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Pigmentation pattern formation in the butterfly wing of *Papilio dardanus*

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Abstract. We investigate pigmentation patterns in the butterfly wing of *Papilio dardanus* by numerical simulations of a reaction-diffusion model on a geometrically accurate wing domain. Our results suggest that the wing coloration is due to a simple underlying stripe-like pattern of some pigment-inducing morphogen. In this paper, we present some of our numerical results and discuss the validity of our model by comparing our results with pictures of male and female wing patterns of the butterfly.

1 Introduction

The species of butterfly *Papilio dardanus* is widely distributed across sub-Saharan Africa and well-known for the spectacular phenotypic polymorphism in females. The females have evolved more than a dozen different wing color patterns, of which several mimic different species of unpalatable danaids, other butterflies and moths. The female wing patterns are very complicated in their appearance. At first glance it seems difficult to find an underlying logical relationship between them even in the single species. The males, on the other hand, are monomorphic and strikingly different from the females, exhibiting a characteristic yellow and black color pattern and tailed hind wing (Fig. 1).

Global pigmentation patterns on lepidopteran wings, which cover whole dorsal and ventral wing monolayers, can be very complicated in structure and they are sometimes used for identification of species. Owing to the pioneering work of Schwanwitsch [10] and Süffert [12] on the nymphalid ground plan, the complicated patterns on the wings can be understood as a composite of a relatively small number of pattern elements. Regarding pigmentation patterns of the butterfly *Papilio dardanus*, Nijhout [8] proposed an idea that the black color pattern elements in the wing constitute the principle pattern elements, even though the background color attracts our attention most. The elements differ in size depending on the mimetic form and this can have dramatic effects on the overall appearance of the pattern. Our problem is, then, largely simplified and our goal is to present a mechanism that can account for only the black pattern elements.

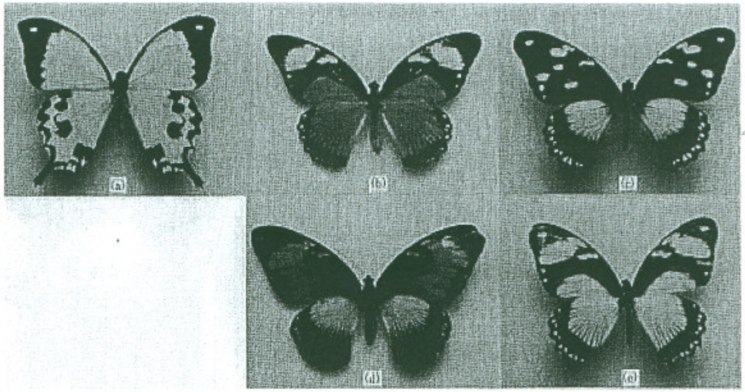

Fig. 1. Male (a) and some mimetic female forms (b)-(e) of *Papilio dardanus*: (b) *trophonius*, (c) *cenea*, (d) *planemoides*, (e) *hippocoon*.

2 Basic idea on pattern formation

Fig. 2 shows Nijhout's basic idea on how different wing patterns of the butterfly *Papilio dardanus* arise from changes in size of the black color pattern elements. The left-hand side of Fig. 2 shows black color wing patterns corresponding to mimetic females in Fig. 1. The arrows in the figure on the right-hand side of Fig. 2 indicate the directions of expansion or contraction of the pattern elements proposed to account for the variety of female wing patterns of *Papilio dardanus*.

Recently, we presented a reaction-diffusion model on a geometrically accurate wing domain for the formation of pigmentation patterns in the butterfly wing of *Papilio dardanus*. Our numerical results reveal that only small changes in the gradient threshold are necessary to generate different female wing patterns of *Papilio dardanus* [11]. The model is based on the idea that a system of reacting and diffusing chemicals could evolve from an initially uniform spatial distribution to concentration profiles that vary spatially - the so-called diffusion driven instability [13].

In the next section, we review briefly the reaction-diffusion model and present some numerical results.

3 Model equations and numerical simulations

Several Turing-type reaction-diffusion models have been proposed [7]. As an illustration of the pattern forming potential of these models, we solve the non-

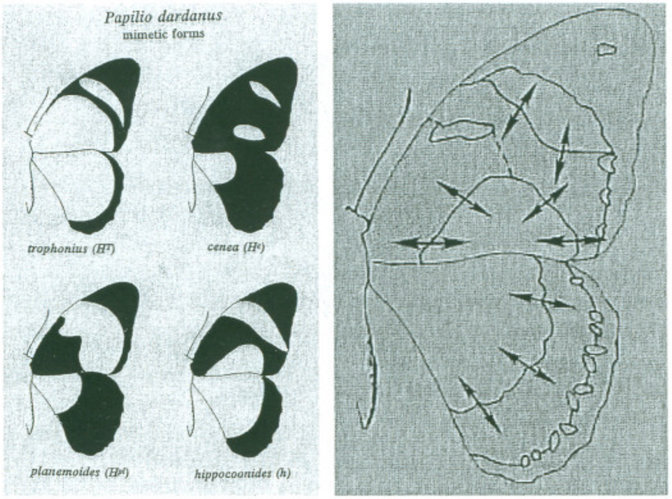

Fig. 2. Basic idea on color pattern formation in the wing of *Papilio dardanus*: Black color patterns (left), abstracted from the mimetic female forms in Fig. 1 (b)-(e), are proposed to arise from a basic pattern (right) by increasing or decreasing the black color pattern elements in size, as shown by the arrows in the figure (see [8]). (Reproduced from [8] with permission.)

dimensionalised reaction-diffusion system with Gierer-Meinhardt [4] reaction kinetics

$$u_t = \gamma \left(a - b\,u + \frac{u^2}{v\,(1 + k\,u^2)} \right) + \nabla^2 u, \tag{1}$$

$$v_t = \gamma \left(u^2 - v \right) + d\,\nabla^2 v \tag{2}$$

using the finite element method on fixed two-dimensional wing domains. Here $u(\underline{x}, t)$ and $v(\underline{x}, t)$ represent chemical (morphogen) concentrations at spatial position $\underline{x}$ and time t; a, b, d, k and γ are positive parameters. The boundary conditions for our simulations are either Dirichlet for one morphogen and Neumann for the other or Neumann conditions for both morphogens. Initial conditions are prescribed as small perturbations about the homogeneous steady state if it exists. We used the finite element method to compute solutions (see [5,9] and the web site [1] for full details of the finite element method). Numerical solutions are illustrated in Fig. 3.

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[1] http://web.comlab.ox.ac.uk/cucl/work/andy.wathen/software.html

Fig. 3. Numerical results of the Gierer-Meinhardt model [4]. Top panel: (from left to right) male, *trophonius*, *cenea*. Bottom panel: *planemoides*, *hippocoon* (the patterns in Fig. 3 simulate the patterns observed in Fig. 1).

4 Discussion

We have shown that the Turing model in two dimensions can account for pigmentation patterning on the adult wing of the butterfly *Papilio dardanus*. We carried out these simulations on a geometrically accurate adult wing shape. Our mathematical analysis and computer simulations of the model equations suggest that the global wing coloration is essentially due to underlying stripe-like patterns of some pigment inducing morphogen. Recently, we used our model to predict the outcome of a number of different types of cutting experiments [6].

Our results also highlighted the importance of a few key factors such as parameter values for mode selection, threshold values which determine color, wing shape and boundary conditions. In particular, slight changes in the gradient threshold could generate diverse pigmentation patterns exhibited in the females of *Papilio dardanus*. This result may be very suggestive and important from the genetic point of view because it agrees with the result that most of the different female color patterns are controlled by a single genetic locus [1–3]. Moreover, we found that we needed to impose slight changes in boundary conditions at the body and wing margins of the forewing to generate the range of patterns shown in Fig. 3 (we refer the reader to [11] for full details). Therefore, whereas [8] invokes local control in growth overlying a basic ground plan pattern as a mechanism for generating the diversity of color patterns exhibited in *Papilio dardanus*, we have shown that, alternatively, local control of boundary conditions can achieve a similar result.

It is known that the pigmentation process occurs as the butterfly wing imaginal disc grows from the larval stage to the adult. We are now solving the model computationally on a growing domain to see if it can exhibit patterns similar to those observed experimentally. We will then use the model to make experimentally testable predictions.

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