

Butterflies

and

Mathematics

“I do not know whether I was then a man dreaming I was a butterfly, or whether I am now a butterfly dreaming I am a man.” (Chang Tzu)

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A Pattern Formation Mechanism for Butterfly Wing Patterns

The variety of different patterns and spectacular colouring on butterfly and moth wings is astonishing.

There are close to a million different types of butterflies and moths.

The study of butterfly wing colours and patterns has a long history.

As with the development of the coat patterns on mammals, the patterns on the wings of lepidoptera (butterflies and moths) appear towards the end of morphogenesis, but they reflect an underlying prepattern that was laid down much earlier.

We will look at a possible model mechanism for wing patterns proposed by Murray (1981).

A major feature of the model is the crucial dependence of the pattern on the geometry and scale of the wing when the pattern is laid down.

Although the diversity of wing patterns might indicate several mechanisms are required, it turns out that seemingly different patterns can be generated by the same mechanism.

Eyespots, or ocelli, are important elements in many butterfly wings.

Nijhout (1980) presents evidence from experiments on the nymphalid butterfly *Precis coenia* that the foci of the eyespots are the influencing factors in their pattern formation.

The foci generate a morphogen, the level of which activates a colour-specific enzyme.

Another model, by Sibatini (1980), is based on the existence of an underlying prepatter and suggests the ocellus-forming process involves several interacting variables.

These two models are not necessarily mutually exclusive.

Experimental work suggests that there are at least two mechanisms in the pattern formation of *Ephestia kuhniella*, since different effects are obtained depending on the time after pupation at which cauterization occurs.

However, the same mechanism could simply be operating at different times, which could imply different parameter values and different geometries and scale produce quite different patterns.

The main reason for studying wing pattern in lepidoptera is to try to understand their formation in hopes of finding a pattern generation mechanism (or mechanisms).

Another reason is to show evidence for the existence of diffusion fields greater than 100 cells.

From a modelling point of view, it is interesting that the evolution of pattern looks essentially two-dimensional, so we must consider the roles of both geometry and scale

The Model

Assume there are sources of a morphogen, with concentration S , situated at A and P on the anterior and posterior edges of the wing. For simplicity, not necessity, this is idealized as a circular sector of angle θ bounded by radii r_1 and r_2 .

The governing equation for the morphogen concentration $S(r, \theta, t)$ is

$$\frac{\partial S}{\partial t} = D \left(\frac{\partial^2 S}{\partial r^2} + \frac{1}{r} \frac{\partial S}{\partial r} + \frac{1}{r^2} \frac{\partial^2 S}{\partial \theta^2} \right) - KS$$

where $D(\text{cm}^2\text{s}^{-1})$ is the diffusion coefficient and $K(\text{s}^{-1})$ is the degradation rate-constant.

S diffuses across the wing surface. Suppose the cells react in response to the local morphogen level and a gene G is activated by S to produce a product g . We assume the kinetics of the gene product exhibits a biochemical switch behaviour.

One model for the switch mechanism gives

$$\frac{dg}{dt} = K_1 S + \frac{K_2 g^2}{K_4 + g^2} - K_3 g$$

where the K 's are positive parameters.

Boundary and initial conditions for the mathematical problem are:

$$S(r, \theta, 0) = 0, \quad r_1 < r < r_2, \quad 0 < \theta < \theta_0$$

$$S(r, 0, 0) = S_0\delta(r-r_P), \quad S(r, \theta_0, 0) = S_0\delta(r-r_A)$$

$$\frac{\partial S}{\partial r} = 0 \quad 0 \leq \theta \leq \theta_0, \quad r = r_1, \quad r = r_2$$

$$\frac{\partial S}{\partial \theta} = 0, \quad r_1 < r < r_2, \quad \theta = 0, \quad \theta = \theta_0$$

$$g(0; r, \theta) = 0$$

where $\delta(t)$ is the Dirac Delta function.

This model uniquely determines S and g for all $t > 0$.

Introduce nondimensional quantities to isolate the key parameter groupings and to indicate the relative importance of different terms in the equations. Let $L(\text{cm})$ be a standard reference length and $a(\text{cm})$ a relevant length of interest in the wing. The dimensionless quantities are:

$$\gamma = \left(\frac{a}{L}\right)^2, \quad S^* = \frac{S}{S_0}, \quad r^* = \frac{r}{a}, \quad t^* = \frac{D}{a^2}t,$$

$$k = \frac{KL^2}{D}, \quad k_1 = \frac{K_1 S_0 L^2}{D\sqrt{K_4}}, \quad k_2 = \frac{K_2 L^2}{D\sqrt{K_4}},$$

$$k_3 = \frac{K_3 L^2}{D}, \quad g^* = \frac{g}{\sqrt{K_4}}$$

The model becomes (after dropping the asterisks):

$$\frac{\partial S}{\partial t} = D \left(\frac{\partial^2 S}{\partial r^2} + \frac{1}{r} \frac{\partial S}{\partial \theta} + \frac{1}{r^2} \frac{\partial^2 S}{\partial \theta^2} \right) - \gamma k S,$$

$$\frac{dg}{dt} = \gamma \left(k_1 S + \frac{k_2 g^2}{1 + g^2} - k_3 g \right) = \gamma f(g; S).$$

The initial and boundary conditions are algebraically the same except that

$$S(r, 0, 0) = \delta(r - r_P), \quad S(r, \theta_0, 0) = \delta(r - r_A)$$

Suppose at a given time $t = 0$ say, $g = 0$ everywhere and a pulse of morphogen S is released. What happens?

The gene product is activated. So g increases with time as in the graph. If S never reaches the critical threshold $S_{th} (> S_C)$, then as S decrease to 0, so does g . But if $S > S_C$ for long enough, then g can increase sufficiently so that there is a switch from $g = 0$ to $g = g_3$. S must reach a threshold is intuitively clear.

Even the linear problem for S with the conditions is not easily solved analytically. S looks like the graph, reaching a different maximum at each r . For a given $S(r, t)$, g has to be found numerically. S_{th} is not trivial to determine analytically.

Intuitively we can see how the mechanism, in which a finite amount of morphogen S_0 is released from A and P can generate a spatial pattern in gene product. The morphogen pulse diffuses and decays as it spreads across the wing surface, and as it does so it activates the gene G to produce g .

The growth in g is not instantaneous and so the critical S_{th} is larger than S_C .

The coupling of the two processes, diffusion and gene transcription, in effect introduces a time lag. Thus, as the pulse of morphogen diffuses across the wing as a quasi-wave, it generates a domain of permanently non-zero values of g , until S has decreased sufficiently so that g returns to 0.

Geometry and Scale

Even with such a simple model the variety of patterns that can be generated is impressive.

- for a fixed geometry, what are the effects of scale?
- for a fixed scale, what are the effects of geometry?

Eyepots

Assume that the eyespot centre emits a pulse of morphogen. The idealized mathematical problem in plane axisymmetric polar coordinates, with the same conditions, is

$$\frac{\partial S}{\partial t} = \frac{\partial^2 S}{\partial r^2} + \frac{1}{r} \frac{\partial S}{\partial r} - \gamma k S,$$

$$S(r, 0) = \delta(r), \quad S(\infty, t) = 0$$

The solution is

$$S(r, t) = \frac{1}{4\pi t} \exp \left[-\gamma k t - \frac{r^2}{4t} \right], \quad t > 0$$

It can be shown that if such mechanisms operate, then the dimension of the diffusion field of pattern formation is of the order of several millimetres. This is much larger than any so far found in other embryonic situations.

It is most likely that several independent mechanisms are operating, possibly at different stages, to produce diverse patterns on butterfly wings. It is reasonable to assume, as a first modelling step, that the number of mechanisms is the same as the number of melanins present.

Perhaps we should turn the question around and ask “What patterns *cannot* be formed by such simple mechanisms?”

The Butterfly Effect

The “Butterfly Effect” is the propensity of a system to be *sensitive to initial conditions*. Such systems over time become unpredictable.

The name seems to come from Edward Lorenz’s paper “Predictability: Does the Flap of a Butterfly’s Wings in Brazil Set Off a Tornado in Texas?” address at the annual meeting of the American Association for the Advancement of Science in Washington, December 1979.

The Butterfly Effect was a starting point for Chaos Theory.

The Butterfly effect has been most commonly associated with weather systems. This is where the discovery of “non-linear” phenomena began.

However, any “Newtonian Classical” system where one system is in competition with another, such as the “chaotic pendulum” (which plays magnetism off against gravity) will exhibit “sensitivity to initial conditions”.

Other examples are predator-prey systems and liquid flow.

Natural systems can present a tangled mix of determinism and randomness, or “order” and “chaos” .

Many shapes that describe non-linear systems are fractal, in the sense that they are a set of shapes that are self-similar on smaller and smaller scales.

Is Nature really fractal, or is it just a better description than the simple geometry of Euclid?

The Butterfly Theorem

Theorem: *Let M be the midpoint of a chord PQ of a circle, through which two other chords AB and CD are drawn; AD cuts PQ at X and BC cuts PQ at Y . Then M is the midpoint of XY .*

The Butterfly Lemma

Lemma (Zassenhaus 1934): Given two normal subgroups G_1 and G_2 of a group, and two normal subgroups H_1 and H_2 of G_1 and G_2 , respectively, then

$$H_1(G_1 \cap H_2) \text{ is normal in } H_1(G_1 \cap G_2),$$

$$(H_1 \cap G_2)H_2 \text{ is normal in } (G_1 \cap G_2)H_2,$$

and one has an isomorphism of quotient groups

$$H_1(G_1 \cap G_2) / H_1(G_1 \cap H_2) \simeq (G_1 \cap G_2)H_2 / (H_1 \cap G_2)H_2$$

This lemma was named by Serge Lang (2002) based on the shape of the corresponding diagram, which Lang derived from Zassenhaus's original publication.

The Butterfly Lemma is used in the following two theorems:

Theorem (Schreier) *Let G be a group. Two normal towers of subgroups ending with the trivial group have equivalent refinements.*

Theorem (Jordan- Hölder) *Let G be a group, and let*

$$G = G_1 \supset G_2 \supset \dots \supset G_r = \{e\}$$

be a normal tower such that each group G_i/G_{i+1} is simple, and $G_i \neq G_{i+1}$ for $i = 1, \dots, r - 1$. Then any other normal tower of G having the same properties is equivalent to this one.

The Butterfly Graph

The n -dimensional butterfly graph is a directed graph whose vertices are pairs (w, i) , where w is a binary string of length n and i is an integer in the range 0 to n and with directed edges from vertex (w, i) to $(w', i + 1)$ iff w' is identical to w in all its bits with the possible exception of the $(i + 1)$ th bit counted from the *left*.

The butterfly graph has $2^n(n + 1)$ vertices and $2^{n+1}n$ edges.

The Butterfly Curves

There are two curves known as butterfly curves:

- The sextic plane curve given by

$$y^6 = x^2 - x^6$$

- A curve with polar equation

$$r = e^{\cos \theta} - 2 \cos(4\theta) + \sin^5 \left(\frac{\theta}{12} \right)$$

with corresponding Cartesian parametric equations:

$$x = \cos t \left[e^{\cos t} - 2 \cos(4t) + \sin^5 \left(\frac{t}{12} \right) \right]$$
$$y = \sin t \left[e^{\cos t} - 2 \cos(4t) + \sin^5 \left(\frac{t}{12} \right) \right]$$

“The butterfly counts not months but moments, and has time enough.” (Rabindranath Tagore)