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# Artificial miniaturization causes eggs laid by crowd-reared (gregarious) desert locusts to produce green (solitarious) offspring in the desert locust, *Schistocerca gregaria*

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ABSTRACT

The mechanism underlying the phase-dependent polyphenism in hatchling body coloration was studied by testing for a possible causal relationship with egg size in the desert locust, *Schistocerca gregaria*. Crowd-reared (gregarious) females typically produce large, black offspring, whereas females reared in isolation (solitarious) deposit small, green offspring. We first tested for possible genetic differences in the role of egg foam by washing or separating eggs from two strains of locust. No solitarizing effect was found in either of the strains tested, supporting a previous finding, using another laboratory strain, to show that the hatchling body coloration and size are pre-determined in the ovary of the mother and no egg foam factor is involved in the control of the hatchling body coloration. Topical application of fenoxycarb, a juvenile hormone analog (JHA), and implantation of extra corpora allata (CA), taken from *Locusta migratoria*, caused gregarious female adults of *S. gregaria* to produce small eggs. Some eggs laid by CA-implanted females produced green hatchlings. All large eggs chosen among those deposited by gregarious females produced black hatchlings. When eggs were either kept on dry filter paper at nearly saturated relative humidity during embryogenesis or pricked with a needle so that some egg yolk was squeezed out, some produced small, green hatchlings. These results suggested that the amount of egg yolk or the availability of yolk material may determine the body coloration of hatchlings.

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## 1. Introduction

The desert locust, *Schistocerca gregaria*, shows phase polyphenism in various traits in response to population density (Faure, 1932; Uvarov, 1966; Dale and Tobe, 1990; Pener, 1991; Pener and Yerushalmi, 1998). For example, locusts grown at a low population density (solitarious phase) are characterized by cryptic body coloration and solitary and sedentary habits, whereas those at a high population density (gregarious phase) are characterized by a dark body coloration and gregarious and migratory habits. The variation in these traits is not discrete but continuous, and intermediate forms (transient phase) with intermediate characteristics are observed under certain conditions. Phase-dependent variation is also found in developmental and reproductive traits, some of which are directly related to the population growth of locusts during outbreaks (Maeno and Tanaka, 2008a).

The maternal control of hatchling body size and color is also a density-dependent phenomenon observed in *S. gregaria*. Green and small hatchlings appear from eggs produced by solitarious adult females, whereas black and large hatchlings are obtained from eggs produced by gregarious adult females (Faure, 1932). This phenotypic variation can be observed in the laboratory by rearing locusts either under isolated or crowded conditions (Hunter-Jones, 1958). The Oxford research group (Islam et al., 1994; McCaffery et al., 1998; Simpson et al., 1999; Hägele et al., 2000; Simpson and Miller, 2007) has proposed that hatchling body melanization is caused by the egg-pod foam factor produced by the gregarious (crowd-reared) female adults. According to their studies, black hatchlings are obtained from eggs laid by crowd-reared adults, but green hatchlings appear if these eggs are washed or separated individually shortly after oviposition (McCaffery et al., 1998; Simpson and Miller, 2007). Recently, this research group suggested an alkylated L-dopa analog as a candidate substance (Miller et al., 2008), although the biological effects of this compound on hatchling coloration have not been tested. Another research group (Tanaka and Maeno, 2006, 2008; Maeno and Tanaka, 2008b) has concluded that the degree of melanization as well as the body size of hatchlings is pre-determined in the ovaries of their mothers and that no egg-pod foam factor is involved in this phenomenon.

A close correlation between body size and the degree of melanization of hatchlings has been noticed for a long time in locusts (Hunter-Jones, 1958). Therefore, it seems reasonable to

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assume that hatchling body coloration is pre-determined in the ovary of the mother because in *S. gregaria*, egg size, which is directly related to hatchling body size, is determined in the ovaries (Tanaka and Maeno, 2008; Maeno and Tanaka, 2008b). However, the causal relationship between the two traits has not been verified. In the present study, we explore the mechanism underlying the expression of melanization in the desert locust by modifying egg size artificially to observe its effects on hatchling body size and coloration in *S. gregaria*. We test the hypothesis that hatchling body coloration is dependent upon egg size, and that artificially miniaturized eggs produce green hatchlings even if they have been deposited by crowd-reared female adults. Several different methods can be used to obtain miniature eggs. In one method, crowd-reared female adults are administered with a juvenile hormone analog or implanted with corpora allata, the glands producing juvenile hormone, as this hormone has been reported to cause crowd-reared locusts to produce smaller eggs than those normally produced (Cassier and Papillon, 1968; Islam, 1995). In other methods, eggs that are thought to produce black hatchlings are either exposed to dry conditions or pricked with a needle to remove some egg yolk. Some of the resulting miniaturized eggs survive and produce hatchlings. Here, we present evidence to indicate that a certain egg size or the availability of a certain amount of egg yolk may be required for melanization in the hatchlings.

## 2. Materials and methods

### 2.1. Insects

Three different laboratory strains of *S. gregaria* were used. One strain came from the International Centre for Insect Physiology and Ecology, Kenya (Tanaka and Yagi, 1997); another strain from Prof. H.J. Ferenz's Laboratory, Germany; and the last strain from Dr. S. Anderson's Laboratory, Denmark, the same laboratory line previously described by Hunter-Jones (1957), Yerushalmi et al. (2000) and Schoofs et al. (2000). The former two strains originated from Ethiopia and Niger, respectively, but information was not available for the last one except that it was brought from the Chemical Defence Experimental Establishment, Porton to the Anti-Locust Research Centre in England (Hunter-Jones, 1957). The first two strains, which will be referred to here as Ethiopian and Niger strains, respectively, were normal (pigmented), but the last strain showed albinism controlled by a simple Mendelian recessive gene (Hunter-Jones, 1957), and it will be referred to as an albino strain. Locusts were reared at 30–32 °C and a 16:8 h photoperiod in groups of approximately 100 individuals kept in wood-framed cages (42 cm × 22 cm × 42 cm) according to the method described previously (Maeno and Tanaka, 2004). Locusts were fed leaves of orchard grass and cabbage and wheat bran. A laboratory colony of the migratory locust, *Locusta migratoria*, originally collected on Iheya Island, Okinawa, Japan (Yamagishi and Tanaka, 2009) was maintained at 30 °C. Sexually mature female adults were sacrificed in order to collect corpora allata for transplantation.

### 2.2. Washing and separation of eggs

Before examining the effect of egg size on hatchling characteristics, we tested the role of the egg-pod foam in the control of hatchling body coloration in different strains of desert locusts. Simpson and Miller (2007) suggested that different strains could have different mechanisms controlling the expression of hatchling characteristics. Therefore, the effects of egg washing and separation on hatchling characteristics were tested on the Niger normal strain and the albino strain, as the Ethiopia strain had been tested already (Tanaka and Maeno, 2006, 2008). Hatchlings of the albino strain are entirely green and no darkening occurs even under crowded conditions. Therefore, female adults were maintained with males of the Ethiopian normal strain for hybridization. Hatchlings of the F1 generation obtained in this way were black in color, as the pigmented phenotype is dominant over the albino phenotype (Hunter-Jones, 1957; Maeno and Tanaka, in press). In this experiment, the first egg pods were discarded, because they tend to produce a mixture of green and black hatchlings, as described by Maeno and Tanaka (2008b). Eggs deposited by crowd-reared adults were washed with saline solution or separated individually within 1 h of oviposition according to the method of McCaffery et al. (1998). Eggs were all individually held on moist filter paper in small dishes (diameter, 4 cm; height, 1 cm) according to the method of Tanaka and Maeno (2008). After 2 weeks at an incubation temperature of 32 °C the eggs hatched and were divided into five hatchling color groups (HCGs 1–5) based on the darkness of their coloration (Maeno and Tanaka, 2007). Hatchlings in HCG 1 were green, as typically observed in solitarious forms, and those in HCG 5 were almost completely black, as observed in gregarious forms. Individuals in HCGs 2–4 were intermediate in color.

### 2.3. Administration of a juvenile hormone analog and implantation of corpora allata

Crowd-reared female adults of the Ethiopian strain were topically applied with a juvenile hormone analog (JHA), fenoxycarb, on the dorsal surface of the abdomen on each of the 1st, 4th and 7th days after adult emergence. The JHA was purchased from Sigma (Tokyo, Japan) and was resolved in acetone. Five μl solution containing 25 or 2.5 μg of JHA was applied onto each individual each time with a micropipette. These dosages were chosen because it was known that no hatching occurred after application of fenoxycarb at doses ≥250 μg in this locust (Islam, 1995). Another group of female adults were implanted with corpora allata taken from *L. migratoria* females using the methods of Tanaka (1993). Our unpublished observations indicated that corpora allata taken from *L. migratoria* were highly effective in inducing green body coloration in *S. gregaria* nymphs when implanted into the latter, indicating that the implanted corpora allata had juvenile hormone activity. In the present study, each *S. gregaria* female received two pairs of corpora allata on each of the 1st, 4th and 7th days after adult emergence. All treated females were kept individually with two sexually mature *S. gregaria* males in small cages (22 cm × 12 cm × 28 cm) to ensure that they were continuously exposed to crowding conditions. The first egg pods deposited were collected and incubated at 32 ± 1 °C to determine the body coloration of the hatchlings obtained as above.

### 2.4. Miniaturization of eggs

Eggs deposited by crowd-reared adults of the Ethiopian strain into moist sand in plastic cups (380 ml in volume) were incubated at 32 ± 1 °C. The day of oviposition was designated as day 0. On day 2 eggs were washed with tap water and those longer than 7.0 mm were chosen for experiments. These large eggs are known to produce black hatchlings (Tanaka and Maeno, 2008). The eggs were held on wet filter paper in Petri dishes (9 cm in diameter; 1.5 cm in height) and incubated until used. Two methods were adopted to make these eggs smaller. In one method, healthy looking eggs were sampled every day from day 3 to day 12 from the prepared groups of large eggs and placed on dry filter paper (9 cm in diameter) in a Petri dish. The eggs in Petri dishes were then held in an air-tight plastic container in which relative humidity was kept close to 100% by putting moist tissue paper at a corner of the container. Eggs lose some water under such conditions, because they cannot absorb water from air (Shulov and Pener, 1963). Fifteen healthy

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