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MIMS EPrint: **2018.7**

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ISSN 1749-9097

SHAKING AND WHIRLING: DYNAMICS OF SPIDERS AND THEIR WEBS

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ABSTRACT. As one of a set of defence strategies, orb-web spiders shake their webs. Other spiders whirl. Mathematical models are introduced which describe these phenomena and throw light on expected oscillation frequencies and behaviour that could be compared with experiments. The models also suggest dynamical interpretations for the design of webs. In particular a new interpretation of the function of stabilimenta is given.

Subject Category: Life Sciences – Mathematics interface

Subject Areas: biomathematics, biomechanics, biophysics

Key words: orb-web, spiders, dynamics, web shaking, web oscillation

1. INTRODUCTION

Many species of spiders respond to threats by moving rapidly with their webs. This web-shaking can also be used to remove detritus from the web. In this paper we consider three different types of motion initiated and maintained by the spider which involve the web moving with the spider. First, rapid oscillation in the direction transverse to the plane of the web is considered in section 3.1. This is observed in orb-web spiders such as *Agriope aurantia*, e.g. [28] where it is called web flexing. Secondly, rapid whirling beneath a horizontal web or from strands of silk fixed above the spider [12]. This behaviour is observed in the cellar spider, *Pholcus phalangioides*. Thirdly, rapid oscillations or vibrations of the position of the spider in the plane of the web itself, which will be referred to as vibrations, are analyzed. Like the shaking of section 3.1 this can also be observed in species of orb-web spiders.

In all three cases the net effect is that the image of the spider becomes blurred. The obvious interpretation is that the spider initiates the motion so that blurred image either makes it harder for a predator to

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attack the spider because of uncertainty over its position, or discourages the predator by giving the impression that the spider is larger and ‘less spider-like’ [5]. Web decorations (*stabilimenta*) may also help change the observed outline of objects in a shaken web, see [5] and references therein.

The mechanical properties of webs and silk strings has been investigated quite extensively, e.g. [15, 16], as has the structure and size of webs, e.g. [25], but there has been relatively little work on the global dynamics of webs. The ways in which spiders might detect collisions with their webs and how they might interpret vibrations of their webs has been discussed [13, 18, 22] and there is a more abstract mathematical interest in networks of elastic strings independent of spiders [21, 23]. Aoyanagi and Okumura [2] consider dynamics, but in the context of high dimensional models that allow only numerical observations. They focus on stress distributions and the effect of damage on structures. Thus the models presented here are the first to probe the mathematical features of web-shaking as a defence mechanism.

The simple models introduced here provide initial insights into the mathematical description of web-shaking. The models are based around simple pendulums and networks of elastic strings. They do not give a complete description of the web structure, but suggest how the web responds to actions of the spiders in ways that make it possible to provide predictions and test hypotheses. All the models presented could be made more complicated and hence more realistic, but they have been chosen because they provide good qualitative agreement with observed behaviour whilst making quantitative comparisons possible as well. The agreement with observations also suggest that webs may be designed to be closer to the models than one might expect, i.e. that by designing webs to behave dynamically in more constrained ways the spider is better able to control the response of the web. In particular, we use the discussion to speculate both on the extent to which the spider excites the web without responding to the web, as is the case in section 3.2, or responds to the motion of the web, pumping it like a swing, e.g. section 3.1. The analysis also suggests ways that the structure of the web, for example the *stabilimenta*, may make the dynamics closer to the models presented.

2. METHODS

2.1. Overview. The aim of the models presented here is to provide insights into the essential biophysics behind web-shaking. The models treat the spider as a point mass with inextensible massless legs, and

the web is treated as a set of elastic strings which exert force when under tension but not when slack. These assumptions make it possible to build theoretical models based on classic pendulums and networks of elastic strings which provide insights into how the oscillations observed are created and maintained.

In each of the three models the spider plays a different role, and this leads to different technical challenges. In the first two models (shaking transverse to the plane of the web and whirling) the spider is active. In web-shaking the spider pumps the web using a strategy analogous to the way a child pumps a swing, and in whirling the spider changes the position of the point at which its body is attached to the web or ceiling above it. In these cases it is natural to use Lagrangian mechanics to describe the position of the spider's body as a function of time in response to a time-dependent forcing term representing the independent actions of the spider.

Lagrangian methods are based on the idea of generalised coordinates. Suppose that the state of a system can be described by n coordinates (positions and angles) $\mathbf{q} = (q_1, \dots, q_n)$. If the kinetic energy of the system is $T(\mathbf{q}, \dot{\mathbf{q}}, t)$ and the potential energy is $V(\mathbf{q}, \dot{\mathbf{q}}, t)$ then the Lagrangian of the system is $L(\mathbf{q}, \dot{\mathbf{q}}, t) = T - V$ and the equations of motion in the absence of external forces are the Euler-Lagrange equations

$$\frac{d}{dt} \left(\frac{\partial L}{\partial \dot{q}_i} \right) - \frac{\partial L}{\partial q_i} = 0, \quad i = 1, \dots, n. \quad (1)$$

In the case of the spider vibrating in the plane of the web the actuation of the vibration by the spider determines the initial conditions for our model, and the passive dynamics of the spider in its web is described by the forces due to the tension in the strings. Since a slack string produces no force (at least to the level of approximation used here) the force is zero if the length ℓ of the string is less than its natural length ℓ_0 , whilst it is proportional to the extension $\ell - \ell_0$ if $\ell > \ell_0$. If

$$\{x\}_+ = \max(0, x)$$

denotes the maximum of x and zero then the force exerted on the spider by the string is

$$\mathbf{F} = k\{\ell - \ell_0\}_+ \hat{\mathbf{r}}, \quad (2)$$

where $k > 0$ is the string constant and $\hat{\mathbf{r}}$ is the unit vector in the direction of the string towards the external point to which the string is fixed. These forces will be summed over the radial strands of the web.

In the remainder of this section the equations used to describe shaking and vibrating are explored in more detail. The model for whirling

has been derived in the context of mechanical cranes [9] and the equations are described as part of the results, subsection 3.2.

2.2. Shaking. The model of shaking is shown in Figure 1. Only the central vertical strand is described, and the spider is attached to the web at two places representing its front and back legs. Gravity is small compared to the elastic forces in the web and is ignored, and to simplify the description the configuration is assumed to be symmetric about the horizontal line through the body of the spider.

Mathematically, in coordinates (x, z) with x horizontal and z vertical, the web strings are fixed at $(0, z_0)$ and $(0, -z_0)$ above and below the spider for some fixed $z_0 > 0$ and the symmetry implies that the spider moves transverse to the plane of the web in the x -direction with $z = 0$. The model involves the following further quantities:

spider's leg length	h ;	
length of upper and lower web strands	ℓ ;	
angle of web strands to vertical	θ ;	
angle of spider's legs to vertical	ϕ ;	(3)
web coefficient of elasticity	k ;	
spider mass	m ;	
natural length of web strand	ℓ_0 .	

Note that h , m and z_0 are constants and the other quantities vary with time. By elementary geometry, if $(x, 0)$ is the position of the spider's centre of mass then

$$\begin{aligned} z_0 &= \ell \cos \theta + h \cos \phi \\ x &= \ell \sin \theta + h \cos \phi. \end{aligned} \tag{4}$$

We shall choose to work with (x, ϕ) as generalized coordinates, in which case (4) determines θ and ℓ in terms of the generalized coordinates. Eliminating θ from (4), or by using the cosine rule

$$\begin{aligned} \ell = \ell(x, \phi) &= \sqrt{x^2 + z_0^2 + h^2 - 2h(x \sin \phi + z_0 \cos \phi)} \\ &= \sqrt{(x - h \sin \phi)^2 + (z_0 - h \cos \phi)^2}. \end{aligned} \tag{5}$$

The potential energy is the elastic energy of the two web strands

$$V(x, \phi) = k(\ell - \ell_0)^2, \tag{6}$$

and assuming the web strands have negligible mass, the kinetic energy of the system is

$$T = \frac{1}{2}m\dot{x}^2. \tag{7}$$

The Lagrangian is $L = T - V$ and the Euler-Lagrange equation for the equations of motion in the x -variable is Using (5),

$$L = \frac{1}{2}m\dot{x}^2 - k \left(\sqrt{(x - h \sin \phi)^2 + (z_0 - h \cos \phi)^2} - \ell_0 \right)^2. \quad (8)$$

Thus the equation of motion is

$$m\ddot{x} = -\frac{2k(x - h \sin \phi) \left(\sqrt{(x - h \sin \phi)^2 + (z_0 - h \cos \phi)^2} - \ell_0 \right)}{\sqrt{(x - h \sin \phi)^2 + (z_0 - h \cos \phi)^2}}. \quad (9)$$

During the swing phases of the motion ϕ is held fixed by the spider and so the Lagrangian has no explicit t dependence. Hence the energy is a first integral during the swing phase and solutions lie on curves of constant E :

$$\frac{1}{2}m\dot{x}^2 + k \left(\sqrt{(x - h \sin \phi)^2 + (z_0 - h \cos \phi)^2} - \ell_0 \right)^2 = E. \quad (10)$$

As the web swings, the spider adjusts the angle between its leading legs in a short period of time which observations suggest to be timed so that $\dot{x} \approx 0$, i.e. at the turning points of the oscillations, a bit like the pumping of a child's swing. During this phase the Lagrangian (8) remains valid, but the actuation by the spider means that the ϕ variable becomes time dependent so the analysis of the previous paragraph leading to (10) is no longer valid. Over a small time the angle changes from ϕ_- to ϕ_+ say, or vice versa, and the corresponding change in x can be analyzed using the methods of [30]. The conclusion will be that the change in x during the short period of time during which the spider re-adjusts its posture by changing ϕ is negligible, unlike the swings of [30], but similar to a car and its suspension going over a bump.

If $\phi = \phi(t)$ then the Euler-Lagrange equation in x is

$$m\ddot{x} + \frac{\partial V}{\partial x} = 0, \quad (11)$$

with V defined by (6) and (5). Suppose that the actuation period is small, Δt . The partial derivative $\frac{\partial V}{\partial x}$ is bounded as ϕ varies, so integrating over a small time from 0 to $t \leq \Delta t$,

$$m\dot{x} = K + O(\Delta t) \quad (12)$$

where K is constant (the value of \dot{x} at the start of the actuation process) and the $O(\Delta t)$ terms arise from integrating the bounded partial derivative. Integrating once more from 0 to Δt and denoting the change in a variable y from 0 to Δt by $[y]$,

$$[x] = O(\Delta t). \quad (13)$$

The change of posture of the spider is fast compared to the oscillations of the web, so as $\Delta t \rightarrow 0$ the right hand side of (13) tends to zero and the left hand side is simply the change in x , i.e.

$$[x] = 0 \quad (14)$$

if the change in posture of the spider is instantaneous.

At first sight this seems quite surprising; it is essentially due to the fact that the kinetic energy term is degenerate as it is independent of $\dot{\phi}$. Had a more sophisticated model with mass in the legs of the spider been used then there would have been a compensating shift in the value of x .

This implies that at the end of each swing of the oscillation the equation of motion changes from (9) with $\phi = \phi_{\pm}$ to the same equations with $\phi = \phi_{\mp}$ whilst x is continuous at the moment of change.

2.3. Vibrating. To model the vibrations of a spider in the plane of its web, the web is considered to consist of N radial elastic strings. Each string is fixed at one end to some external frame at position \mathbf{Z}_j and at the other end to the spider at position \mathbf{X} . From (2) the motion of the spider is determined by the equation

$$m\ddot{\mathbf{X}} = \sum_1^N k\{|\mathbf{Z}_j - \mathbf{X}| - \ell_0\}_+ \mathbf{r}_j, \quad \mathbf{r}_j = \frac{\mathbf{Z}_j - \mathbf{X}}{|\mathbf{Z}_j - \mathbf{X}|}. \quad (15)$$

Equation (15) can be applied to three-dimensional motion with the points \mathbf{Z}_j at arbitrarily chosen positions, but for simplicity only the two-dimensional case will be considered, looking at motion in the plane of the web.

If the points \mathbf{Z}_j are regularly spaced on a circular frame of radius $\ell_0 + a$ where ℓ_0 is the natural length of each string and $a > 0$ is the extension of each string when the spider is at the centre of them web, then we can choose coordinates

$$\mathbf{Z}_j = (\ell_0 + a)\left(\cos \frac{2\pi j}{N}, \sin \frac{2\pi j}{N}\right), \quad j = 1, \dots, N.$$

With this assumption the right hand side of (15) is zero if $\mathbf{X} = (0, 0)$, i.e. $(0, 0)$ is an equilibrium point for the system with all the strings in tension having length $\ell_0 + a$. For sufficiently small perturbations from the equilibrium point, all strings remain under tension and we can ignore the curly brackets in (15). Thus if $\mathbf{X} = \epsilon \mathbf{U}$ with $\epsilon > 0$ small, then if $\ell = \ell_0 + a$ and $\mathbf{U} = \epsilon \ell(u, v)$ the lowest order perturbations give

$$|\mathbf{Z}_j - \mathbf{X}| - \ell_0 \sim a - \epsilon \ell \left(u \cos \frac{2\pi j}{N} + v \sin \frac{2\pi j}{N} \right) + O(\epsilon^2).$$

Setting $c_j = \cos \frac{2\pi j}{N}$ and $s_j = \sin \frac{2\pi j}{N}$ then

$$\mathbf{r}_j = (c_j, s_j) - \epsilon (a(u, v) - (c_j u + s_j v)(c_j, s_j)) + O(\epsilon^2).$$

Substituting these expressions into (15) and retaining only the leading order terms gives

$$(\ddot{u}, \ddot{v}) = -\frac{Nk}{2m} \left(1 + \frac{a}{\ell_0 + a}\right) (u, v). \quad (16)$$

So in a sufficiently small neighbourhood of the origin *in this symmetric case* the motion is oscillatory, and the origin is stable.

If there are infinitely many strings the sum in (15) is replaced by an integral with respect to the angle coordinate θ labelling the points \mathbf{Z}_j on the hoop. The configuration then has radial symmetry and we can calculate the force at any \mathbf{X} with $|\mathbf{X}| = r$ by considering the force at $\mathbf{X} = (r, 0)$ and using the symmetry. The symmetry also implies that this will be a central force regardless of the proportion of strings under tension.

Suppose that $\mathbf{Z} = (\ell_0 + a)(\cos \theta, \sin \theta)$ is a point on the boundary of the hoop and $\mathbf{O} = (0, 0)$. Then provided the string is in tension, the extension of the string from \mathbf{Z} to \mathbf{X} is

$$|\mathbf{XZ}| - \ell_0 = \sqrt{((\ell_0 + a) \cos \theta - r)^2 + (\ell_0 + a)^2 \sin^2 \theta} - \ell_0$$

or, setting $p = \ell_0 + a$,

$$|\mathbf{XZ}| - \ell_0 = \sqrt{p^2 + r^2 - 2rp \cos \theta} - \ell_0. \quad (17)$$

If the angle $\angle OXZ$ is denoted by ϕ then the component of the force in the x -direction which stands for the radial direction in the general case by symmetry is

$$k(\sqrt{p^2 + r^2 - 2rp \cos \theta} - \ell_0)(-\cos \phi), \quad (18)$$

with the minus sign on the last term so that the positive direction is the positive x -direction. Using the cosine rule, $|\mathbf{OZ}|^2 = |\mathbf{OX}|^2 + |\mathbf{XZ}|^2 - 2|\mathbf{OX}||\mathbf{XZ}| \cos \phi$ and so

$$2r|\mathbf{XZ}| \cos \phi = |\mathbf{OX}|^2 + |\mathbf{XZ}|^2 - |\mathbf{OZ}|^2 = 2r^2 - 2rp \cos \theta. \quad (19)$$

Thus $|\mathbf{XZ}| \cos \phi = r - p \cos \theta$ and the component of the force in the x -direction from (18) is

$$-k \left(r - p \cos \theta - \ell_0 \frac{r - p \cos \theta}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} \right). \quad (20)$$

The total force on the mass at \mathbf{X} is found by integrating over all angles θ such that the string from \mathbf{X} to \mathbf{Z} is under tension, i.e. $|\mathbf{XZ}|^2 \geq \ell_0^2$.

If all the strings are under tension then let $\psi = 0$, otherwise let ψ be the solution in $0 \leq \psi \leq \pi$ such that

$$p^2 + r^2 - 2pr \cos \psi = \ell_0^2. \quad (21)$$

Then the total force on the mass at radius r is

$$\mathbf{F} = -\hat{\mathbf{r}}2k \int_{\psi}^{\pi} \left(r - p \cos \theta - \ell_0 \frac{r - p \cos \theta}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} \right) d\theta \quad (22)$$

where $\hat{\mathbf{r}}$ is the unit vector from the origin \mathbf{O} to the centre of mass of the spider \mathbf{X} . Thus

$$\mathbf{F} = -\hat{\mathbf{r}}2k \left((\pi - \psi)r + p \sin \psi - \ell_0 \int_{\psi}^{\pi} \frac{r - p \cos \theta}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} d\theta \right). \quad (23)$$

The last term of (23) can be evaluated using elliptic integrals, and we will use this to obtain a lowest order approximation to the force for small r when all the strings are tense, i.e. when $\psi = 0$. This calculation is long and technical so it is deferred to the appendix.

3. RESULTS

3.1. Shaking: webs under tension. Orb-web spiders have been observed to create fast oscillations of their webs in the direction transverse to the plane of their web. Cedhagen and Björklund [4] observe that

- the spider shakes the web by altering the angle of its legs to its body; and
- the spider is able to bring the vibrations to a rapid stop.

The first observation may not appear controversial, there are many examples of elastic structures with vibrational modes that can be set in motion by appropriate oscillation of a part of the structure or its surroundings. If the vibration is a classic (approximately) conservative oscillation then the second is harder to explain dynamically, although it is always possible to invoke dissipative forces. In this section we develop a model of a web under tension which explains both these phenomena via a simple behavioural rule.

A simple model of the tensioned web is sketched in Figure 1a and is described in subsection 2.2. Note that we assume that when the spider flexes its legs it stretches the web as though the web were attached to its legs and that the web is under tension throughout the motion, i.e. the length of the web is always greater than the natural length of the web. The symmetry of the configuration simplifies the dynamics, though experimental observations [27] suggest that the spider pulls more with

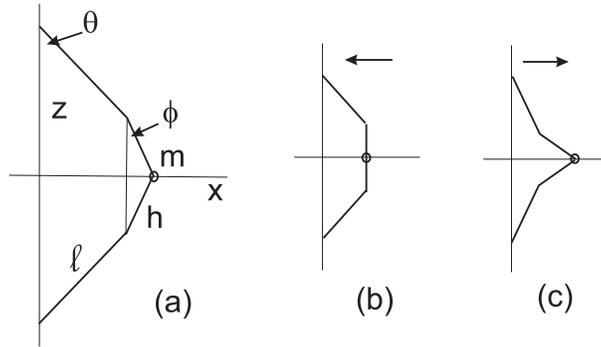


FIGURE 1. Schematic view of the web model. (a) Side view of the web showing the variables used to describe the configuration; (b) the spider in vertical position with $\phi = \phi_- = 0$; (c) the spider in the alternative position with $\phi = \phi_+ > 0$.

its front legs (i.e. lower legs, as it is upside down in the web) rather than with both front and back legs equally.

The dynamics of the spider and its web is described by two variables, the horizontal displacement x of the centre of mass of the spider, and the angle ϕ between the spider's legs and the vertical. Observations suggest that the spider adjusts the angle ϕ (more accurately, the angle between its front and back legs, which determines ϕ by geometry) at the end of each swing. During one swing ($\dot{x} < 0$ if the spider is on the right of the web as shown in Figure 1) the spider is aligned with the web with $\phi = \phi_- \approx 0$ and during the other part of the swing ϕ is fixed at some value, ϕ_+ .

The analysis of subsection 2.2 shows that if the spider changes position quickly then there is a simple change from (9) with $\phi = \phi_{\pm}$ to the same equations with $\phi = \phi_{\mp}$ at the end of each oscillation. Unlike the case of a child's swing there is no jump in the x variable caused by this re-positioning. This can be interpreted as saying that all the work done by the spider goes into stretching the web rather than moving its centre of mass. If $0 \leq \phi_{\pm} < \frac{\pi}{2}$ then by (9) there is a stationary point at $x = h \sin \phi_{\pm} > 0$, and the curves (10) are closed curves in the (x, \dot{x}) phase space around $(h \sin \phi_{\pm}, 0)$. For small oscillations and $h \ll z_0$ the dynamics is approximately simple harmonic motion with frequency (in Hertz)

$$f_a = \frac{1}{2\pi} \sqrt{\frac{2k(z_0 - \ell_0)}{mz_0}}. \quad (24)$$

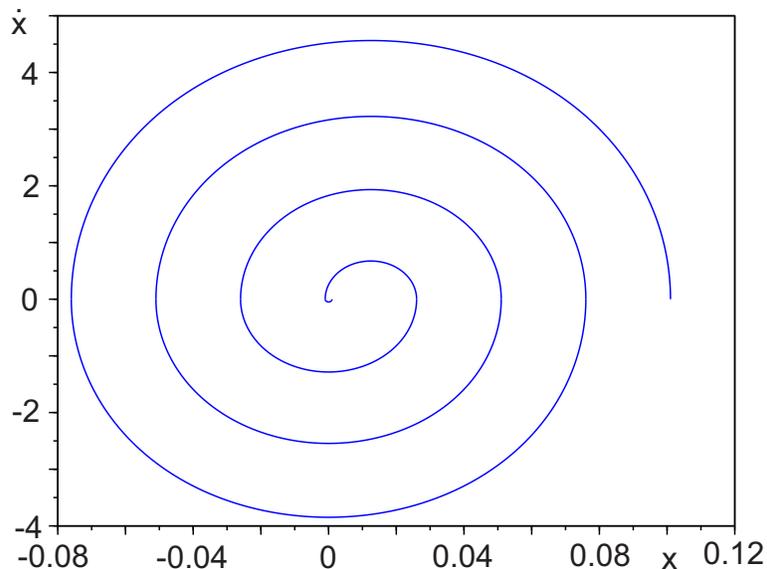


FIGURE 2. Phase portrait of the growth in amplitude of the oscillations using (9) with $\phi = \phi_- = 0$ if $\dot{x} < 0$ and with $\phi = \phi_+ = 30^\circ$ if $\dot{x} > 0$. The initial condition is $(x, \dot{x}) = (0.001, 0)$ with $\phi = 0$ (i.e. a displacement of 1 mm from the vertical). Other parameters are as in the text.

Now suppose that the spider is on the right of the web, as shown in Figure 1, and that it is able to sense the swinging of the web. The phase curves (10) show that the strategy described above will lead to an increase in amplitude as shown in Figure 2.

It is now necessary to put some numbers into the equations to determine the behaviour in more detail (we will work with standard *SI* units). Risch [25] shows that it is reasonable to take

$$m = 0.2 \times 10^{-3} kg, \quad z_0 = 0.2 m, \quad h = 0.025 m. \quad (25)$$

It is difficult to determine the natural length of the web strands, and we will use

$$\ell_0 = \frac{1}{2}z_0 = 0.1 m \quad (26)$$

to ensure that the web remains under tension. Risch [25] notes that the strings are highly elastic allowing around 300% extension or more, so this is not unreasonable, though it may be on the low side. The Young's modulus E of spider strands are variable, but values in the region of 2 GPa, or $2 \times 10^9 Nm^{-2}$ is in keeping with [15] though possibly a little low [16]. The radius of the string is commonly given to be in the region of 3 μm ($3 \times 10^{-6} m$) and so the coefficient of elasticity $k = EA/\ell_0$ where

A is the cross-sectional area of the strand. Substituting the various constants already given implies that

$$k = 10EA = 20 \times 10^9 \times 9\pi \times 10^{-12} = 18\pi \times 10^{-2}. \quad (27)$$

This is already enough to approximate the expected small amplitude frequency of oscillations during each phase using (24):

$$f_a = \frac{1}{2\pi} \sqrt{\frac{k}{m}} = 15 \sqrt{\frac{1}{\pi}} \approx 8.5. \quad (28)$$

This suggests a natural frequency of around $8 - 9 \text{ Hz}$, which is not unreasonable given the observations and the simplicity of the modelling.

The choice of ϕ_+ is again hard to determine from the literature. We have chosen to use 30° , and solutions are similar for other values of ϕ_+ that have been tried. Note that the solution shown in Figure 2 grows rapidly from an initial amplitude of 1 mm to 10 cm within four oscillations. This takes just under half a second and the numerically computed frequency over this period of time is 8.03 Hz . Dissipative effects caused by the movement of the whole web are likely to become important at this amplitude and speed, preventing the amplitude from becoming too large.

This fast increase in amplitude can be understood from the equations of motion. During each oscillation of the web with constant ϕ the equations of motion (9) are symmetric about the point $x = h \sin \phi$ since the x -dependence is only via terms in $(x - h \sin \phi)$ multiplied by a function of $(x - h \sin \phi)^2$. Hence during a half oscillation with $\dot{x} < 0$ and $\phi = \phi_- = 0$, the spider moves from $(x, \dot{x}) = (x, 0)$ with $x > 0$ to $(-x, 0)$. Similarly, during the half oscillation with $\dot{x} > 0$ the motion is from $(-x, 0)$ to $(2h \sin \phi_+ + x, 0)$. In other words, during a complete oscillation the spider moves from $(x, 0)$ to $(x + 2h \sin \phi_+, 0)$, and more generally a factor of ΔA is added to the amplitude of the motion during every complete oscillation where

$$\Delta A = 2h \sin \phi_+. \quad (29)$$

This model provides an explanation for the growth in amplitude of the oscillation. On the other hand, if the spider starts with relatively large amplitude, but adopts the opposite strategy (small ϕ in $\dot{x} > 0$ and larger ϕ in $\dot{x} < 0$) then the oscillations are rapidly damped and after a finite number of oscillations the solution intersects $\dot{x} = 0$ between $x = 0$ and $x = h \sin \phi_+$. At this point solution curves from above and below both tend towards $\dot{x} = 0$ and the motion stops (technically this represents a pseudo-stationary point of the Filippov flow, see e.g. [8]). The approach to this point involves a finite time approach to a

stationary state at this level of approximation – this could well be an indication of the ‘abrupt’ halt to the oscillations observed [4]. It would be interesting to have more data on this phenomenon.

3.2. Whirling. The cellar spider, *Pholcus phalangioides*, has long thin legs. It rests upside down with its legs attached to the web above it. If threatened, it initiates a whirling motion with its body. More careful observation [11, 12] suggests that the spider initiates a wave of flexing in its legs, successively lengthening and shortening its legs in a wave that moves around its body.

Mathematically, this means that the pivot point of the spider moves around a closed curve, as the weight of the spider is taken by the shortest leg, and this wave moves around the curve on which the ends of the legs are tethered to the ceiling. This could be modelled accurately, but as a first approximation and as a simple model that can shed light on the dynamic response of the spider’s body to this strategy, we consider the case of the ‘infinitely-legged’ spider such that the shortest leg is tethered to the ceiling on a circle and the wave moves around this ellipse with angular velocity $\omega > 0$ actuated by the spider. Note that this implies a different neurological strategy to the motion in section 3.1. In the case considered in section 3.1 the spider is assumed to respond to the position and speed of the web; in this section the spider initiates an independent flexing of its legs.

As an approximation then, the spider’s whirl is modelled by a parametrically forced spherical pendulum for which the pivot point moves in the plane of the ceiling. There is, of course, a slight up-and-down modulation of the length of the pendulum as the spider shifts the load bearing legs around the circle, and the circle is more accurately an ellipse or more complicated closed curve, but as a first approximation we will ignore these effects and consider only the forcing due to the circular rotation of the pivot point. This simplifies the algebra. The system is an example of a parametrically forced spherical pendulum with a literature that goes back at least to Miles in the 1980s [20] although the pivot moves on a line segment in that case. However, in Miles’ work and many of the subsequent analyses of the parametrically forced spherical pendulum the focus has been on resonance, where the forcing frequency is close to the natural frequency of the pendulum; see also [14, 17] for experiments and the effects of dissipation. In our case there is no attempt by the spider, consciously or otherwise, to create a resonant frequency. This non-resonant case has been considered in [9] for weights supported by mechanical cranes, so although the equations are the same, the parameters are very different. However, the

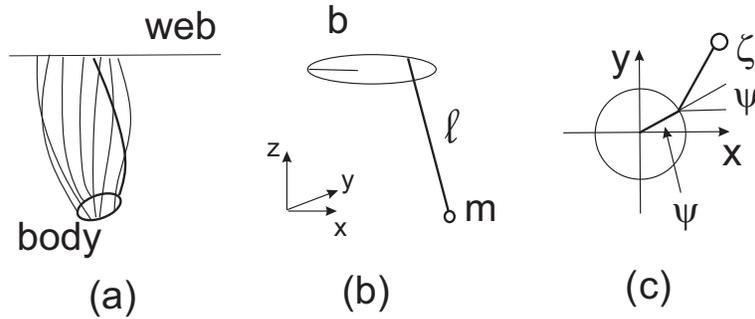


FIGURE 3. Schematic view of (a) the spider; (b) the pendulum model; and (c) the definition of the rotational angles ψ and ζ , note $\phi = \psi + \zeta$, in the projection of the model onto the plane $z = 0$.

mathematical description of the problem and some consequences can be taken from [9], and this is where we start. Note that the nature of our problem, in particular the angles that the spider is able to influence directly, means that we will use a slightly different coordinate system to that in [9].

The model is as shown in Figure 3. An inextensible string modelling the spider's legs is attached to the ceiling at a moving point

$$P = (b \cos \psi, b \sin \psi, 0), \quad \psi = \omega t$$

so that it moves around a circle of radius $b > 0$ in the plane $z = 0$ with period $\frac{2\pi}{\omega}$ and the origin of time is chosen so that $y = 0$ with $x > 0$. The frequency $\frac{1}{2\pi}\omega$ is chosen by the spider, and from observations it is a little lower than the shaking frequency in section 3.1. The variable ω is defined without the factor of 2π for ease of comparison with [9].

The centre of mass of the spider is at a point C which can be expressed in terms of an azimuthal angle θ between the load bearing leg and the downward vertical, so $0 \leq \theta \leq \pi$, and a rotational angle $\psi + \zeta$. Thus we define ζ so that the angle from the positive x -axis to the projection of C in the (x, y) -plane. The angle that would normally be labelled as ϕ in classical mechanics textbooks is $\psi + \zeta$, see Figure 3c. This differs slightly from the notation of [9]; they use an angle $\delta = -\zeta$; the choice of sign here makes the connection to the classical total angle ϕ as $b \rightarrow 0$ more straightforward. In these coordinates $C = (x, y, z)$ where if the effective length of the load bearing leg (i.e. the string) is ℓ then

$$\begin{aligned} x &= b \cos \psi + \ell \sin \theta \cos(\psi + \zeta) \\ y &= b \sin \psi + \ell \sin \theta \sin(\psi + \zeta) \\ z &= -\ell \cos \theta. \end{aligned} \tag{30}$$

The Lagrangian is then

$$L(\zeta, \theta, t) = \frac{1}{2}m(\dot{x}^2 + \dot{y}^2 + \dot{z}^2) + mgz$$

with (x, y, z) given by (30) and $\psi = \omega t$.

In these coordinates the equations of motion (the Euler-Lagrange equations) are [9]

$$\ell\ddot{\theta} - \ell(\omega + \dot{\zeta})^2 \cos \theta \sin \theta - b\omega^2 \cos \theta \cos \zeta + g \sin \theta = 0, \quad (31)$$

and

$$\ell\ddot{\zeta} \sin \theta + 2\ell(\omega + \dot{\zeta})\dot{\theta} \cos \theta + b\omega^2 \sin \zeta = 0. \quad (32)$$

If $b = 0$ the equations are the classic equations of the spherical pendulum with first integral $\ell^2\dot{\theta} \sin^2 \theta = H$, constant, from which an effective potential can be deduced for the θ equation and hence find that typical solutions oscillate between two allowed values of θ as the mass rotates around the z -axis with angle $\phi = \psi + \zeta$. However, we are more interested in whether low amplitude oscillation with speed initially almost zero can be amplified by the new forcing terms introduced by the parametric forcing which represents the spider's actuation of its legs. Note that although there is an extensive literature on *resonant* forcing, where the forcing frequency $\frac{1}{2\pi}\omega$ is close to the natural frequency of the pendulum, $\frac{1}{2\pi}\sqrt{\frac{g}{\ell}}$, the mechanism described here does not need such a precise alignment of parameters.

Ghigliazza and Holmes [9] describe the basic bifurcations of (31), (32). The simple solutions (relative equilibria) that circle the z -axis with θ and ζ constant must have $\sin \zeta = 0$ from (32), so $\zeta = 0$ or $\zeta = \pi$.

If $\zeta = 0$ then (31) implies that there is a fixed θ solution $\theta_+ \in (0, \frac{\pi}{2})$ and no other solutions, and that this is stable [9]. This corresponds to solutions in which the spider's body co-rotates with its legs, lying outside the circle of radius B in the direction of the load-bearing leg. Note that the stability is local, and since the equations are Hamiltonian, nearby solutions will oscillate about the stable solution.

If $\zeta = \pi$ then there is another solution $\theta_- \in (\frac{\pi}{2}, \pi)$ lying above the plane of the spider's legs, and this is unstable [9]. In addition, Ghigliazza and Holmes [9] show that there is a saddle node bifurcation creating a pair of new solutions which exist if $b < \ell$ and

$$\omega > \sqrt{\frac{g}{\ell}} \left[1 - \left(\frac{b}{\ell} \right)^{\frac{2}{3}} \right]^{-\frac{3}{4}}. \quad (33)$$

In our problem $g \approx 9.8 \text{ m s}^{-2}$, $\ell \approx 0.05 \text{ m}$ and so the right hand side is greater than the resonant value $\sqrt{\frac{g}{\ell}} \approx 14$. We will restrict attention

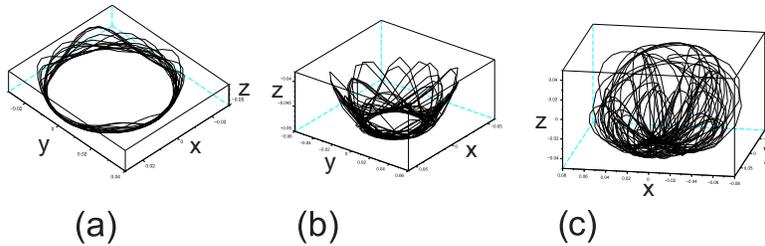


FIGURE 4. Projection onto the spatial coordinates (x, y, z) (30) of solutions of (31) and (32) with parameters given by (34) for time $0 < t < 20$. (a) $\omega = 5$ and initial conditions $(\theta, \dot{\theta}, \zeta, \dot{\zeta}) = (0.04, 0.01, 0.01, 0.05)$; (b) $\omega = 9$ and initial conditions $(\theta, \dot{\theta}, \zeta, \dot{\zeta}) = (0.04, 0.01, 0.01, 0.05)$; (c) $\omega = 12$ and initial conditions $(\theta, \dot{\theta}, \zeta, \dot{\zeta}) = (0.02, 0.07, -0.05, 0.01)$.

to $\omega < 13$ to ensure that these solutions do not exist and the system is not close to resonance.

Numerical simulations with parameters

$$g = 9.8, \quad \ell = 0.05, \quad \text{and} \quad b = \frac{1}{2}\ell. \quad (34)$$

and with various values of ω between 5 and 13 (between 0.7 and 2 Hz roughly) reveal a number of different types of solution. (Note that in this case the equations are independent of the spider's mass and lengths are in metres.) Figure 4 shows three solutions, where the curve traces out the position of the spider's body as a function of time. The motion in Figure 4a with $\omega = 5$ makes small oscillations around the stable periodic solution. In Figure 4b ($\omega = 9$) the motion is further from the periodic orbit and less regular, with larger variation in the height of the motion, and this example also has preferred direction.

As ω increases it is also possible to find more complicated solutions which spend periods of time in $z > 0$. Since $z = 0$ represents the plane of the web, this would involve collisions between the spider and its web which are not modelled by the equations here, and this suggests the existence of dynamical reasons for limits on the speed of actuation. An example is shown in Figure 4c.

These numerical experiments suggest that a more systematic analysis of the features of the rotating spider and their relation with (a more systematic treatment of) the dynamics of this model would be worthwhile, but also that this very simple model is able to reflect the observations available.

3.3. Vibrating. In the presence of danger, or if poked by a pencil, many spiders will perform rapid oscillations in the plane of the web. Since these oscillations are in the plane of the web it is reasonable to assume that the radial spokes of the web, in tension, play the major role in the dynamics observed, and the aim of this subsection is to investigate the dynamics of connected elastic strings under tension. The analysis of subsection 2.3 shows that there is a ‘stable’ region near the centre of the web where the dynamics is regular – presumably a comfortable place for the spider to sit – but that if the spider is displaced outside this central region the dynamical description of solutions becomes more complicated. We conjecture that under threat the spider pulls itself out of the stable zone and uses the high frequency dynamics of the web to create the blurred illusion of size.

If the web is modelled using only three strings, symmetrically placed, then

$$\mathbf{Z}_1 = (\ell_0 + a) \left(\frac{\sqrt{3}}{2}, -\frac{1}{2} \right), \quad \mathbf{Z}_2 = (\ell_0 + a) \left(-\frac{\sqrt{3}}{2}, -\frac{1}{2} \right),$$

and

$$\mathbf{Z}_3 = (\ell_0 + a)(0, 1).$$

This choice is motivated to provide a vertical ($x = 0$) axis of symmetry. The equations of motion, (15) are therefore

$$m\ddot{\mathbf{X}} = \sum_1^3 k \{ |\mathbf{Z}_j - \mathbf{X}| - \ell_0 \}_+ \frac{(\mathbf{Z}_j - \mathbf{X})}{|\mathbf{Z}_j - \mathbf{X}|}. \quad (35)$$

This is a piecewise smooth dynamical system which can be simulated numerically. We choose parameters similar to those in section 3.1 but with less stretching of the strings:

$$m = 0.2 \times 10^{-3}, \quad \ell_0 = 0.17, \quad a = 0.03, \quad k = 18\pi \times 10^{-2} \quad (36)$$

and assume that by displacing its centre of mass the spider can create initial conditions with positions within a leg-span of the origin, i.e. up to $0.05 m$ away from the origin (the centre of the web). The important thing about this quantity is that it should be larger than a , so the spider can displace itself into regions where not all strings are under tension. Under these conditions, retaining only the planar displacements, two different dynamical classes of solutions can be observed in the model.

In Figure 5a the spider’s body oscillates up and down in a fairly narrow range of x -values, and similar solutions at different angles to the horizontal can be found at other initial conditions with zero velocity. If the spider is able to give itself an initial impetus as well, rotational solutions can also be observed, see Figure 5b. Both of these types of

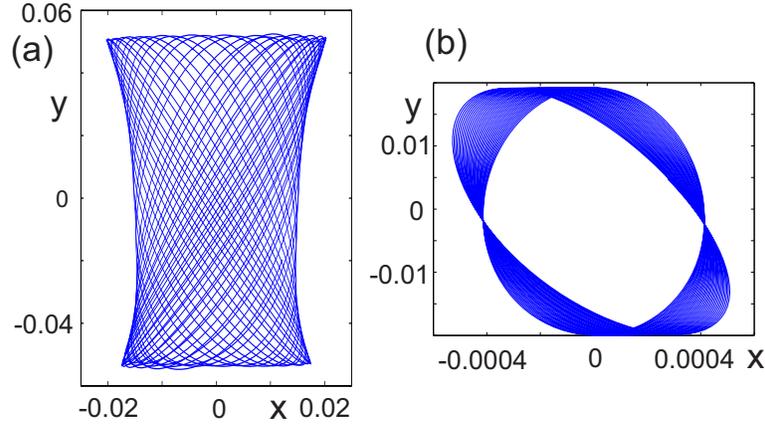


FIGURE 5. Solutions of (35) projected onto the physical space coordinates (x, y) with parameters given by (36) for time $0 < t < 3$. (a) Initial conditions $(x, \dot{x}, y, \dot{y}) = (0.02, 0, 0.05, 0)$; and (b) initial conditions $(x, \dot{x}, y, \dot{y}) = (0, 0.03, -0.02, 0)$.

motion can be observed in the behaviour of spiders. These classes of solutions are sometimes called box orbits and loop orbits respectively [19] and can be found in many mechanical systems.

In the case of infinitely many strings symmetrically distributed the force on the spider is central and given by (23). The integral can be solved in terms of special functions, details of which can be found in the appendix. The small r approximation to this motion is also described in the appendix. Working in standard polar coordinates with $A = 2\pi \frac{k}{m} (1 - \frac{\ell_0}{2p}) > 0$ the equations become

$$\ddot{r} - r\dot{\theta}^2 = -Ar + O(r^2), \quad r^2\dot{\theta} = H \quad (37)$$

where H is the initial angular momentum per unit mass. Hence, ignoring terms of order r^2 and higher

$$\ddot{r} = -Ar + \frac{H^2}{r^3} = -\frac{\partial}{\partial r} \left(\frac{1}{2}Ar^2 + \frac{H^2}{2r^2} \right). \quad (38)$$

Thus the motion is equivalent to motion in a potential

$$V(r) = \frac{1}{2}Ar^2 + \frac{H^2}{2r^2}$$

which has a unique minimum in $r > 0$ with $r^2 = H/\sqrt{A}$. Solutions oscillate about this relative equilibrium with frequency approximately $\frac{1}{2\pi} \sqrt{-V''(r)} = \frac{1}{2\pi} \sqrt{2A}$.

Typically the spider stays still with $H = 0$, in which case the equilibrium at $r = 0$ is stable (small oscillations), but once again if the spider creates some angular momentum then larger amplitude oscillations in the plane of the web are possible.

4. DISCUSSION

This paper has introduced a number of models to describe web-shaking by spiders. The models cover shaking in the direction perpendicular to the web (subsection 3.1), whirling from a higher support (subsection 3.2) and vibration in the plane of the web (subsection 3.3). All of these are in some sense minimal models: models that seem to capture the essentials of the phenomenon without becoming so complicated that they become hard to visualise or analyse. As such, all can be criticised for not including certain aspects of the web dynamics, and in particular the models of subsection 3.3 could easily be extended to three dimensions simply by making the vectors three dimensional, and so the combination of the effects of subsection 3.1 and 3.3, and the competition between in plane and out of plane motion could be explored in more detail.

Apart from the general features described in the introduction and detailed in the relevant sections a number of features stand out. First, simple models are able to capture the qualitative dynamics observed when spiders are threatened, and the models make some quantitative predictions that could be used to investigate (for example) the relationship between tension and frequency in a web.

Second, the models involve very different strategies on the part of the spider. In the case of shaking by orb-spiders the model assumes that the spider is able to detect the change in motion of the web and react by altering its position at the correct time. This implies that there is feedback in the actuation on the part of the spider. In the case of whirling the assumption is that the spider sets up a circular wave of motion around its body (shortening and lengthening its legs around the circle of its body) and that this induces the whirling motion. Thus for whirling the spider does not react to the motion, but creates it. Of course, it needs to monitor other features such as the height of the oscillations to ensure it does not collide with the web or ceiling above it. It would be interesting to prove that these are indeed the strategies taken by the spiders, and whether the whirling spider is able to moderate the speed of rotation as a function (for example) of the height of its trajectory. Finally, the in plane vibrations are actuated by an initial displacement and possibly a change in velocity (for example

by dropping a short distance). Thereafter the spider is passive and it is the elastic tension in the web and the geometry of the web which determine the nature of the vibrations of the spider. Dissipative effects would soon damp this motion, and it would be interesting to know how the spider moves so as to maintain the energy of the motion. In particular, does it pump the web (as a second order effect) as in shaking?

This leads on to a third point. The out of plane shaking and in plane vibrating described here have been modelled separately. Can spiders choose which strategy to use, or is it a function of properties of the web which determine whether the oscillations are in plane, out of plane, or both? Theoretical studies in three dimensions could certainly suggest answers, but is the behaviour of individual spiders understood well enough to determine whether it is external properties or the spider's preference that determines which dynamic strategy is used. Moreover, is the choice between box orbit almost linear oscillations and loop orbits to do with the tension of the web, the individual spider, or is it random. Numerical simulations with three, four and six string models suggest that box orbits appear more often than loop orbits in tense webs. Is this reflected in experimental observations?

The frequency of the spider's wave actuation for whirling used in subsection 3.2 is a little slower than observations would suggest. This was chosen to avoid complications due to resonance [20] and the extra periodic solutions described in [9]. The results of subsection 3.2 show that these complications are not necessary for the model to exhibit the qualitative features of observations, but more precise observations may show that the higher ω effects are needed to explain the detailed behaviour observed. We have chosen not investigate the effect of higher ω values without the information from more detailed observations.

A further hypothesis emerges from the apparent validity of simple models. Many spiders' webs have decorations (stabilimenta) on them. There are a number of different explanations for these apparent advertisements of the position of the web, and hence invitation to predators [3]. They could be flags to large non-predators to avoid accidental damage [7, 29], they could camouflage the position of the spider itself [26] or they could attract potential prey [6]. To these three hypotheses we add a fourth. Decorations provide a strengthening of the web along particular axes. If there is one stabilimentum, as often seems the case, then the dynamics of the web will be closer to the linear model of section 3.1 and hence make this form of defensive strategy easier to initiate by giving the motion a preferred axis (and so it supports the predator-defence hypothesis but in a different form). Multiple decorations may

make the behaviour closer to that of the models of section 3.3. In other words, the decorations are likely to have dynamical consequences by making parts of the web more rigid and creating preferred directions, and spiders may select those that are beneficial. Whether or not this is the primary reason for decorations, it certainly has consequences which need to be part of the debate. One immediate avenue of investigation would be to look at the relative prevalence of box orbits and loop orbits in models based on the geometry of the stabilimenta and compare these with observations.

The limit of infinitely many strings the models of subsection 3.3 was shown in the appendix to reduce to a central force defined by elliptic functions. It is not clear how much the precise form of the central force matters to an understanding of web dynamics, but it provides another avenue that could be investigated further.

Acknowledgements: I am grateful to Mark Muldoon and James Montaldi for helpful conversations. I was able to observe spiders in their webs in slow motion from numerous video clips such as [27] available on the web; these helped to inform the models developed here.

Competing Interests: I have no competing interests.

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APPENDIX A. INFINITELY MANY STRINGS

In this appendix the force (23) for infinitely many strings is simplified using the theory of elliptic integrals. This makes it possible to calculate the ‘small r ’ approximation used in subsection 3.3 and also defines an intriguing situation in which elliptic integrals appear as the forcing terms of a dynamical system rather than in their usual role as solutions. All the notation is as introduced in subsection 2.3.

It is the last term of (??), the integral, that is hard to simplify. First note that

$$I = -\ell_0 \int_{\psi}^{\pi} \frac{r - p \cos \theta}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} d\theta = \frac{\ell_0}{2r} \int_{\psi}^{\pi} \frac{2r^2 - 2rp \cos \theta}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} d\theta$$

and so by adding and subtracting p^2 to the numerator and rearranging

$$I = \frac{\ell_0}{2r} \left(\int_{\psi}^{\pi} \frac{p^2 - r^2}{\sqrt{p^2 + r^2 - 2rp \cos \theta}} d\theta + \int_{\psi}^{\pi} \sqrt{p^2 + r^2 - 2rp \cos \theta} d\theta \right). \quad (39)$$

These are standard elliptic integrals of the first and second kind respectively. Different sources use slightly different notation, so we will briefly recall definitions and basic results. The elliptic integral of the first kind $F(\phi, k)$ and the elliptic integral of the second kind, $E(\phi, k)$ are defined by

$$F(\phi, k) = \int_0^{\phi} \frac{d\theta}{\sqrt{1 - k^2 \sin^2 \theta}}, \quad E(\phi, k) = \int_0^{\phi} \sqrt{1 - k^2 \sin^2 \theta} d\theta.$$

If $\phi = \frac{\pi}{2}$ then these become complete elliptic integrals and [1]

$$F\left(\frac{\pi}{2}, k\right) = \frac{\pi}{2} \left(1 + \frac{1}{4}k^2 + \frac{9}{64}k^4 + O(k^6)\right), \quad E\left(\frac{\pi}{2}, k\right) = \frac{\pi}{2} \left(1 - \frac{1}{4}k^2 - \frac{3}{64}k^4 + O(k^6)\right). \quad (40)$$

From Gradshteyn and Ryzhik [10] (2.571.5) and (2.576.2) if $A > B > 0$ and $0 \leq x \leq \pi$,

$$\int \frac{1}{\sqrt{A - B \cos \theta}} d\theta = \frac{2}{\sqrt{A + B}} F(\delta, R)$$

and

$$\int \sqrt{A - B \cos \theta} d\theta = 2\sqrt{A + B} E(\delta, R) - \frac{2B \sin \theta}{\sqrt{A - B \cos \theta}}.$$

where

$$\delta = \sin^{-1} \sqrt{\frac{(A+B)(1-\cos\theta)}{2(A-B\cos\theta)}}, \quad R = \sqrt{\frac{2B}{A+B}}.$$

Substituting these results back into (39) gives

$$I = \frac{\ell_0}{r} \left[(p-r)F(\delta_\theta, s) - (p+r)E(\delta_\theta, s) + \frac{4pr \sin \theta}{\sqrt{p^2 + r^2 - 2pr \cos \theta}} \right]_\psi^\pi, \quad (41)$$

where we have used a subscript θ on δ to emphasise that δ is a function of the end-points, and

$$s = \frac{2}{p+r} \sqrt{pr}. \quad (42)$$

In principle this provides a closed form for the force which could be integrated to obtain solutions. To simplify matters we will consider only the behaviour when r is small, in which case we may assume that all the strings are under tension so $\psi = 0$ and using (23) and (41) the force is

$$\mathbf{F} = -\hat{\mathbf{r}}2k \left(\pi r + \frac{\ell_0}{r} ((p-r)F(\frac{\pi}{2}, s) - (p+r)E(\frac{\pi}{2}, s)) \right). \quad (43)$$

Using (40) and (42) and expanding in powers of r this becomes

$$\mathbf{F} = -\hat{\mathbf{r}}2k \left(\pi - \frac{\ell_0}{2p} \right) r + O(r^2). \quad (44)$$