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*Volume 36*

*Series Editors* STEPHEN J. SIMPSON  
and JÉRÔME CASAS





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# Advances in Insect Physiology

*Series Editors*

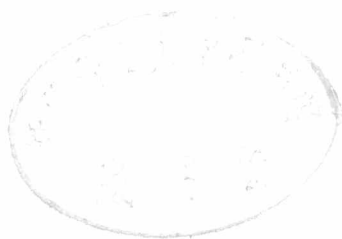
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# Locust Phase Polyphenism: An Update

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## 1 Introduction

### 1.1 SCOPE OF THE PRESENT REVIEW

The present review updates two former reviews by the senior author (Pener, 1991; Pener and Yerushalmi, 1998). It is devoted mostly to recent findings; within the past 9- to 10-year period, well over 200 articles were published in scientific journals on various aspects of locust phase polyphenism, markedly advancing the knowledge of the subject. However, we refer also to the older literature when background information is necessary for complementary and better treatment, or because of historical importance. We already stress here that some of the recent publications report contradictory findings, and such contradictions are especially emphasized in the present review.

## 1.2 LOCUST MENACE

From the practical standpoint, the locust menace is far from being over (as an example for a particular year, see Thomas *et al.*, 2000). After the major plague of the desert locust, *Schistocerca gregaria* (Forskål), in 1986–1989 (Skaf, 1990; Skaf *et al.*, 1990; Showler and Potter, 1991; Showler, 2002), several outbreaks/upsurges occurred (Showler, 1995). A recent outbreak led to an upsurge/plague of the desert locust, in 2003–2004, from the Sahel of western Africa, with swarms reaching northern Africa (Bell, 2005), southern Europe, Cyprus and the Middle East (Lecoq, 2005; FAO, 2006, p. 11 and pp. 46–50; Ceccato *et al.*, 2007). It may be mentioned that the FAO differentiates between the three terms: ‘outbreak’, ‘upsurge’ and ‘plague’, respectively, connoting mild, major and extremely massive concentrations of locusts, their damage and control measures (for more detailed definitions and discussion, see Van Huis *et al.*, 2007). However, not all authors adopt the hierarchical meaning of these terms. Some authors do not use the term upsurge, some others use outbreak and upsurge as synonyms. Some authors employ different kinds of classification to characterize the intensity of locust concentration (Hunter, 2004).

The general biology, with field data, and recession and invasion areas of the desert locust are detailed by Steedman (1990), Duranton and Lecoq (1990) and Latchininsky and Launois-Luong (1997). Lessons from the recent upsurge/plague of the desert locust are discussed by Lecoq (2005). Cheke and Tratalos (2007) analyse the migrations of the desert locust. Steedman (1990) also deals with other African locusts, namely, the African migratory locust, *Locusta migratoria migratorioides* (Reiche and Fairmaire), the red locust, *Nomadacris septemfasciata* (Serville) and the South African brown locust, *Locustana pardalina* (Walker). The outbreaks and population dynamics of the brown locust are reported and analysed in relation to climatic factors by Todd *et al.* (2002). Price and Brown (2000) summarize a century of locust control in southern Africa, emphasizing the history of the brown locust. Lecoq (1995) deals with field conditions leading to gregarization of the Malagasy strain of *Locusta migratoria* (L.), also known as *Locusta migratoria capito* (Saussure), and presents some details on a recent outbreak of this strain. There are different opinions on the subspecies status of different geographic races of *L. migratoria*. Uvarov (1966) recognized eight geographically distinct subspecies, whereas Farrow and Colless (1980) advocated that all subtropical and tropical non-diapausing geographical strains are best regarded as spatially and temporally variable populations of a single subspecies, *L. m. migratorioides*. Instead of naming other subspecies (with egg diapause, or with adult diapause, or with both), these authors characterize the different strains by their geographic areas.

Chen’s (1999) booklet provides a review on morphology, life cycle, habitats, food plants, natural enemies, breeding areas, fecundity and distribution of *L. migratoria* in China, distinguishing three subspecies: *L. migratoria manilensis* (Meyen) that is polyvoltine at favourable temperatures, *L. m. migratoria* (L.) and

*L. migratoria tibetensis* (Chen) (synonymized in Uvarov (1966) as *L. m. burmana* Ramme), which are usually univoltine. Although most of the references are in Chinese, or Chinese with English summary, and they cover the period 1930–1986 (except for some of the author's own papers and three other articles from the late 1980s to the early 1990s), the booklet is a useful summary in English on *L. migratoria* and some other acridids in China.

More recent publications on *L. migratoria* in China are also available. In Central and South China, outbreaks of *L. migratoria*, considered from this geographic area as *L. m. manilensis*, were reported (Ji *et al.*, 2004a; Ma *et al.*, 2005; and references therein). Zhang and Kang (2005), employing random amplified polymorphic DNA technique, analysed the genetic divergence within and among 11 geographical populations of *L. migratoria* in China. They found four regional groups: the populations from Xinjiang and Inner Mongolia (northeastern China) may be considered as *L. m. migratoria*, that from Hainan as *L. m. manilensis*, and two populations from Tibet as *L. m. tibetensis*. The fourth group was found in the Great Plains of northern China and the authors postulated that it resulted from mutual pervasions of *L. m. migratoria* and *L. m. manilensis*, constituting a kind of hybrid zone. Stige *et al.* (2007) analysed a 1000-year-long Chinese record of the annual abundance of *L. m. manilensis* and revealed climatic forcing of decadal dynamics of this locust. They also paid attention to global warming studies relevant to such dynamics. *L. migratoria*, also considered as *L. m. migratoria* (see earlier), causes damage in the northern parts of China (Tanaka and Zhu, 2005), in south Russia and in some southern countries of the former USSR, such as Kazakhstan (Sivanpillai *et al.*, 2006), though its economic importance decreased in the Aral Sea basin as a result of man made ecological interference (Gapparov and Latchininsky, 2000). In the former Soviet countries, Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan, Tajikistan and Georgia, as well as in the southern Siberian plains of Russia and Afghanistan, the univoltine Moroccan locust, *Dociostaurus maroccanus* (Thunberg), and the Italian locust, *Calliptamus italicus* (L.), are serious pests (Abashidze *et al.*, 1998; Evdokimov *et al.*, 1999; Abashidze, 2000; Latchininsky, 2000; Anarbaev, 2001; Gapparov, 2001; Khassenov, 2001; Wilps *et al.*, 2002; Stride *et al.*, 2003; Sergeev and Vanjakova, 2005 and further references in these publications); for a comprehensive review on the Moroccan locust, see the book by Latchininsky and Launois-Luong (1992) and an update by Latchininsky (1998).

Plagues of the Australian plague locust, *Chortoicetes terminifera* (Walker), also occur, though the Australian Plague Locust Commission successfully prevents most plagues in an early stage of an outbreak as reported by Hunter (2004), who uses three grades of outbreaks and two grades of plagues, hierarchically superimposed upon one another, from mild to extremely massive concentrations of *C. terminifera*. Aerial detection of nymphal bands much improves the preventative control measures against this locust (Hunter *et al.*, 2008). Occasional outbreaks of the Australian spur-throated locust, *Austracris*



*guttulosa* (Walker), known for a while in the past as *Nomadacris guttulosa* (Key and Rentz, 1994), were also observed (Hunter and Elder, 1999). Baker (1993) summarizes the biology, plague dynamics and economic impacts of these two species and of other Australian locusts, *Austroicetes cruciata* (Saussure), *Gastrimargus musicus* (Fabricius), the Australian strain of *L. migratoria*, as well as a few acridid species on the verge of the definition of locusts.

There seems to be no recent update on the South American and Central American locusts, *Schistocerca cancellata* (Serville) and *Schistocerca piceifrons* (Walker), respectively. However, an older article by Hunter and Cosenzo (1990 and references therein) may be consulted for the former and Dirección General de Sanidad Vegetal (1998) for the latter. The names of these two species are presented herewith according to Harvey's (1981) reclassification of the *Schistocerca americana* complex. Before Harvey's study, *S. piceifrons* was designated as *Schistocerca paranensis*.

Better understanding of locust phase polyphenism has an applied potential; interference with gregarization, migration, or band or swarm formation by physiological or ecophysiological manipulations may lead to non-conventional control of locusts. This is especially important because present control measures are based mostly on chemical pesticides that conflict with environmental conservation (Peveling, 2001, and references therein), though recently biological control with mycopesticides became promising (Milner and Hunter, 2001; Long and Hunter, 2005). Such mycopesticides act slowly and are best applied to an early outbreak of a locust population (Lomer *et al.*, 2001). The best known mycopesticide against locusts and grasshoppers is *Metarhizium anisopliae* var. *acridum*; its state in integrated pest management is discussed by Hunter (2005). Klass *et al.* (2007a,b) developed a model on effectiveness of the control of several locust species by *M. anisopliae* var. *acridum*.

## 2 Insect polyphenism

The meaning and considerations related to the term 'polyphenism' in insects, equivalent to the former terms 'facultative polymorphism', or 'environmentally regulated polymorphism', were discussed in detail by Pener (1991, pp. 1–2). Briefly, Michener (1961) suggested the term 'polyphenic', instead of 'polymorphic', for connoting environmentally induced major physiological or behavioural differences or both in the same insect species. Lüscher (1976) extended the term to include morphological differences. Hardie and Lees (1985, p. 473) defined polyphenism as "occurrence of two or more distinct phenotypes which can be induced in individuals of the same genotype by extrinsic factors". This definition emphasizes the causative role of the extrinsic factors in the same genotype. Most of the relevant recent literature uses the term 'polyphenism' that gradually replaces the older term 'polymorphism'. From the etymological standpoint, polyphenism is more correct. Moreover, with recent advances in

molecular biology, such as genomics, proteomics and peptidomics, polymorphism has gained a somewhat different and much wider meaning. Therefore, accepting the present trend, we use the term polyphenism.

According to Nijhout (1994, p. 176), "Polyphenisms are formally distinguished from polymorphisms by the fact that in the latter the alternative phenotypes are due to genetic differences", whereas in polyphenism, "the alternative phenotypes are developmental variants that are genetically identical". However, the strict distinction is somewhat blurred by the fact that some bivoltine species, exhibiting two distinctly different phenotypes in different seasons, are capable of producing intermediate phenotypes by experimentally created intermediate environmental conditions, or by experimental manipulation of the physiological mechanism (Nijhout, 1994, 2003 – see especially p. 13 and Fig. 4 – and references therein). Therefore, different phenotypes of the same species that are presently considered as polymorphic may actually turn out to be polyphenic.

The present review does not deal with sequential polyphenism such as different forms (larva, pupa, imago) of Holometabola and refers to sexual diphenism (male versus female) only when it is relevant to locust phases. Also, sexual diphenism may be better considered as sexual dimorphism, because generally male and female insects of the same species are not identical genetically.

Insect polyphenism received considerable attention in recent years. Applebaum and Heifetz (1999) reviewed density-dependent physiological phase polyphenism in insects. Nijhout (1999, 2003), as well as Evans and Wheeler (2001), contributed theoretical considerations, with examples, to insect polyphenism. Hartfelder (2000) reviewed polyphenism in social insects, Miura (2004) added to this subject and Roisin (2000) published a review on caste polyphenism in termites. Zera and Denno (1997), then Zera (2004), devoted reviews to dispersal and wing polyphenism in insects. Emlen and Nijhout (2000) dealt with continuous and discontinuous polyphenism of exaggerated morphologies in insects. Dingle (2002) treated endocrine aspects of insect polyphenism in a chapter on hormonal mediation of insect life histories. More recently, Hartfelder and Emlen (2005) reviewed the whole subject of insect polyphenism, and their section on aphid polyphenism seems to be the sole recent summary for this group of insects. Zera (2007) devoted an article to the methods employed for investigating endocrine (mostly juvenile hormone [JH]) regulation of insect polyphenism, outlining the limitations of simple 'hormone manipulations' that usually means application of a hormone or a hormone analogue.

Although locust phase polyphenism is among the most striking examples of phenotypic plasticity in the Animal Kingdom, it has not featured prominently in the burgeoning literature in this area, perhaps because of perceived applied theme of much of the older work (Simpson and Sword, 2009). For example, there are no references to locusts in four major texts on phenotypic plasticity

(Schlichting and Pigliucci, 1998; Pigliucci, 2001; DeWitt and Scheiner, 2004; Pigliucci and Preston, 2004). An exception is the book by West-Eberhard (2003), where locusts are covered briefly but are, at least, considered to be “among the most striking coordinated alternative phenotypes known” (West-Eberhard, 2003, p. 132).

### 3 Density-dependent phase polyphenism

#### 3.1 LOCUSTS

The theory of locust phases was formed by Uvarov (1921) in a taxonomic revision of the genus *Locusta*. He found that *L. migratoria* and *Locusta danica* are respectively the swarming and the solitary forms or ‘phases’ of the same species. In the same article, he also indicated that the South African brown locust, *L. pardalina*, has similar swarming and solitary phases. The advancement and generalization of the locust phase theory was reviewed by Uvarov (1966 and earlier references therein) and extensively discussed by Pener (1991, pp. 4–7). According to present concepts, locusts show density-dependent phase polyphenism in morphology, anatomy, colouration, development, reproduction, physiology, biochemistry, molecular biology, behaviour, chemical ecology (pheromones) and other aspects of ecology. The two phases are named ‘gregarious’ and ‘solitarious’. The term ‘solitarious’ was introduced by Uvarov (1966, p. 332) instead of the former term ‘solitary’, to avoid the ambiguity of the latter (a gregarious phase insect may be alone, in which case it would be solitary but not yet solitarious), but both terms are used in the recent literature. Extreme phase differences are found only in the field; locusts maintained in the laboratory under conditions of crowding and in isolation only approach the full suite of features of the gregarious and solitarious phases, respectively. The features differing between the gregarious and the solitarious phases are termed ‘phase characteristics’.

Locust phase polyphenism is continuous in two senses: (1) all kind of intermediates can be found between the two extreme phases and (2) induction of a phase change is not stage-specific. The latter means that phase characteristics can be shifted to either direction and the direction of the shift is reversible in any stadium, all in response to changes in the density of the population in the field or in the laboratory (Pener, 1991, pp. 5–6). Even the eggs are subject to phase transformation; experimental treatment within a short while after oviposition induced some gregarious phase characteristics in hatchlings from eggs laid by solitarious females of *S. gregaria* (McCaffery *et al.*, 1998; Simpson *et al.*, 1999) (see Section 16).

The term ‘locust’ was defined by the senior author as short-horned grasshoppers (Orthoptera: Acrididae) that “meet two criteria: (1) they form at some (rather irregular) periods dense groups, comprising huge numbers, bands of

hoppers and/or swarms of winged adults which migrate; and (2) they are polymorphic in the sense that individuals living separately differ in many characteristics from those living in groups'' (Pener, 1983, p. 379, 1991, p. 6). In this definition, 'polymorphic' should be altered to 'polyphenic', but otherwise this definition seems to be valid to date. The first criterion does not need explanation; it is known from biblical times (the plague inflicted on Pharaoh and the people of Egypt, Exodus, Chapter 10, verses 4–19; the prophecy of Joel, Chapters 1 and 2). As for the second criterion, phase characteristics or the amplitude of their change or both differ in different locust species. Some authors define locusts by only one of these two criteria. For example, Pierozzi and Lecoq (1998, p. 25, abstract and p. 27) define locusts as acridid species that exhibit phase polyphenism (see later discussion on *Rhammatocerus schistocercoides*). In contrast, some Australian authors define locusts as swarming acridids (see, e.g., Elder, 1997, p. 63, first sentence of the discussion).

*L. migratoria* and *S. gregaria* exhibit the most extreme, externally very distinct differences between the solitary and gregarious phases, whereas *C. terminifera* shows externally only slightly distinguishable phase differences. According to Uvarov (1977, p. 356), gregarious males of *C. terminifera* are larger than solitary males, but in the females, such difference is scarcely observable. In other locust species (Table 1), phase characteristics are in between these extreme cases. It is important to realize that different locust species belong to several different subfamilies of the family of Acrididae (Table 1, subfamilies according to Uvarov, 1966). Therefore, in this family, phase polyphenism presumably evolved several times, by convergent, or partially convergent, evolution. In fact, many acridid species show some tendency to aggregation and swarming (see also Song, 2005). Such species may be considered as less typical locusts or aggregating/swarming grasshoppers (Table 1, species marked by an asterisk). For example, *Melanoplus differentialis* Uhler was claimed to exhibit some phase polyphenism (Dingle and Haskell, 1967); crowded insects were smaller and darker than isolated ones, though morphometric ratios  $E/F$  and  $F/C$  ( $E$  = length of tegmina,  $F$  = length of hind femora,  $C$  = maximum width of head) did not seem to be different. More recently, Fielding and DeFoliart (2005) reported that high density induced darkening in another species of the same genus, *Melanoplus sanguinipes* (Fabricius). Also, in this species, 'good fliers', supposed to be migrants, showed a higher hyperlipaemic response to adipokinetic hormone I (Locmi AKH I) than 'bad fliers' considered to be non-migrants (Min *et al.*, 2004). Although the effect of density on adipokinetic response was not investigated in *M. sanguinipes*, it is known that this response in crowded *L. m. migratorioides* adults is much higher than in isolated conspecifics (Ayali and Pener, 1992), and young crowded adults of *S. gregaria* show a higher flight-induced hyperlipaemic response than isolated young adults (Schneider and Dorn, 1994). Moreover, the distinction between good fliers and bad fliers is also somewhat similar to locust phase polyphenism. Studying the neural correlates to flight-related phase polyphenism

TABLE 1 Acrididae that show elements of density-dependent polyphenism

Species Name	Common Name	Subfamily
<i>Schistocerca gregaria</i>	Desert locust	Cyrtacanthacridinae
<i>Schistocerca piceifrons</i>	Central American locust	Cyrtacanthacridinae
<i>Schistocerca cancellata</i>	South American locust	Cyrtacanthacridinae
<i>Schistocerca interrita</i>	Peru locust	Cyrtacanthacridinae
<i>Nomadacris septemfasciata</i>	Red locust	Cyrtacanthacridinae
<i>Nomadacris succincta</i> <sup>a,b</sup>	Bombay locust	Cyrtacanthacridinae
<i>Austracris guttulosa</i> <sup>a</sup>	Spur-throated locust	Cyrtacanthacridinae
<i>Anacridium melanorhodon</i>	Sahelian tree locust	Cyrtacanthacridinae
<i>Locusta migratoria</i>	Migratory locust	Oedipodinae
<i>Locustana pardalina</i>	Brown locust	Oedipodinae
<i>Chortoicetes terminifera</i>	Australian plague locust	Oedipodinae
<i>Aiolopus simulatrix</i> <sup>a</sup>	Sudan plague locust	Oedipodinae
<i>Austroicetes cruciata</i> <sup>a</sup>	Small plague grasshopper	Oedipodinae
<i>Oedaleus senegalensis</i>	Senegalese grasshopper	Oedipodinae
<i>Gastrimargus musicus</i> <sup>a</sup>	Yellow-winged locust	Oedipodinae
<i>Calliptamus italicus</i>	Italian locust	Calliptaminae
<i>Dociostaurus maroccanus</i>	Moroccan locust	Gomphocerinae
<i>Gomphocerus sibiricus</i>	Siberian locust	Gomphocerinae
<i>Rhammatocerus schistocercoides</i> <sup>a</sup>	Mato Grosso grasshopper	Gomphocerinae
<i>Ceracris kiangsu</i>	Yellow-spined bamboo locust	Acridinae
<i>Melanoplus spretus</i> (extinct)	Rocky Mountain locust	Catantopinae
<i>Melanoplus differentialis</i> <sup>a</sup>	Differential grasshopper	Catantopinae
<i>Melanoplus sanguinipes</i> <sup>a</sup>	Migratory grasshopper	Catantopinae

Note: Subfamilies are according to Uvarov (1966).

<sup>a</sup>Partial phase change; as also occurs in other species not listed, suggesting that the entire family is predisposed to evolving phase polyphenism.

<sup>b</sup>Also known as *Patanga succincta*.

in *S. gregaria*, Fuchs *et al.* (2003) and Ayali *et al.* (2004) found a lower threshold for wind-induced flight initiation in crowded than in isolated adults.

Another example is the Brazilian Mato Grosso acridid, *Rhammatocerus schistocercoides* (Rehn), that exhibits conspicuous gregarious behaviour, forming hopper bands (Lecoq *et al.*, 1999) and swarms of adults that migrate, though the displacement of the swarms is rather limited, up to 2.5 km per day (Lecoq and Pierozzi, 1996a). The species shows no morphological, morphometrical or colour-related phase differences (Pierozzi and Lecoq, 1998). As a result, these authors concluded that this insect is a grasshopper and not a locust (see earlier for their definition of locusts). However, in a later publication, *R. schistocercoides* was nevertheless connoted as a locust (Lecoq, 2000), presumably just reflecting the difficulty of a sharp distinction between locusts and grasshoppers. No experiments were reported on possible physiological or behavioural phase differences in this species. On the contrary, *A. guttulosa* is considered to be a locust by some Australian authors, despite that it exhibits only swarming of prereproductive adults and no overtly discernible phase polyphenism (see Section 8.5 for some additional details). Heifetz and Applebaum (1995) found some density-dependent physiological and behavioural changes,

resembling locust phase characteristics, in the grasshopper, *Aiolopus thalassinus* (Fabricius), though density did not affect colouration and morphometrics, and no marching or swarming of this species have been recorded. However, another species of the genus, the Sudan plague locust, *Ailopus simulatrix* (Walker), possibly migrates (Steedman, 1990, p. 118). It seems that the whole family of Acrididae has some tendency of aggregation and swarming, as outlined by Uvarov (1977, pp. 142–150) and termed by him as ‘antecedents of gregarious behaviour’ (see also Song, 2005; Song and Wenzel, 2007). In conclusion, it is difficult to make a strict demarcation between locusts and grasshoppers. Density-dependent physiological and behavioural studies are needed to demonstrate that an aggregating and swarming acridid species shows at least some aspects of phase polyphenism.

Mapping information about phase characteristics onto independently derived phylogenetic trees for the acridids offers the opportunity to explore issues regarding the evolution of phase characteristics. Such issues include to what extent have phase characteristics arisen independently within and across acridid lineages; how are different phase characteristics coupled (if at all); and what are the environmental correlates that have accompanied the acquisition or loss of phase characteristics? (Simpson and Sword, 2009).

Several aspects of locust phase polyphenism were reviewed recently. They are as follows: Simpson *et al.* (1999) on phase-related behaviour and factors affecting behavioural phase state in *S. gregaria* (see Sections 11, 14 and 15); Hassanali and Torto (1999), Ferenz and Seidelmann (2003) and Hassanali *et al.* (2005a) on locust pheromones with some contradictory conclusions (see Sections 8.1 and 12); Dorn *et al.* (2000) and Breuer *et al.* (2003) on endocrine aspects of locust phase polyphenism (see Section 9); De Loof *et al.* (2006) on molecular markers of locust phase characteristics (see Section 10). Recently, Tanaka (2005) reviewed the effects of the dark-colour-inducing neurohormone (DCIN, also termed [His<sup>7</sup>]-corazonin; see Sections 7.2.2 and 9.3.4) on certain phase characteristics such as colouration (Section 7.2.2), morphometrics (Section 5.2) and number of antennal sensilla (Section 5.3.1). In another, more detailed, review on the same subject, Tanaka (2006) extended the discussion in a wider context of locust phase polyphenism. Additionally, there are two recent reviews dealing among other topics with the adaptive significance and evolution of phase polyphenism (Simpson *et al.*, 2005; Simpson and Sword, 2009) and two articles on phylogenetic perspectives of the evolution of locust phase polyphenism, based on Cyrtacanthacridinae (Song, 2005), as well as on cladistic analysis of this subfamily (Song and Wenzel, 2007).

The review of Hartfelder and Emlen (2005) devotes a section to locust phase polyphenism, but these authors have been much influenced by Dorn *et al.* (2000) who claimed that JH has a major causative role in locust phase polyphenism. Hartfelder and Emlen (2005) strongly supported the claim of Dorn *et al.* (2000), despite many findings that disagree with this claim (see Section 9.1). In contrast, Dingle (2002), devoting a section to locust phase

polyphenism, accepts that although JH promotes some solitary phase characteristics, such as green colour and higher fecundity, "it is not the primary physiological factor responsible for the solitary syndrome" (Dingle, 2002, p. 260).

When the present review had been completed and when we were checking the list of references, an additional review appeared by Verlinden *et al.* (2009), devoted to endocrinological aspects of reproduction and phase change in locusts.

### 3.2 SOME OTHER INSECTS

Phase polyphenism is not limited to locusts. Pener (1991, p. 8) listed some references on density-dependent polyphenism in other, non-acridid, insects, all from the Orthopteroid complex.

The case of the Mormon cricket, *Anabrus simplex* Haldeman, which belongs to the katydids or bush-cricket (Tettigoniidae) should also be mentioned. This brachypterous species may show phase polyphenism (Gwynne, 2001, pp. 85–87 and Table 4.3); the gregarious insects have dark colour and migrate by marching, whereas the solitary insects are more sedentary and have green or brown colouration (Lorch and Gwynne, 2000; Gwynne, 2001, pp. 64–65 and Plate 9). The coulee cricket, *Peranabrus scabricollis* Thomas, again a flightless tettigoniid, also can form marching bands that migrate (Lorch and Gwynne, 2000). Recently, however, Sword (2005) questioned the true nature of phase polyphenism in the Mormon cricket. He quantified the effects of long-term differences in rearing density versus short-term presence or absence of conspecifics on behaviour. Short-term presence of conspecifics played a greater role in inducing movements of migratory band-forming Mormon crickets than did endogenous behavioural phase changes mediated by high local rearing density. Also, Sword (personal communication) was unable to obtain green solitary colouration by individual separation of field-collected first-instar nymphs that were progeny of gregarious parents. Certainly, further investigations are needed to clarify the effect of density on possible physiological and other differences between 'gregarious' and 'solitary' Mormon crickets. It is interesting to note that a recent analysis indicated substantial genetic divergence between Mormon cricket populations from the eastern and western slopes of the American Rocky Mountains. The former are solitary, whereas the latter are mainly, but not always, gregarious migrants. This finding suggests that the difference in appearance between the two forms may be genetically based rather than environmentally induced (Bailey *et al.*, 2005).

Finally, certain moth larvae exhibit phase polyphenism. The colour of such larvae depends on population density; they are dark under conditions of crowding, but cryptic, green or light coloured, under isolation. This polyphenism is similar in certain features to locust phase polyphenism, though the major component of its endocrine control differs from that of the locusts. Dark

colouration in these lepidopteran larvae is induced by the melanization and reddish colouration hormone (MRCH) and related neurohormones of the pyrokinin (PK) and pheromone biosynthesis activating neuropeptide (PBAN) (see later) family, whereas dark colouration in locusts is induced by the DCIN (DCIN, also termed [His<sup>7</sup>]-corazonin) (see Sections 7.2.2 and 9.3.4). The MRCH in adult female moths has a completely different function; it acts as a PBAN. There is no recent review on the phase polyphenism in larvae (though there are several reviews on PBAN). However, treatment of the subject by Applebaum and Heifetz (1999), Dingle (2002, pp. 262–263), in the introduction to a recent research article (Ben-Aziz *et al.*, 2005) and by another research report (Lee and Wilson, 2006), as well as the references cited in these publications, provides a fairly comprehensive picture.

#### 4 Locust phase characteristics

Phase characteristics of locusts not only depend on the species (see Section 3.1) but also on developmental stadium, sex and even geographic strains within the same species. There are many stadium-dependent differences in phase characteristics. For example, hatchlings of gregarious *L. m. migratorioides* are blackish, whereas conspecific solitary hatchlings are light grey. However, gregarious hoppers in the fifth (last) nymphal instar have a dirty orange background colour and black patterns, whereas solitary hoppers are either green or homochrome. Similarly, gregarious hatchlings of *S. gregaria* are usually blackish, whereas solitary hatchlings are mostly light greenish. In the last nymphal instar, gregarious *S. gregaria* hoppers have a bright yellow background colour and black patterns, whereas solitary hoppers are green or greenish, or at low humidity, beige-brown without marked black patterns (Hunter-Jones, 1962). For a detailed account and relevant references on phase- and stadium-dependent colour polyphenism in *L. migratoria* and *S. gregaria*, as well as in other locusts, the reader may refer the work by Pener's (1991, pp. 12–16) review as well as Section 7 later in the present review.

Stadium-dependent differences in phase characteristics are even more marked between hoppers and adults. For example, the yellow background colour and black patterns characteristic of last-instar gregarious *S. gregaria* nymphs disappear in the adults; the latter are pinkish after the last moult, then become pinkish-beige, beige and eventually yellow. On the contrary, conspecific solitary adults are mostly beige and never become yellow (Pener, 1991, pp. 18–19, and references therein); for a recent interpretation of this phase difference, see Sas *et al.* (2007).

Sex-dependent differences in phase characteristics are also considerable. In adults of *L. migratoria*, *S. gregaria* and *N. septemfasciata*, solitary females are larger than conspecific gregarious females, but in adult males of these



species, the situation is reversed. Therefore, the relative difference in body size between the phases is sex-dependent; the difference in size between the females and the males is smaller in the gregarious than in the solitary phase (for body size of locusts, see also Section 5.1).

Another example of stadium-, sex- and even age-dependent difference in phase characteristics is the production of the pheromone, phenylacetonitrile (PAN) (also termed as benzyl cyanide), by sexually mature gregarious adult males of *S. gregaria* (see Sections 8.1, 12.1.3, 12.4 and 12.5). Nymphs, solitary adults of both sexes, sexually immature gregarious adult males and females and mature gregarious adult females do not produce this substance; moreover, isolation of crowd-reared males soon results in cessation of PAN production (Deng *et al.*, 1996; Seidelmann *et al.*, 2000).

There are even strain-dependent differences in phase characteristics of the same species. The best known example is *Schistocerca gregaria gregaria* (usually connoted only as *Schistocerca gregaria*) that exhibits major phase differences, contrasting to *Schistocerca gregaria flaviventris* (Burmeister), the South African strain (or subspecies) that shows much smaller phase differences in every investigated aspect (Uvarov, 1966, pp. 363–364 and pp. 374–375; Uvarov, 1977, p. 522). Other cases of strain-dependent differences in the phase characteristics of *L. migratoria* were reviewed by Pener and Yerushalmi (1998). In laboratory experiments, Schmidt and Albütz (1996) found differences in morphometrics between two populations of *L. migratoria*, one originating from Greece and the other from Nigeria. The same authors (Schmidt and Albütz, 1999) reported differences in development time between crowded and isolated *S. gregaria* of various geographical origin. More recently, morphometrical differences (see Section 5.2) between crowded (gregarious) and isolated (solitary) adults of the Okinawa (Japan) strain were found to be much smaller than in a West African strain of *L. migratoria* (Yerushalmi *et al.*, 2001). Also, adults of the former showed a higher response to the DCIN of locusts (see Section 7.2.2) than the latter (Grach *et al.*, 2004). Zhang and Kang (2005) found genetic divergence among different geographical populations of *L. migratoria* in China. Recently, Chapuis *et al.* (2008a) found that a historically outbreaking population of *L. migratoria* from Madagascar (presumably *L. m. capito*) exhibited parentally inherited density-dependent phase changes to a greater degree than a historically non-outbreaking population from France (presumably *Locusta migratoria cinerascens*). See also Sections 11.2 and 16.3 for strain-dependent differences in phase characteristics and Section 17.6 for population genetics of various geographic strains of *L. migratoria*.

In the following sections, we review recent data on phase characteristics, and factors affecting them, mostly published after compilation of the reviews by Pener (1991) and Pener and Yerushalmi (1998). Older publications, overlooked or not related to the subjects treated in the preceding reviews, are also included.