

Review

# Maternal effects on phase characteristics in the desert locust, *Schistocerca gregaria*: A review of current understanding

Stephen J. Simpson<sup>a,b,\*</sup>, Gabriel A. Miller<sup>a,b</sup>

<sup>a</sup>*School of Biological Sciences, The University of Sydney, Heydon-Laurence Building A08, NSW 2006, Australia*

<sup>b</sup>*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

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## Abstract

Desert locusts demonstrate pronounced density-dependent polyphenism: a complex suite of traits shifts over the lifetime of an individual in response to crowding or isolation. These changes also accumulate across generations through a maternal effect. Female desert locusts alter the developmental trajectory of their offspring in response to their own experience of crowding. The mother possesses a memory of both the recency and extent of crowding and shifts the phase state of her hatchlings accordingly. Extensive experimental work has shown that offspring behaviour is controlled by a low molecular weight, polar compound (or compounds) released from the mother's accessory glands. The chemical identity of this agent is not yet known.

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## 1. The maternal control of phase state in the desert locust

The desert locust, *Schistocerca gregaria*, demonstrates an extreme form of density-dependent polyphenism known as phase change. Local population density induces the expression of graded changes in a suite of traits that

include colouration, morphometry, anatomy, egg mass, food selection, nutritional physiology, reproductive physiology, metabolism, neurophysiology, endocrine physiology, molecular biology, immune responses, longevity and pheromone production (Pener, 1991; Pener and Yerushalmi, 1998; Simpson et al., 1999, 2005; Tanaka, 2001, 2006; Ferez and Seidelmann, 2003; Kang et al., 2004; Hassanali et al., 2005; De Loof et al., 2006; Simpson and Sword, 2007). The extreme forms are termed *solitaria* (the solitary phase) and *gregaria* (the gregarious phase). Uvarov (1966, p. 332) argued that the term 'solitary' is

\*Corresponding author. School of Biological Sciences, The University of Sydney, Heydon-Laurence Building A08, NSW 2006, Australia. Tel.: +61 293515633; fax: +61 293514119.

E-mail address: [stephen.simpson@bio.usyd.edu.au](mailto:stephen.simpson@bio.usyd.edu.au) (S.J. Simpson).

should be used instead of the ambiguous ‘solitary’; we apply this convention here.

Behaviour is the phase trait which responds most rapidly to a change in population density, and provides positive feedback which couples other less labile traits and drives the process of phase change at a population level (Simpson et al., 1999; Simpson and Sword, 2007). Gregarious locust behaviour differs from that of solitary counterparts; most notably, gregarious individuals (1) are attracted to rather than repelled by other locusts, (2) exhibit increased locomotor activity, and (3) demonstrate a tendency to form marching bands as nymphs and day-flying swarms as adults (Simpson et al., 1999).

Phase state not only changes within an individual’s lifetime but also transmits epigenetically between generations. Present understanding of transgenerational phase control stems from early studies (Faure, 1932; Gunn and Hunter-Jones, 1952; Hunter-Jones, 1958) in which hatchling colouration was shown to depend on parental rearing density; crowded parents produce darker hatchlings characteristic of the gregarious phase, while solitary locusts produce light green coloured hatchlings (Uvarov, 1966). These observations have since been extended: many offspring features, including morphometry, behaviour, hatchling mass and development time, are related to parental rearing density (Pener and Yerushalmi, 1998; Simpson et al., 1999; Rahman et al., 2002).

At least 45 independent experiments and associated controls have investigated which aspects of parental and egg treatments affect hatchling behaviour and colouration. These experiments are summarised in Table 1, which deals with treatments applied to solitary-reared mothers and their eggs, and Table 2, which concerns crowd-reared mothers and their progeny. We will first précis the phenomenon of transgenerational accumulation of phase state by reference to the experiments as numbered in Tables 1 and 2. We next consider evidence for the nature of agent responsible for the phenomenon.

## 2. Transmitting gregarious characteristics across generations

The extent to which solitary-reared mothers produce hatchlings that behave gregariously depends upon the recency of crowding relative to oviposition (e.g., Table 1, exp. 9, Bouaïchi et al., 1995). The female need not experience crowding directly: mating with a crowd-reared male results in a majority of behaviourally gregarized hatchlings (exp. 8, Islam et al., 1994a). Such effects translate into the field situation, as shown by the observation that hatchling behavioural gregarization could be induced by food plants distributed in a clumped rather than a dispersed manner when solitary-reared adults were kept in field enclosures (exp. 16, Despland and Simpson, 2000). Clumped resource distribution at small spatial scales encourages congregation and subsequent gregarization of

solitary locusts (Collett et al., 1998; Despland et al., 2000).

Behavioural phase state correlates with colouration; treatments that induce behavioural gregarization tend to produce darker-coloured hatchlings. However, the correlation is relatively weak, with colouration only explaining 10% of the variance in behaviour (Islam et al. 1994a). The experiments summarised in Table 1 illustrate an overwhelming trend: behaviour precedes colouration as an indicator of gregarious phase transformation. In only one case of the 23 experiments surveyed in Table 1 did colour change appear to precede behavioural gregarization—the case (exp. 7) in which solitary-reared adults laid in tubes containing greater than three recently laid gregarious egg pods (McCaffery et al., 1998).

## 3. Transmitting solitary characteristics across generations

The effect of parental population density on hatchling phase state occurs in both gregarizing and solitarizing contexts. Whereas crowding solitary-reared parents leads to development of gregarious features in hatchlings, isolating crowd-reared adults results in only partial solitarization of hatchlings. However, the effect on hatchling phase state of a short period of isolation in gregarious females does not last as long as does a period of crowding in solitary-reared females (Table 1, exp. 9, Bouaïchi et al., 1995). Hence, solitarization of hatchlings was partially induced when crowd-reared females were isolated at the time of oviposition (Table 2, exp. 38), but not if females or their mates were separated from the crowd at the time of mating and then returned to the crowd (exp. 26, Islam et al., 1994b).

Rather than behaviour being more labile than colouration, as is the case for acquisition of gregarious characters, gregarious behaviour and colouration are ‘lost’ (i.e., behavioural and pigmentary solitarization occurs) at roughly equal rates. In only three cases of the 11 for which both behaviour and colouration were measured did partial colour change precede behavioural change (exps. 34 and 35) or vice versa (exp. 45). In exp. 45 (Hägele et al., 2000), there was a clear disconnection between colour and behaviour, further indicating that, although these traits are correlated, they do not necessarily share the same underlying mechanisms. In that experiment, the accessory glands were ligatured in gregarious females; hatchlings emerged behaviourally solitarized but black rather than green in colour.

## 4. The nature of the maternally produced gregarizing agent

A series of experiments indicates that gregarizing activity is found in the foam deposited with the eggs during oviposition (exps. 6, 13, 22 and 32). The active material is present in aqueous extracts of egg foam and degrades rapidly, losing its effect if stored for more than 24 h.

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