wavelength (λ) for various angles of incidence (α). **1**, This chart depicts diffraction for a grid with line separation (d) of 330 nm, the mean value reported for *Maratus robinsoni* scales. **2**, Only a slight increase in d ($= 350 \text{ nm}$) has a large impact on diffraction. Dashed lines mark diffraction toward the top of each scale.

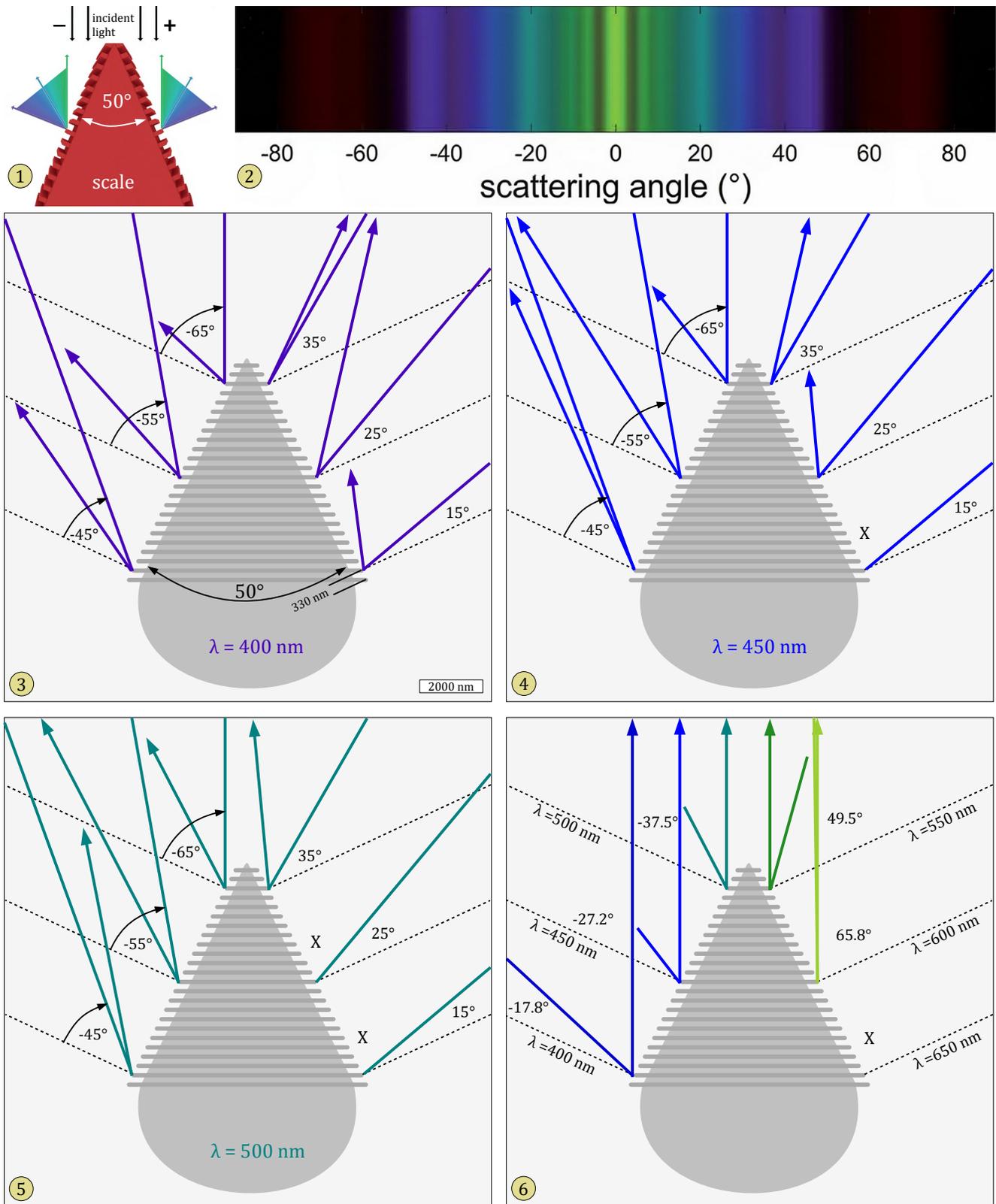


Figure 15. Examples of diffraction or scattering of light from scales of *Maratus robinsoni*. **1-2,** Note the 50° separation of the two flat sides of each scale, at the top (1, transverse section). *Scattering angle*, or the direction that light coming from above is diffracted relative to a vertical (sagittal) plane through the axis of each scale, is greater for shorter (blue) wavelengths (blue light) than for longer (green) wavelengths (modified from Wilts et al. 2020). **3-5,** Calculated diffraction for various angles of incidence. Scattering, or lateral redirection of incoming light, is much greater for shorter wavelengths. Since diffraction >90° is not possible, some light is not diffracted (X). **6,** Angle of incidence corresponding to diffraction of light toward the top of the scale, as a function of wavelength (λ).

The top-down direction of incident light that has been studied in detail (Hsiung et al. 2017; Wilts et al. 2020) may have little relevance in nature, however, and studies at a wider range of incidence that include measurement with a spectrophotometer are needed. There is a possibility that the internal structure of scales plays a role in their colour (see Figure 12.8). Finally, we know nothing about the reactions of the female *Maratus robinsoni* to the details of this display. Is mating success contingent on the direction of approach by the male relative to the position of the sun, or even the time of day? We do not know.

Superposition and diffraction. Much of what is taught to students of physics is comprised of *formulas that work*, and this includes the standard diffraction formula (Figure 13). These formulas are useful and provide much insight, but do not fully explain what is really happening. Diffraction is a remarkable phenomenon, related to the ability to sort out the various frequencies (or wavelengths) of light, and to send each wavelength in a different direction. A simple example of diffraction is represented by the famous *two-slit experiment*, which employs a transmissive diffraction grating with only two alternative pathways. Historically this served as an important demonstration for the wave nature of light as, like water waves emerging from a barrier, the two emerging wave fronts on the far side of the slits appeared to interfere both constructively and destructively, producing a predictable interference pattern. However, it has been demonstrated that photons arriving singly at a pair of narrow slits, one by one, can also produce this pattern (*one-photon interference*; Abouraddy et al. 2001; Kolenderski et al. 2013). A series of single photons can also produce the more complicated kind of multiple slit or line interference that is described in this paper (Deachapunya et al. 2016; Schwarz et al. 2020; Diniz et al. 2025).

Figure 13 depicts the kind of interference (constructive reinforcement) that has most often been interpreted as an interaction between two *coherent* photons, aligned in parallel as they approach the grid. However, in nature light is far from coherent. With quantum physics we have a different understanding based on *superposition* of multiple states. The red and blue lines shown in Figure 13 can be interpreted as two states (tracks or positions) of one incoming photon, and the interaction of these states determines the angle at which that photon is diffracted.

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