Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Insect Science

The mechanism controlling phenotypic plasticity of body color in the desert locust: some recent progress

Seiji Tanaka[1], Ken-ichi Harano[2], Yudai Nishide[1] and Ryohei Sugahara[1]

Schistocerca gregaria exhibits density-dependent body color polyphenism. Nymphs occurring at low population densities show green–brown polyphenism. They show phase polyphenism and develop black patterns at high population densities. Recent studies suggest a third type of polyphensim, that is, homochromy, a response to background color. Laboratory experiments that considered homochromy suggest that humidity is not directly involved in green–brown polyphenism and that odor from other individuals does not induce black patterns. Black patterns can be induced in isolated nymphs by video images of locusts and tadpoles. Juvenile hormone and [His^7]-corazonin control body color in locusts. The gene encoding the latter has been identified for *S. gregaria* and *Locusta migratoria*, and its key role in controlling black patterning has been demonstrated.

Addresses
[1] National Agriculture and Food Research Organization (NAFO), Institute of Agro-biological Sciences, Ohwashi 1-2, Tsukuba, Ibaraki 305-8634, Japan
[2] Brain Science Institute, Faculty of Agriculture, Tamagawa University, Machida City, Tokyo 194-8610, Japan

Corresponding author: Tanaka, Seiji (stanaka117@yahoo.co.jp)

Current Opinion in Insect Science 2016, **17**:10–15
This review comes from a themed issue on **Molecular physiology**
Edited by **Takema Fukatsu** and **Ryo Futahashi**
For a complete overview see the Issue and the Editorial
Available online 17th May 2016
http://dx.doi.org/10.1016/j.cois.2016.05.011

Introduction

The desert locust, *Schistocerca gregaria*, shows density-dependent phase polyphenism, in which various behavioral, morphological and physiological traits are strikingly affected by changes in population density [1–5]. For example, the locusts occurring at a low population density are sedentary, whereas those occurring at a high population density are migratory and move actively as bands or swarms. The former is called the solitarious phase, and the latter is called the gregarious phase. During the transitional period from the solitarious to the gregarious phase and vice versa, an intermediate form called the transient phase also appears.

Body coloration can play a major role in the biology of animals, especially small invertebrates, such as grasshoppers [6]. Body coloration is, in general, related to various phenomena, including prey–predator relationships, species and mate-recognition, microhabitat utilization and thermoregulation [6–11,12•] and is often controlled by biotic and abiotic factors [5,13,14].

According to a widely accepted model [3–5,15], the nymphs of *Schistocerca gregaria* exhibit two types of body-color polyphenism after the first instar: green/brown polyphenism controlled by humidity and color polyphenism of the phase (black patterning) controlled by crowding. Green/brown polyphenism is observed only in nymphs in the solitarious phase in this locust. Green morphs have a green or greenish body color, whereas individuals in the brown morph are not necessarily brown and develop various non-green background colors, including brown, gray, dark gray, yellow and whitish colors. The variation is continuous, and there are endless intermediates in between. Unlike other acridids, such as the migratory locust, *Locusta migratoria* [16], it has been considered that *S. gregaria* does not show homochromy, a response to the background color of the growing environment [3,5,15]. In response to crowding, *S. gregaria* nymphs develop black patterns with a white, yellow or orange background color, depending on the nymphal instar. Tactile, visual and olfactory (smell) factors derived from other individuals have been suggested as being involved in the induction of black patterning [17–19].

Body-color polyphenism in Orthoptera has been studied most intensively for *S. gregaria* and *L. migratoria* [3–5,16]. Recently, it has been suggested that some widely accepted ideas may need to be revised [20]. This review will describe these ideas and related findings and outline information on the endocrine and molecular control of body color in these locusts.

Solitarious body coloration

Green/brown polyphenism: Body color of locusts is composed of background color and black patterns. In *S. gregaria*, it has been reported that nymphs reared in high humidity develop a green background color, whereas those reared in low humidity assume various none-green

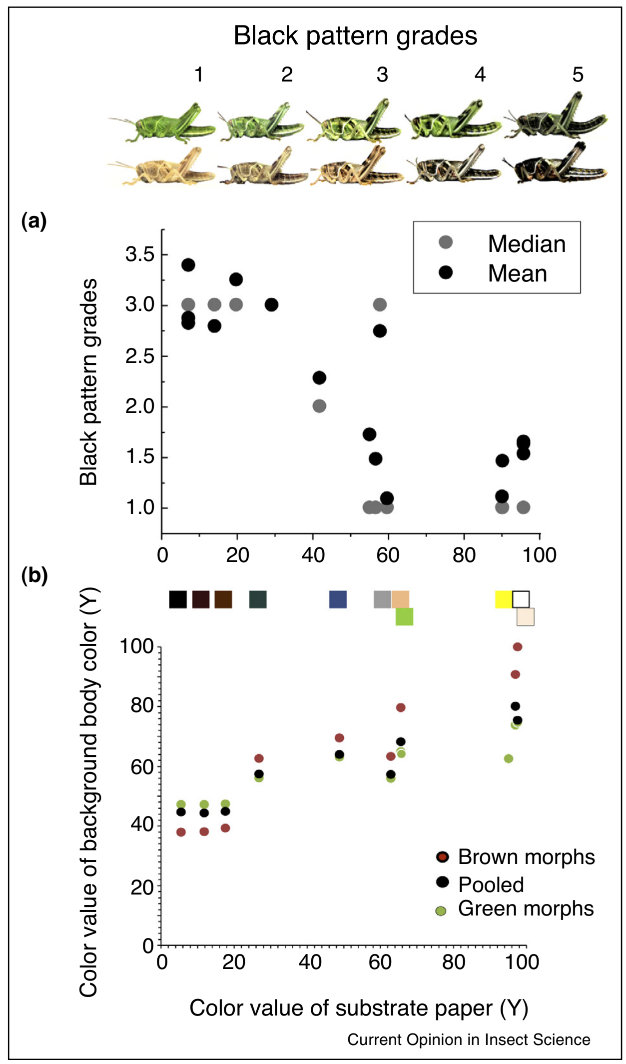
Box 1 To compare different body colors, it is important to use objective methods to quantify them. One such method is the DIC color guide part II (Dainippon Ink and Chemicals Co., Tokyo), which has 1280 different color samples. The samples from the color guide that are most similar to a color paper or locust body color are picked and the *x*, *y* and *Y* values of these samples are measured using a handy colorimeter (NR-3000, Nippon Denshoku Co., Tokyo, Japan). The values of *x* and *y* represent chromaticity, and Y represents a color value. The color value represents the relative brightness of the color as perceived by the human eye. Because all eyes may be different, this is an approximation based on experimental data [Jukette R: RGB Color Space Conversion — XYZ Color Space and Chromaticity. 2010, http://www.ryanjuckett.com/programming/graphics/27-rgb-color-space-conversion?start=2]. Colors with higher color values are perceived to be brighter, and colors with equal color values are perceived to have the same brightness. Chromaticity (PC1), which can be converted from the chromaticity values, *x* and *y* by a principal component analysis, represents an objective specification of the quality of a color, regardless of its luminance.

background colors [21]. The important role of humidity in controlling green/brown polyphenism is also known in other acridid species, such as *S. vaga* [22] and *Gastrimargus africanus* (mistaken identity, now considered to be *G. determinatus*, [23]) [24], and is widely accepted for *S. gregaria* [3,4,19]. However, field observations show that green solitarious nymphs of this locust are common in desert areas where the relative humidity is below 20% [25]. The role of humidity was re-examined by rearing solitarious nymphs individually in white containers under high (75%) and low (35%) humidity conditions [20]. In this experiment, grass was supplied as food only during the dark period (8 h) because it turned darker under low humidity conditions. The results demonstrate that humidity does not affect green/brown polyphenism in *S. gregaria*. The discrepancy between the two studies may have been caused by an indirect influence of humidity on this polyphenism by affecting the color of grass and locust behavior [20]. However, this interpretation is based on an undocumented assumption that green/brown polyphenism in the desert locust is influenced by the background color of the growing environment.

This assumption was tested by rearing 2nd instar nymphs of *S. gregaria* individually in containers with 11 different substrate colors and recording their color morph during the last (6th) nymphal instar [20]. The proportions of green and non-green morphs differ from one substrate color to another. For example, the proportion of green morphs is 40–55% in white, gray, zinc and black substrates, whereas it is 100% in yellow-green and yellow substrates. However, when the proportions of green morphs are plotted against the color value (*Y*, see Box 1) of substrate paper in the containers, no significant correlation is observed between the two variables. The green/brown polyphenism in this locust is influenced by certain colors of the growing environment but is not directly associated with the brightness of the color.

Black patterning: Black patterning is a characteristic of gregarious hoppers in the desert locust [1,16,26]. In the laboratory, black patterns can be easily observed by rearing locusts in a group. However, such patterns often appear even among nymphs reared in isolation [3,21,27] and in solitarious populations in the field [25,26]. Analysis of the relationships between black patterning and substrate color indicates that the hoppers growing in containers with a darker substrate tend to develop more intense black patterns (Figure 1a) [20].

Figure 1



(a) Relationships between grades of black patterns and the color values of substrate colors in *S. gregaria* last stadium nymphs reared in containers with different substrate colors. **(b)** Relationships between the color values of substrate paper and those of the background body colors in *S. gregaria* last stadium nymphs reared in containers with different substrate colors. Hoppers grown on green–yellow and yellow substrates produced green morphs only. Means of all individuals (•), green morphs (●) and brown morphs (●) were plotted separately. Bars indicate SD. Squares with different colors indicate substrate colors.*Source*: modified from [20].