

DYNAMICS OF A BISTABLE SYSTEM: THE CLICK MECHANISM IN DIPTERAN FLIGHT

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SUMMARY

A mathematical model based upon catastrophe theory is derived to describe the kinematics of the wing beat in Dipteran flight. The parameters of the model correspond to anatomical and physiological characteristics of the insect.

INTRODUCTION

Biologists have long been hampered by the lack of mathematical means for describing occasional discontinuities in otherwise continuous biological systems. Recently, however, a powerful mathematical tool, catastrophe theory, has been developed by René Thom (1969, 1975) which can be used to describe dynamical systems characterized by any of the four properties of bimodality, divergence, catastrophic jumps and hysteresis delays. The key to this approach lies in modeling the dynamics of a system rather than the underlying causal structure (*e.g.* Boyle's law models macroscopic properties of a gas without reference to the underlying causal relationships). Applications include such diverse topics as models of heartbeat and nerve impulse (Zeeman, 1972), national defense (Isnard & Zeeman, 1974), stock exchanges (Zeeman, 1974), phase transition (Fowler, 1972, Shulman & Revzen, 1972, Thom, 1971), light caustics (Thom, 1969, 1975), wage bargaining (Zeeman, 1973*a*), evolution (Waddington, 1974), cellular differentiation (Woodcock, 1974) and protein denaturation (Kozak & Benham, 1974). The purpose of the present study is to describe the kinematics of the click mechanism of Diptera using the principles of catastrophe theory.

Of the many attempts to describe the aerodynamics of insect flight, the most successful have been those in which measurements of the aerodynamic forces produced by flying insects on a balance in a wind tunnel were made simultaneously with a cinematographic record of the kinematics of the wing beat

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(Weis-Fogh, 1956; Nachtigall, 1966). In the majority of studies, however, the kinematics have not been measured exactly, a simple sinusoidal movement of the wing stroke being assumed (Weis-Fogh & Jensen, 1956). The general failure of such studies to describe the observed aerodynamics of insects is due to the fact that the movement of the wing stroke is '... far from sinusoidal and incapable of description by any simple mathematical formula' (Pringle, 1957). This is especially so in the Diptera where the thoracic and axillary articulations form a bistable system which can 'click' from one stable configuration to the other (Boettiger & Furshpan, 1952; Boettiger, 1957; Nachtigall, 1974). Catastrophe theory provides a mathematical framework to model this behavior.

The click mechanism of the dipteran wing

We shall begin with a brief description of the anatomy of the click mechanism, based on the studies of Boettiger & Furshpan (1952) and Snodgrass (1909).

Consider the wing at the start of the downstroke (fig. 1*a*). Distortion of the notum by the longitudinal muscles results in upward movement of the tip of the scutellar lever, forcing $ax1$ upward. Owing to the configuration of the linkage chain (wing process - $ax2$ - paranotum - notum), $ax1$ may only move upward by forcing the wing process outward and the lateral wall of the notum inward. These movements are resisted by the elasticity of the cuticle and also by the action of the pleurosternal muscle (fig 1*b*). As the configuration of the wing articulation changes from that illustrated in figure 1*a* to that in figure 1*b*, the angles α and β increase. The resisting force of the cuticular elasticity is directly proportional to α and β . The rate of change from configuration 1*a* to 1*b*, for a constant force applied through the scutellar lever, is therefore directly proportional to α and β , and also to the force developed by the pleurosternal muscle, which resists outward movement of the wing process. A third force which will resist the upward movement of $ax1$, and thus the downward movement of the wing is the force of the relative wind, produced by the movement of the fly through the air. This latter force acts in a direction opposite to the wing movement. The rate of change of the wing angle γ is therefore slow until position 1*b* is reached, *i.e.* $d\gamma/dt$ small for $\phi > 180^\circ$.

When the scutellar level pushes $ax1$ above the level indicated in figure 1*b* (*i.e.* $\phi < 180^\circ$), the resultant of the cuticular elastic forces and the pleurosternal tension now acts in the same direction as the movement of the scutellar level, forcing $ax1$ to rise rapidly, resulting in a large increase in $d\gamma/dt$. Thus, $d\gamma/dt >> 0$, for $\phi < 180^\circ$.

However, during this period, α and β decrease until the cuticular elastic restoring force has been completely dissipated. At approximately the same time, the articulations encounter anatomical stops which limit the upward movement of $ax1$.

The movement of the notum which drives the scutellar lever results not only

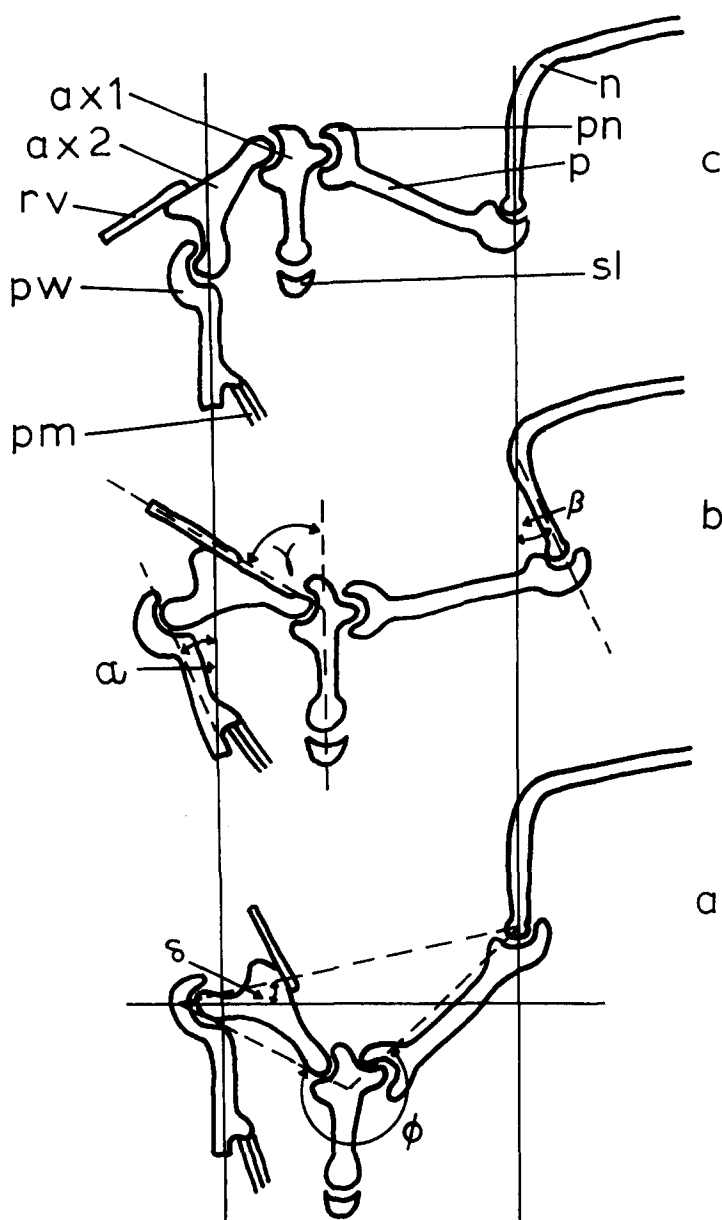


Fig. 1. a-c Three successive positions of the wing articulation in the course of a beat, from the up position (1a) to the down position (1c). The key to the anatomy is as follows: *ax 1, ax 2*—axillary sclerites 1 and 2; *n*—notum; *p*—parascutum; *pm*—pleurosternal muscle; *pn*—anterior notal process; *pw*—wing process; *rv*—base of radial vein; *sl*—section through tip of scutellar level. For further description see text.

from tension development in the longitudinal muscles but also from tension development in the dorso-ventral muscles, the tension developed being directly proportional to the muscle length (Boettiger, 1957). With the release of cuticular tension during the 'click' upwards of $ax1$ (and 'click' downwards of the wing), the notum bulges upward, stretching the dorso-ventral muscles to the extent where their tension exceeds the tension in the longitudinal muscles. The dorso-ventral muscles in their turn distort the notum, but in such a manner as to force the scutellar lever downwards, drawing down $ax1$ by virtue of a tight ligamentous coupling. The click mechanism then operates in the opposite direction to that described for the downward wing stroke, the relative wind acting with the movement instead of against it.

There is one important difference between the upstroke and the downstroke: the action of the dorso-ventral muscles compresses the whole thorax in addition to causing local distortion. This general compression results in the angle ϕ decreasing considerably. As ϕ must still change beyond the 180° level before the click mechanism operates, the angle γ will be different on the upstroke; *i.e.* the click mechanism operates at different wing angles on the upstroke and downstroke.

It can be seen, therefore, that the click mechanism depends on the vertical force of the scutellar lever being opposed by the lateral force of the cuticular elasticity and the tension developed by the pleurosternal muscle. In the absence of the pleurosternal tension the click mechanism does not function, the wing angle γ changing at an approximately constant rate (Boettiger & Furshpan, 1952). The use of catastrophe theory to describe the dynamics of the system should therefore be based on the relationship of wing angle γ to both lateral and vertical tension, and should incorporate the following properties of the system: (a) failure of the click mechanism in the absence of pleurosternal tension; (b) rapid switch in direction of the vertical force at the extreme values of γ ; (c) occurrence of the click at different values of γ on the up and down strokes.

Catastrophe theory

As mentioned above, catastrophe theory provides a mathematical tool for describing bistable systems which 'click.' Provided that the control space is of dimension 5 or less, the theorems of catastrophe theory provide a finite classification of the possible 'catastrophes' (Thom, 1975; Zeeman, 1973a), a 'catastrophe' being a sudden jump in a system from one state to another. The number and type of these catastrophes depends only upon the dimension of the control space (exogenous variables). The state space (endogenous variables) may be arbitrarily large dimension (but finite). Poston & Woodcock (1974) provide graphic illustrations of the elementary catastrophes.

Let us examine the simplest of the elementary catastrophes, the fold catas-

trophe. Consider

$$\epsilon \dot{x} = -(x^3 - 3x + b) \quad (1)$$

where x is some one-dimensional measure of the system, $\dot{x} = dx/dt$, b is an external parameter which can vary, and ϵ is a small positive number.

We will refer to (1) as the 'fast' equation, since for small ϵ , x will vary much faster than b . The equation(s) governing the change in b will be called the slow equation(s). In fact x will vary fast enough that the system will always be near the manifold of stationary points defined by $x^3 - 3x + b = 0$. Let us examine the behavior of this system as we vary b (see figure 2). Beginning at $P1$ ($b = 0, x = \sqrt{3}$), we increase b slowly. The system follows the curve until $P2$ ($b = 2, x = 1$). Now, any increase in b causes the system to jump to the lower branch of the curve, $P3$ ($b = 2, x = -2$). Reversing the process, as b decreases, the system follows the lower branch until it jumps from $P4$ ($b = -2, x = -1$) to $P5$ ($b = -2, x = 2$). Thus, slow variation of one parameter (b) can produce 'catastrophic' jumps in the system (x). Note that the lower and upper branches of the curve are attractors while the folded section of the curve (dotted in fig. 2) is a repellor.

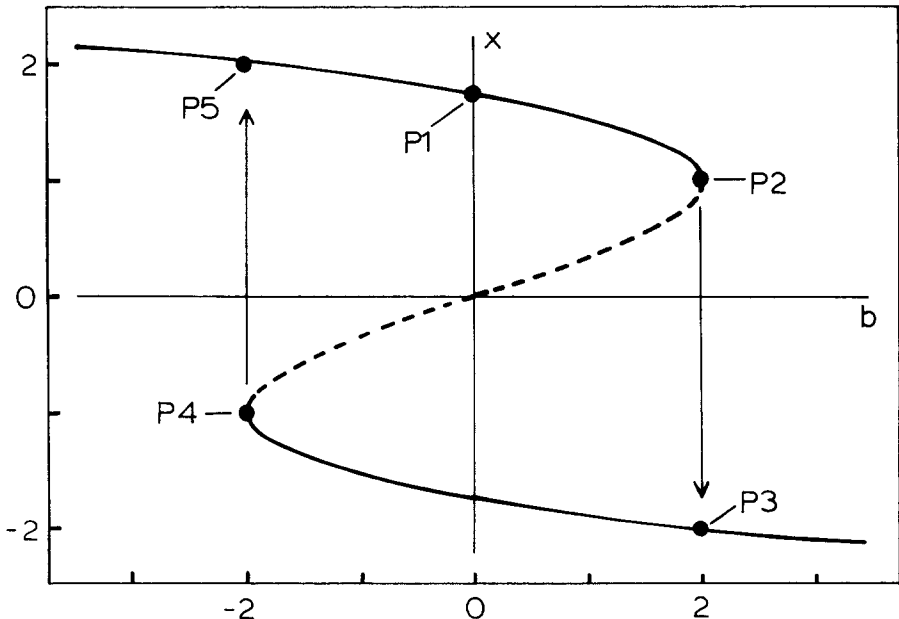


Fig. 2. The fold catastrophe. The solid portions of the curve are attractors of system trajectories, the dotted portion is a repellor. For resultant system behavior see text.

Although the fold catastrophe is sufficient to model the click, other aspects of Dipteran flight will require a more complex model, one with two control parameters. The simplest (and locally unique) choice is

$$\epsilon \dot{x} = -(x^3 - ax + b) \quad (2)$$

where a is now a second control parameter.

The fast manifold defined by equation (2) is depicted in figure 3. Notice that for fixed $a > 0$, we recover the fold catastrophe, while for fixed $a \leq 0$ the manifold is single sheeted – the click disappears.

We are now ready to model the Dipteran click mechanism. Equation (2) will form the core of our model, with x referring to wing tip position in the line of stroke, ϵ to wing inertia and drag, a to a proportion, dependent upon how far forward the wing is drawn by the direct muscles of the fly (Pringle, 1968), of pleurosternal muscular tension greater than some minimum value a^* , s to pleurosternal muscular tension, and b to the muscular driving force transmitted to the scutellar lever. We shall assume that ϵ is constant, although it may in fact vary somewhat through the wing beat. Since the longitudinal and dorso-ventral flight muscles contract in response to a sharp pull rather than a CNS impulse (Nachtigall & Wilson, 1967), our model for variation in b must be endogenous. As a first approximation we chose

$$b = rx$$

where r is a physical parameter giving the rate at which muscular tension develops following a stretch of the muscle.

The system (2) – (3) has the following properties for $a > 0$. For small ϵ we have $\dot{x} \gg \dot{b}$. Hence, x is termed the fast variable and b the slow variable. Points (b, x) on the system trajectory will lie on or near the fast manifold. Thus, qualitative behavior of the system can be determined by considering the slow equation(s), equation (3) in this case, with the constraint $x^3 - ax + b = 0$ (see fig. 2). Beginning with $b = 0$ and $x = \sqrt{a}$, b increases and x decreases slowly. Finally at the point $b = 2\sqrt{a/3}$, $x = \sqrt{a/3}$, the system ‘clicks’, with $\dot{x} \ll 0$ until x reaches the lower branch of the constraint curve. Then the process is repeated in reverse. However, if a goes to zero, the system experiences damped oscillations with no clicks, eventually reaching the stable point $x = b = 0$. Amplitude depends only upon the parameter a , $A = (4/3)\sqrt{3a}$, where A is amplitude. When the wings are drawn back, a is reduced, consequently reducing the wing beat amplitude. Wing beat frequency depends upon ϵ , a and r . For ϵ fixed we find that the frequency is approximately proportional to r/a .

However, the system described above is not yet sufficient, failing to satisfy (c) of the previous section. In addition we require that b have an upper bound,

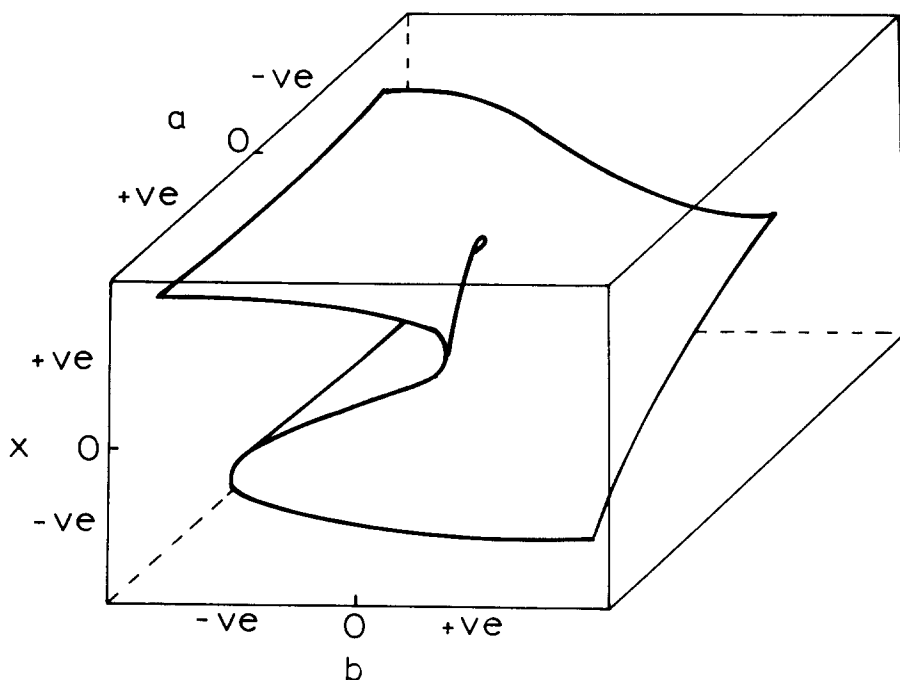


Fig. 3. The catastrophe manifold with one fast variable, x , and two slow variables, a and b . In the single-sheeted region the manifold is an attractor of system trajectories. In the triple-sheeted region the middle sheet is a repeller, the upper and lower sheets attractors. Thus, for a > 0 a trajectory on the upper sheet will jump to the lower sheet when an increase in b brings the system past the edge of the fold.

corresponding to a maximum tension which can be developed in the flight muscles. These problems can be rectified by adding a term in b to the right side of equation (3) and varying a with wing position. That is, the proportion of pleurosternal tension transmitted is greater when the wing is farther forward (as it is at the end of the downbeat) (Pringle, 1968). We shall assume that this difference is small and approximately linear in wing position. The new set of equations becomes

$$\epsilon \dot{x} = -(x^3 - a'x + b) \quad (4)$$

$$(5) \quad b = r(sx - b) \quad (5)$$

$$a' = a - cx \quad (6)$$

$$a = \lambda f(s) - a^* \quad (7)$$

with s the pleurosternal tension, c the cosine of the angle of the wing stroke to the horizontal plane, λ the angle to which the wing is drawn forward at the

midpoint of the wing stroke, $f(s)$ a positive monotonically increasing function in s , and r, s, c, λ and $a^* \geq 0$.

The click now occurs at $x = [-c \pm \sqrt{c^2 + 3a}]/3$ (+ for downbeat, - for upbeat). Thus, the click down is retarded and the click up advanced. The amplitude of the wing beat increases with c , $A = (4/3)\sqrt{c^2 + 3a}$. Amplitude may be reduced by decreasing c . The fly is capable of altering the position of mechanical stops which limit the movement of the articulations; the effect of varying c would appear to reflect such alterations of position. Alternatively, a may be reduced, altering the pleurosternal tension transmitted to the wing by moving the entire locus of wing movement toward the rear. Wing beat frequency now depends upon the values of ϵ, r, s and a in a complex fashion. Estimating parameter values for *Phormia* from Nachtigall (1974) - $\epsilon = .00025, r = 300, s = 2.05, c = .7, f(s) = .4s, a^* = 0$ and $\lambda = 1.6$ - yields a wingbeat frequency of 150 Hz.

DISCUSSION

If the wingbeat is treated as an harmonic oscillator, we have $x(t) = x(0) \sin(\sqrt{k/m} t)$, for x maximal at $t = 0$, k the muscular elastic force, and m the wing inertia. However, this formulation lacks parameters whose variation can be involved in flight control. In addition, empirical study has shown that the click mechanism results in a wingbeat frequency approximately proportional to $m^{-.22}$, not $m^{-.5}$ (for *Calliphora*) (Danzar, 1956).

The catastrophe model of Dipteran flight improves upon the traditional model in several respects.

1. The graph of wing position will not be a sinusoidal curve, but rather a flatter curve near the extremes and a steeper one in between. Figure 4 shows this curve along with a sine curve and a cinematographically derived curve of the actual wing beat (Nachtigall, 1974).

2. Using the parameters given above, we find the wingbeat frequency proportional to $\epsilon^{-.29}$; in good agreement with Danzar's (1956) measurements.

3. When the wings are drawn back, the transmitted pleurosternal tension is reduced, parameter a goes to zero and the click disappears. The wings will come to rest in mid-position following a series of damped oscillations. This prediction is corroborated by Nachtigall (1966, fig. 29).

4. The observation that the upstroke is faster than the downstroke is replicated in our model since the click up occurs earlier in the upbeat than the corresponding click down. However, since variation in wing pitch with wing position has been ignored (drag has been assumed constant throughout the wing beat), we underestimate the difference in rate between upstroke and downstroke.

5. The fly turns by decreasing the amplitude of the beat of one wing and varying the pitch on that side (Nachtigall, 1974). The turn is made toward the

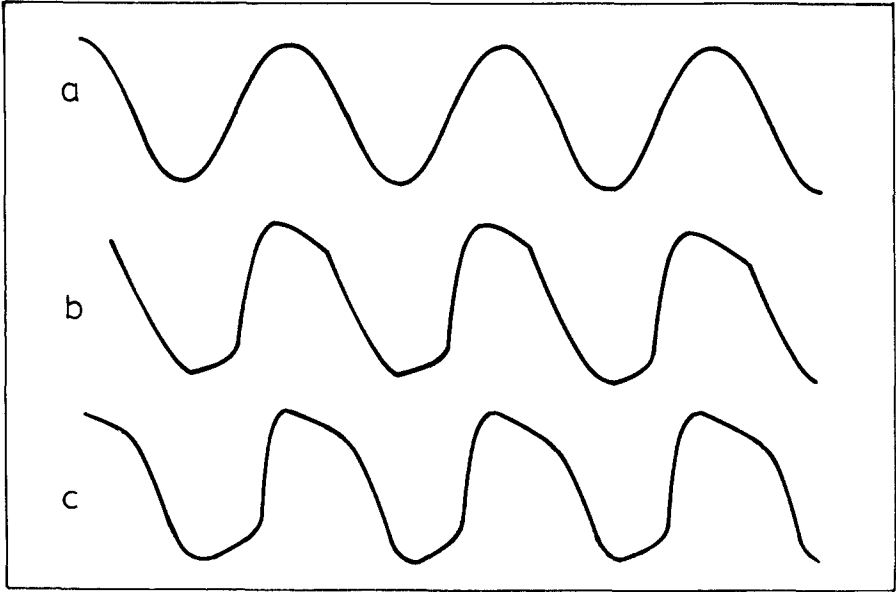


Fig. 4. Three plots of wing tip position relative to the fly plotted against time: a) a sine wave, b) a real fly (*Phormia regina* (Meig.)) (After Nachtigall) and c) a catastrophe model curve.

wing of shorter beat. In our model parameters r and s must be the same for both wings. Thus, turning can only be accomplished by varying parameters a , c and ϵ for one wing so as to reduce wing beat amplitude while maintaining the same frequency as the other wing. Since the wing beating with greater amplitude receives the majority of the driving force, it is largely responsible for determining the frequency. Thus, to turn the fly draws back the wing (reducing a), varies the wing pitch (reducing ϵ), and reduces the relative movement of the wing forward and back as compared to up and down (reducing c). This latter is likely accomplished by repositioning the mechanical stops. Such adjustments might also alter a parameter which has been implicit in the model so far, namely the coefficient of the x^3 term in equation (4). These predictions are compatible with the observation that flight control is accomplished with different muscles than those supplying the driving force (Nachtigall & Wilson, 1967).

6. Boettiger (1957) has shown that wingbeat frequency varies with wing inertia. Varying inertia corresponds to varying ϵ in our model. If ϵ goes to zero, equation (4) becomes a constraint and equation (5) determines the frequency. Hence, if pleurosternal tension and wing angle λ remain constant, we predict an upper bound to the wingbeat frequency.

7. Very high frequency, low amplitude vibrations of the wings have oc-

casionally been recorded in which the click mechanism fails to operate (Boettiger, 1957). The catastrophe model yields this behavior when $s \approx a/\epsilon$ (the slow equation becomes a fast equation).

As the model given here provides a number of insights into the Dipteran click mechanism, several refinements may be worth pursuing. One is to account for variations in drag with wing position. This might be accomplished by assuming pitch independent of wing position and introducing pitch as a second fast variable, or by assuming that pitch varies in a defined way with wing position and replacing ϵ with $\epsilon(x)$ in the fast equation. A second extension would be to model the wing tip position in two dimensions, in order to capture the details of the wing tip's path (a figure-eight) (Nachtigall, 1974). A third possibility is to bring the asynchronous nervous impulses to the flight muscles into the model. Duffing's equation may have applicability here (Zeeman, 1973*b*). Such a framework would also provide a natural place for explicit representation of wing inertia and an alternative explanation for the high frequency, but small amplitude vibrations which are occasionally observed.

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