HIROSHIMA MATH. J.
32 (2002), 325–336

A predictive model for color pattern formation in the butterfly wing of *Papilio dardanus*

This paper is dedicated to Professor Masayasu Mimura on his sixtieth birthday.

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(Received September 25, 2001)

Previously, we have proposed a mathematical model based on a modified Turing mechanism to account for pigmentation patterning in the butterfly wing of *Papilio dardanus*, well-known for the spectacular phenotypic polymorphism in the female of the species (Sekimura, *et al.*, Proc. Roy. Soc. Lond. **B 267**, 851–859 (2000)). In the present paper, we use our model to predict the outcome of a number of different types of cutting experiments and compare our results with those of a model based on different hypotheses.

1. Introduction

Pigmentation patterns on lepidopteran wings, which cover the whole dorsal and ventral wing monolayers, can be complicated in structure and they are sometimes used for identification of species. However, owing to the pioneering work of Schwanwitsch (1924) and Süffert (1927) 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 (for details, see Nijhout, 1991). In spite of these simplifications, the problem of color pattern formation in wings is still not fully resolved and there exist few mathematical models to account for the diversity of color pattern in wings except for some specific features.

Among them, the development of eyespot patterns is the best understood mechanism at present. Nijhout (1990) presented a model for eyespot formation based on experimental evidence, in which a spatial distribution of sources and sinks of pattern organisers is firstly set up and the organising centers induce color patterns in their surroundings. Nijhout succeeded in producing point-like patterns in the exact locations of the organizing centers by an activator-inhibitor mechanism (Meinhardt, 1982) that assumes that the

2000 *Mathematics Subject Classification*. 92O15, 35K57, 65N30.
Key words and phrases: reaction-diffusion; color pattern formation; butterfly wing; *Papilio dardanus*, Gierer-Meinhardt, finite elements.

wing veins act as fixed boundary conditions for the activator and as reflecting boundaries for the inhibitor (Nijhout, 1990, 1994).

Regarding global patterns covering the entire wing surface, Murray (1981) proposed a simple diffusion model for the development of the commonly observed crossbands of pigmentation shortly after pupation. Murray's model extends the idea of a determination stream proposed by Kühn and von Engelhardt (1933), namely, that the anterior and posterior margins of the wing are sources from which emanates a wave of morphogen concentration. Murray showed that this simple model could exhibit a wide variety of observed patterns. For example, it exhibits patterns consistent with those observed after microcautery surgery. The theoretical results are consistent with the observation of Schwantwitsch (1924).

By use of a geometrically accurate wing domain, Sekimura *et. al.*, (2000) presented a reaction-diffusion model for the formation of global pigmentation patterns in the butterfly wing of *Papilio dardanus*. The model is based on the idea that a system of reacting and diffusing chemicals can evolve from an initially uniform spatial distribution to concentration profiles that vary spatially—so-called diffusion driven instability (Turing, 1952). By mathematical analysis and computer simulation of the model equations, Sekimura *et. al.*, (2000) suggested that the global wing coloration is essentially due to underlying stripe-like patterns of some pigment inducing morphogen. The generality of the model should allow it to be applied to a wide variety of problems related to wing color patterns.

In the following sections, we review the model framework briefly and then present numerical results which show how the model can be used to make theoretical predictions on cutting experiments.

2. A model for color pattern formation in the butterfly wing of *Papilio dardanus*

Papilio dardanus is a species of butterfly widely distributed across sub-Saharan Africa, and it is well known for its spectacular phenotypic polymorphism in females (see Figure 1). The female wing patterns look very complicated in their appearance and at first glance it seems difficult to find an underlying logical relationship between them even in the single species. However, the work of Nijhout suggests that the black color pattern elements in the wing constitute the principle pattern elements, even though the background color attracts our attention most (Nijhout, 1991). The elements differ in size depending on the mimetic form and this can have dramatic effects on the overall appearance of the pattern (see Figure 2). Our problem is, then, largely