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PHEROMONES AND CHEMICAL ECOLOGY OF LOCUSTS

By JOHN A. BYERS
Department of Ecology, Lund University, S-223 62 Lund, Sweden

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I. INTRODUCTION

Of the several species of desert and migratory locusts, two species cause most of the economic losses and have consequently received much attention, the desert locust, *Schistocerca gregaria* (Forskål), and the African migratory locust, *Locusta migratoria* L. (Orthoptera: Acrididae). These two species have served as model experimental animals for a great number of studies. Over 4500 research papers have dealt with locusts since 1970 according to Biological Abstracts (BIOSIS). A personal computer search of the titles and keyword listings from BIOSIS showed that 69% of the papers concerned these two species. Most papers are physiological and involve laboratory experiments, while the fewer behavioural and ecological studies are also mostly in the laboratory, using insects reared in cultures. Relatively few behavioural and ecological studies in nature have been undertaken in the last 20 years. Thus it is often difficult to assess the more numerous laboratory studies in terms of how they relate to properties of natural

populations. Earlier investigations on natural population ecology, however, are reported in the Anti-Locust Bulletin (Johnston & Buxton, 1949; Ellis, 1951; Joyce, 1952; Popov, 1953, 1958; Dirsh, 1953; Guichard, 1955; Davey & Johnston, 1956; Ellis & Ashall, 1957; Stower, Popov & Greathead, 1958; Ashall & Ellis, 1961).

This review will attempt to cover in some detail the evidence for the various pheromones hypothesized for locusts. The physiological, morphological and behavioural aspects of pheromone studies will be integrated with concepts of ecology, with the idea of developing control strategies. Aspects of chemical ecology related to pheromones, such as feeding stimulants and deterrents, will be covered briefly as well as some other topics for the sake of clarity and interest. The earlier work on locust pheromones will be shown to be incomplete and sometimes contradictory. Thus, it is not often possible to compare the knowledge of locust pheromones to recent findings in other groups of insects.

A recent review of pheromones and phase transformation in locusts by Loher (1990) also points out certain problems with earlier work although it stresses aspects different from those treated here. Chemical communication in grasshoppers, including locusts, is also discussed by Whitman (1990). For comparisons with other insect systems, the reader is referred to recent reviews on the pheromone systems of bark beetles (Scolytidae: Coleoptera), moths (Lepidoptera) and social insects (Byers, 1989; Baker, 1989; Ali & Morgan, 1990).

(1) *Host plants and feeding*

Schistocerca gregaria has been termed polyphagous (Evans & Bell, 1979) and its food preferences have been investigated by several authors (Mann & Burns, 1927; Bhatia, 1940; Husain, Mathur & Roonwal, 1946; Alam, 1952; Pradhan, Jotwani & Rai, 1962; Rao & Mehrotra, 1977; Singh & Plant, 1980). Of 198 plant species from a variety of families screened by Husain *et al.* (1946), nine were not eaten at all, 29 were eaten with reluctance while 160 were eaten readily. *Locusta migratoria*, in contrast, has been termed a 'specialist' feeder (Evans & Bell, 1979) or oligophagous (Simpson, Simmonds, & Blaney, 1988), because individuals eat only the grass family (Poaceae, formerly Gramineae), although a variety of species.

In Mali, Ohabuike (1979) found no relationship between the abundance of grass species found in faecal pellets of *Locusta migratoria* and the abundance of these grasses found living in the field, indicating that certain grass species were preferentially eaten. Preference for certain species also changed during the season depending on water content. Thus during the dry periods perennial grasses of higher water content were chosen over drier annual grasses that formerly were preferred in the rainy or flood-retreating seasons. However, practically all species were eaten to some extent, even those suspected of containing feeding deterrents. These latter species retarded locust growth but were preferred during the dry season due to their higher water content.

(2) *Life history and pheromones*

In the core outbreak area in Mali where the flood plains of the Niger and Bani rivers converge, *Locusta migratoria* usually has four generations per year (Ohabuike, 1979). Depending on periodic rainfall and grass growth, the population of *L. migratoria* may increase in density resulting in behavioural, physiological and morphological changes

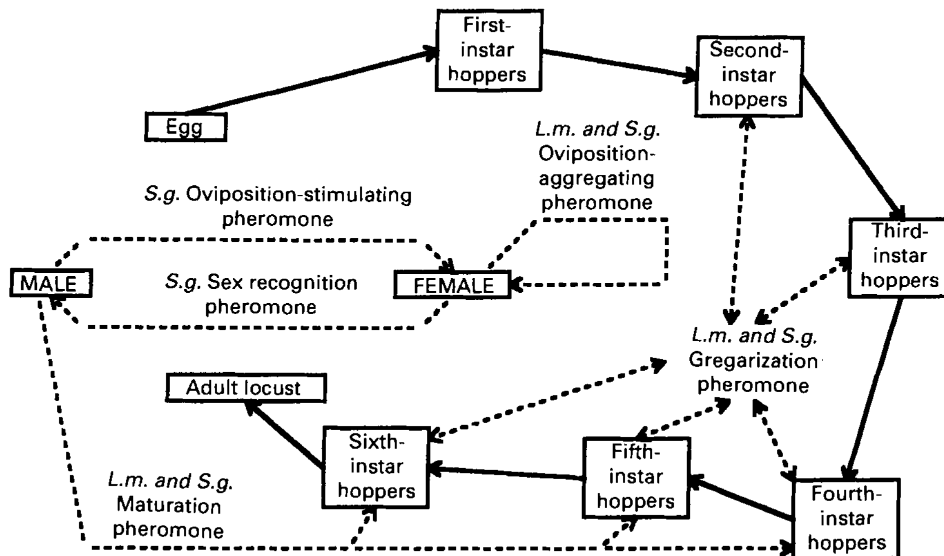

Fig. 1. Experimental evidence of pheromone effects on various stages of locust (*Locusta migratoria, L.m.*, and *Schistocerca gregaria, S.g.*). Dashed lines and arrows indicate the relationship between the stages producing pheromone and those affected by pheromone. See text for more details.

as the young hoppers develop to adults. Similar development of locust plagues for *Schistocerca gregaria* has been reported (Bennett, 1975; Waloff & Green, 1975). These changes, induced by favourable climatic conditions and resurgent food supplies, were first documented by Uvarov (1921) in his theory of periodicity of locust migrations.

Under endemic conditions the 'solitary phase' or form predominates. In *Locusta migratoria*, these young hoppers are green and remain so as adults, but under epidemic high-density conditions individuals show various degrees of the 'gregarious phase', where the hoppers darken and as adults are highly pigmented with melanin (Nolte, 1977). Other morphological features (morphometric ratios) change, such as the ratios of the hind femur length to the head capsule width or pronotal length to width. The same general phenomenon occurs in *Schistocerca gregaria*, but the colour and morphological changes are different (Dirsh, 1953; Nolte, 1976; Gillett, 1975*b*). Not only does the colour darken, but also gregarious behaviour develops and large increases in flight capacity are evident (Nolte, 1977; Michel, 1980). The transformation of phases can be in either direction during development, depending on the local population density, but is usually toward the gregarious form in preparation for migration. A pheromone called the 'gregarization pheromone' (Fig. 1) and possibly other pheromones are involved in phase transformation and social cohesion (Nolte, May & Thomas, 1970; Nolte, Eggers & May, 1973; Gillett, 1975*a*; Fuzeau-Braesch *et al.*, 1988).

The life cycle of both species begins with the hatching of eggs, laid in groups of about 50 per egg pod in the sand (Harjai & Sikka, 1970). The hoppers undergo six or seven instars (seven if they remain solitary, Gillett, 1975*b*) before becoming adult. In *Locusta migratoria*, adults attain sexual maturity within a week or so, while *Schistocerca gregaria* requires from two weeks to one month depending on the presence of other locusts

(Norris, 1964). An adult maturation pheromone (Fig. 1), produced by males of *S. gregaria*, has been shown to promote the sexual development of both sexes and synchronize the maturation of the group (Norris, 1954; Loher, 1960). An anti-maturation pheromone produced by young nymphs may retard the maturation of adults (Norris, 1954, 1962). After maturing, females of *S. gregaria* that have mated develop mature eggs, due in part to a male pheromone transferred during copulation (Fig. 1, Lange & Loughton, 1985), and begin seeking suitable places in the sand to oviposit. In *L. migratoria* a 'long-range' (many decimetres) pheromone seems to attract females to an area previously used by other females for oviposition (Fig. 1, Lauga & Hatte, 1977, 1978). Another pheromone attracts female *S. gregaria* over a few centimetres to areas with locusts where oviposition is then stimulated (Fig. 1, Norris, 1963, 1970). Each of the above pheromones (depicted in Fig. 1) will be discussed in the remainder of the paper in terms of (1) the evidence for the pheromone, (2) isolation and source of pheromone, (3) identification of chemical structure, (4) sensory perception, and (5) ecological and evolutionary aspects. Before beginning a discussion of the various pheromones, it is appropriate to explain the chemical and behavioural methods for isolation and identification of pheromones. A firm understanding of the requisite pheromone components of a particular species is crucial before one can proceed with other basic studies or with development of control methods using pheromones.

(3) *Principles of isolation of pheromone components*

As mentioned above, most locust research, including that with pheromones, has been undertaken in the laboratory with artificially reared insects. This situation is ill advised is basic studies of behaviour and ecology, with regard to modern principles, have not been well investigated in the field. The first step in the study of a pheromone is the observation of the natural phenomenon. Once this knowledge is obtained it is possible to develop relevant bioassays in the laboratory as part of the methodology required for pheromone isolation. Some insight into the source of the pheromone, how and when it is transferred or released to other individuals, and the conditions necessary for response must be obtained in order to construct a bioassay. This is often difficult since several factors may vary simultaneously. Therefore, without a reliable bioassay that is relevant to the natural behaviour there is no point in continuing with the isolation work.

Once a suitable bioassay is developed, and it can be shown that extracts of the emitting insect have specific effects on receiving insects, then chromatographic separation of the chemical blend can proceed. At every stage of further separation of the pheromone extract into various chemicals, bioassays are used to locate the activity among the fractions. Unfortunately, no studies of the various locust pheromones have advanced beyond the initial separation stage and bioassay of individual fractions or compounds (Nolte *et al.*, 1973; Nolte, 1976), or they have assayed compounds based on their dominance in an extract (Fuzeau-Braesch *et al.*, 1988). Synergism, where several compounds often widely separated during chromatography must be presented together to elicit maximal response, is usually the case in most insects (Silverstein, 1981; Byers *et al.*, 1990). Tests for synergism among compounds have rarely been done with locust pheromones, and then only with a mixture of all compounds identified in the extract (Fuzeau-Braesch *et al.*, 1988).

During the isolation, extracts as well as purified compounds must be released at

known rates in the behavioural bioassay (or in electrophysiological recordings of the antenna or sensillum). Otherwise it is possible that biologically insignificant compounds would seem active because of their release at unusually high concentrations compared to biologically significant compounds released at relatively low rates. Rigorous quantification of these semiochemical rates is lacking in locust studies and is a shortcoming of pheromone studies in general (Byers, 1988). Ultimately, the compounds indicated from the laboratory investigations must be tested in the field at release rates comparable to those expected from insects in nature. A recent technique called 'diffusion-dilution', where release rate is predicted from the mole percentage dilution of the component in solvent and the dimensions of the releasing tube, should make it easier to obtain precise release rates of volatile pheromone components and semiochemicals in both the laboratory and field (Byers, 1988).

II. GREGARIZATION PHEROMONE

There is little doubt that a gregarization pheromone exists in *Schistocerca gregaria* (and another in *Locusta migratoria*) that mediates phase transformation toward the gregarious form and elicits aggregation behaviour. However, it is not clear whether one compound (locustol) or several participate in one or more of the various changes, which include colour, morphometric ratios (elytron/femur lengths, femur length/head width), chiasma formation rate during meiosis, development time and moulting synchronization, and cohesive behaviour. Solutions to these questions have been hindered by (1) the relatively slow changes induced by pheromone (up to several weeks), (2) the possible application of inappropriate bioassays, and (3) the shortage or absence of attempts to confirm effects in the field.

(1) *Physiological effects*

Nolte (1963) observed that after third-instar 'crowded' hoppers were isolated individually in another room they gradually lost their black pigment at each moult and became green or sandy-coloured. Experiments that transplanted nymphs from either isolated or crowded environments indicated the presence of a pheromone in the air surrounding crowded hoppers. The pheromone induced both melanization and to some extent the morphometric ratios characteristic of the gregarious phase. A few years later Nolte (1967, 1968, 1969) reported that spermatocytes of *Schistocerca gregaria* exhibited a higher frequency of chiasmata (crossover points of DNA between non-sister chromatids of a chromosome during the diplotene stage of meiosis I) in laboratory-reared individuals exposed to crowded conditions (pheromone present) as well as adults of the gregarious phase from an outbreak in the field. These crowded locust nymphs remained gregarious in form (dark colour) when compared with isolated individuals that became more solitary in form and lighter in colour with subsequent moulting.

Chiasma frequency increases have been suggested to be the most sensitive and reliable indicator of pheromone-induced phase transformation to the gregarious form (Nolte *et al.*, 1970; Nolte, 1973; Nolte, 1976). However, Dearn (1974*a*, *b*) criticized earlier work on chiasma frequencies because of small sample size, and more importantly he found no significant difference between solitary and gregarious locusts of *Schistocerca gregaria* and *Locusta migratoria* in terms of chiasmata. Nolte (1976) countered with the hypothesis that Dearn's use of white paper during rearing caused homochromy, so that

solitaries were pale creamy to off-white colour instead of the usual green. The experiments showed individuals reared on white paper had chiasma frequencies that increased up to 29 % compared with green controls (Nolte, 1976), and these magnitudes are comparable to gregarious phase frequencies for chiasmata (Nolte, 1967, 1973). He concluded that his method when employed properly was valid for discriminating the solitary from the gregarious phase and for quantification of the effects of the gregarization pheromone. However, Nolte's method and results have not been confirmed by other workers. Also it seems possible that chiasma frequency changes are associated with colour changes and not directly with pheromone dosage, so this method may not be the most reliable and relevant bioassay for the pheromone. This hypothesis is strengthened by results with albino *L. migratoria* in which neither crowding nor 'synthetic pheromone' increased the chiasma frequencies (Nolte, 1976).

Gillett (1968) found evidence for the gregarization pheromone, or other airborne pheromone, in *Schistocerca gregaria* which had a behavioural effect, causing solitary hoppers to show grouping behaviour after exposure to air from crowded hoppers, or to lose such behaviour if reared in 'clean' air. The term 'gregarization pheromone' was then introduced by Nolte *et al.* (1970) to include all of the above effects. However, the 'pheromone' has not yet been shown to have a common chemical structure in both locust species and in fact appears to have different behavioural and physiological effects (Nolte, 1973; Gillett, 1983).

Still another effect of the gregarization pheromone was added by Gillett (1975*b*). She found that isolated hoppers of *Schistocerca gregaria* reared in 'clean' air often undergo an extra instar compared to hoppers isolated but exposed to pheromone in the air from crowded hoppers. The development time to reach the fifth instar was significantly less for crowded, pheromone-exposed hoppers (21 days) than for isolated hoppers exposed to pheromone-laden air (29 days), while it was still more for isolated hoppers in 'clean' air (37 days). However, the data for crowded hoppers is not comparable to the latter two values since the crowded individuals were free to approach the light bulb and thus optimize their temperature regime. This freedom of movement may also have resulted in the 'moulting synchronization' of crowded hoppers compared with isolated hoppers.

The only valid comparison is between the isolated hoppers exposed or not to pheromone. The crowded hoppers had different opportunities to regulate their temperature, while field-collected F_1 solitaria were of a different genetic line and history. The valid comparison did show that pheromone-exposed hoppers were more synchronized (lower variance in length of fifth instar) than control, isolated hoppers (Gillett, 1975*b*).

In *Locusta migratoria* it was also found that pheromone from hoppers, but not adults, shortens the duration of the fifth instar and thus synchronizes moulting (Nolte, 1976). Loher (1960) first reported that the epidermis of mature males of the gregarious form of *Schistocerca gregaria* is thicker and contains vacuolated cells that appear to produce the maturation pheromone. This finding was confirmed by Thomas (1970) and Strong (1970, 1971). The maturation pheromone will be discussed later, but it appears to shorten the maturation period of adults and thus synchronizes development of locusts. Other phase characteristics in *S. gregaria*, such as number of eye stripes and morphometric ratios, were little affected by pheromone treatment, although colour was affected as expected (Gillett, 1975*b*). Nolte *et al.* (1970) also found little effect of

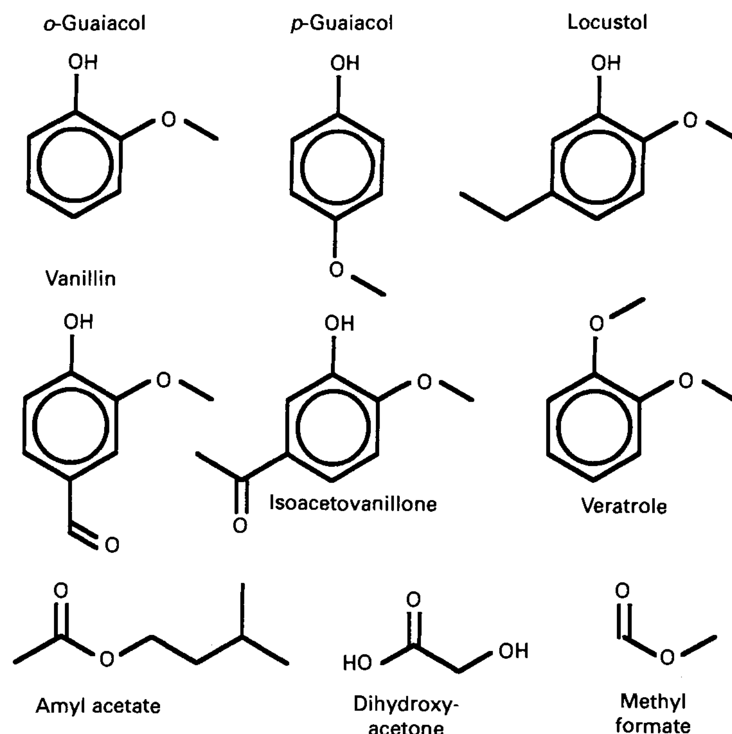

Fig. 2. Potential pheromone candidates affecting melanization, chiasma frequencies and social grouping behaviour in locusts.

pheromone on morphometric ratios in *L. migratoria*, although in other studies they found stronger morphometric effects (Gillett, 1968; Nolte *et al.*, 1973; Nolte, 1976). The problem with these studies is that the concentration or release rate of pheromone is not known, so quantitative comparisons between treatments in various experiments are not possible.

(*a*) Isolation of pheromone

The first attempt to isolate a gregarization pheromone used as solvents either risella oil or dimethyl sulphoxide to extract the air from a locust (*Locusta migratoria*) breeding room (Nolte 1968). Hoppers that had been reared crowded until the third instar were isolated and exposed to extracts, after evaporation of solvent, during the fourth and fifth instars. High chiasma frequencies in young adults compared to controls were found, as well as a retention of the dark coloration (subjectively judged, Nolte *et al.*, 1970). Oil extracts of the head, thorax and abdomen and portions of the alimentary tract were tested similarly on isolated hoppers and revealed that the highest chiasma frequencies were associated with extracts of the crop. Further experiments indicated that the pheromone is excreted with the faeces in both sexes, regardless of whether the hoppers are crowded or not. More pheromone is released by crowded hoppers simply due to the higher numbers and quantity of faeces. In contrast, adult locusts or their faeces did not affect phase transformation (or chiasma frequencies) (Nolte *et al.*, 1970, 1973; Nolte, 1976). Gillett & Phillips (1977) agree that nymphal faeces (fourth and fifth instar) of

Schistocerca gregaria are also active in promoting social aggregation and a dark coloration in hoppers, while adult faeces appear to have no effect.

With the advent of a supposedly reliable bioassay and knowledge of the source of pheromone it was possible to attempt isolation of the chemical components. Nolte *et al.* (1973) steam distilled 1 kg of faeces from crowded *Locusta migratoria* hoppers and then extracted the distillate with pentane. The pentane extract when concentrated *in vacuo* and subjected to silica-gel thin-layer chromatography and gas chromatography (GC) showed two major and several minor constituents. One major component was guaiacol, of which the *o*- and *p*-isomers (Fig. 1) were most active in the chiasma frequency bioassay, although which of these isomers, or the *m*-isomer, were present was not determined. The second major component was identified by gas chromatography–mass spectrometry (GC–MS) and nuclear magnetic resonance spectrometry, synthesis of the indicated possible structures, and comparison by GC–MS of the synthetic with the biological substance. The compound was called 'locustol' (2-methoxy-5-ethylphenol, also called 5-ethylguaiacol, Fig. 2), and it was the most active of any tested substance in the chiasma bioassay. Locustol at an unknown concentration when volatilized in cages with isolated hoppers was able to prolong the retention of dark pigmentation in formerly crowded hoppers by about 80% (as judged subjectively) compared to controls. Morphometric ratios were slightly affected by locustol but not significantly by isomers of guaiacol. An immediate effect of locustol but not guaiacol (*o*-isomer, Fig. 2) on the marching behaviour and aggregation near a source of release was also noted. Nolte *et al.* (1973) state that locustol 'comes closest' to being the gregarization pheromone. They caution that there are 'several other compounds each possessing varying degrees of activity, affecting one or other of the gregarization traits'.

Locusta migratoria nymphs were subjected to hopper faeces from each of four locust species to ascertain the effects on melanin retention and chiasma frequency (when adult). Faeces from the red locust, *Nomadacris septemfasciata*, and Australian locust, *Chortoicetes terminifera*, had no effect while faeces from *Schistocerca gregaria* and the brown locust, *Locustana pardalina*, both reduced the loss of black pigment and increased the chiasma frequency (Nolte, 1973). No effects of crowding the grasshopper, *Paracinema tricolor*, were observed on the colour or the chiasma frequency, indicating no pheromonal effects. Ba-Angood (1976) reared *S. gregaria* individuals alone, crowded in groups of 10 and individually with 9 grasshoppers (mixture of *Oedalens*, *Aiolopus* and *Kraussaria* spp.). There was no gregarizing effect of the grasshoppers on morphometric ratios or eye stripes of *S. gregaria* compared to the solitaries, while the crowded *S. gregaria* showed phase transformation to gregaria. These results indicate that the gregarization pheromone is general only to certain of the locust species.

Nolte (1976) proceeded to further purify locustol, which he admitted was previously 'synthesized by the old method' and 'this was impure'. He also steam distilled and extracted with diethyl ether 2 kg faeces of hoppers and of adults, as well as a smaller amount of grasshopper faeces (probably *P. tricolor*). The infrared spectra of hopper faeces extract showed a strong aromatic peak, while adult or grasshopper faeces extracts had no such peak, consistent with the aromatic structure of locustol and the bioassay activity of hopper faeces. However, GC was unable to confirm the presence of locustol, although Nolte (1976) unfortunately looked 'two months after the bioassay so that any pheromone present could have sublimed'. This seems unlikely, assuming the ether

extract was intact, since locustol is much less volatile than ether and thus would have tended to concentrate.

In any case, the hopper faeces extracts of *Locusta migratoria* were active in increasing the chiasma frequency, the retention of melanin (subjective), and the F/C (ratio of hind femur to headwidth) in the same species, and synchronized moulting by shortening the fifth instar period (Nolte, 1976). Although locustol was most active in increasing chiasma frequencies there were several other analogues, including guaiacol isomers, vanillin, as well as dihydroxyacetone (Fig. 2) which elicited significant increases in chiasma frequencies. However, air from crowded hoppers was most active in reducing or slowing melanin loss, while hopper faeces extracts were significantly less active. Little effect could be observed from locustol alone, and this was not significantly different from isoacetovanillone, guaiacol, amyl acetate (Fig. 2), or adult faeces extract. The F/C ratios were most affected by air from crowded hoppers and by amyl acetate, and less so but significantly by hopper faeces extracts and by locustol. Methyl formate (Fig. 2) stimulates melanin production in solitaries to the level of that of crowded controls (Nolte *et al.*, 1973; Nolte, 1976). Gillett (1983) tested locustol as well as extracts of faeces of either *L. migratoria* or *Schistocerca gregaria* for their effect on *S. gregaria*. In this case only the *S. gregaria* faeces were active in affecting melanization and grouping behaviour. Thus, while *S. gregaria* faeces may effect *L. migratoria* phase transformation the converse does not seem true (Nolte, 1973; Gillett, 1983).

The apparently pheromonal effects caused by solvent chemicals again indicate the need for more reliable, specific and relevant bioassays for further progress in elucidating the components of the gregarization pheromone. The fact that locustol was given at 0·1 %, and guaiacol among others at 0·5 %, while 0·25 % locustol and 1 % guaiacol are 'lethal', seriously jeopardizes the validity of the results (Nolte, 1976). A re-isolation of the gregarization pheromone is necessary using modern analytical methods and the subtractive-combination bioassay (Byers *et al.*, 1990). The latter method allows isolation of synergistic components with a minimum number of tests (compared to additive methods) and is thus optimally suited to the problem.

(2) *Behavioural effects*

In addition to the 'primer' effects of the gregarization pheromone there are apparently immediate 'releaser' effects on the behaviour. The effect of locustol on marching behaviour has already been mentioned. Gillett and co-workers have studied the immediate and longer-term behavioural effects of the gregarization pheromone (Gillett, 1968, 1975*a*, 1988; Gillett, Packham & Papworth, 1976; Gillett & Phillips, 1977). Gillett (1975*a*) placed 10 second-instar nymphs or 10 immature adults, reared either isolated or crowded, in a 90 cm diameter arena. At intervals of 15 min for adults or 30 min for nymphs, the locusts were disturbed and then allowed to resettle during the next interval, whereupon their grouping positions were noted. It was found that significantly more grouping behaviour (number of groups of three individuals or more) was shown by the crowded nymphs or adults than the respective controls that had been reared isolated (no pheromone). However, in several experiments the rates of grouping behaviour, touching and numbers at arena edges were sometimes inversely correlated with crowded rearing time, which is not easily explained. One mathematical problem with this method may be that strong grouping behaviour would tend to include larger

groups and lower the number of possible groups of three or more. When locust nymphs or adults were observed for two hours they tended to 'learn to group' (i.e. increase grouping behaviour), regardless of their past exposure to pheromone, except for the crowded nymphs, who showed a high level of grouping throughout. It is not known if this is a phenomenon of social learning or an immediate effect of the pheromone.

Gillett *et al.* (1976) tried another bioassay in which individual nymphs or adults of *Schistocerca gregaria* were attracted down an 8 × 64 cm walkway to a light source. A porous floor of about 6 cm length was used to release volatiles from live locusts or moult skins, while aqueous or chloroform/methanol extracts of these were evaporated on filter paper over the porous floor. The ratios of the time to traverse the walkway to the time spent over the odour source (floor or paper) were determined. A control was carried out on the same day as the respective treatment (it is not clear if the same or different locusts were used). The results showed that adults were slowed in their progress to the light (arrested) only by either adult faeces smeared on the filter paper (ratio of 4·53) or extracts of adult cuticle (5·62, which may have contained sex-maturation pheromone). Nymphs were arrested by nymphal faeces on filter paper (4·96) or living immature adults (6·45). In contrast, they were repelled by aqueous or solvent extracts of nymphal faeces, as well as by living nymphs. These conflicting results are difficult to explain. Both adults and nymphs appeared unresponsive to solvent extracts from adults or moult skins. These results are further confounded by the fact that the above time ratios for the controls in the various experiments with nymphs varied from 4·26 to 9·34, thus widely overlapping the differences between a specific treatment ratio and its control. With such wide variation possible between controls (and treatments) it seems the bioassay was inconsistent.

The possibility of an anti-gregarization pheromone or 'solitarizing' pheromone was first proposed by Gillett & Phillips (1977). They based their hypothesis on the finding that isolated nymphs treated with adult faeces were even less 'gregarious' in behaviour and colour than untreated isolated nymphs when compared with crowded controls, although the differences between the isolated, treated and untreated, nymphs were not statistically significant. This evidence, admittedly weak, was examined again by Gillett (1983). She reared first-instar nymphs crowded and then separated them under various treatments until mid second instar, when their social behaviour was appraised. The grouping behaviour of nymphs with adult faeces was much less than nymphs with nymphal faeces and not significantly different from fully isolated nymphs. This indicates that adult faeces are ineffective in gregarizing nymphs but does not provide evidence for a solitarizing pheromone. In another experiment (III), two nymphs were reared per jar with or without adult faeces added, but no effect on grouping behaviour could be observed and the behaviour was not different from crowded controls. Therefore, there is no evidence to support her conclusion that there is 'evidence of a previously proposed (Gillett & Phillips, 1977) stimulus in the faeces of locusts which modifies the phase polymorphism: a solitarizing stimulus produced by crowd-reared adults'.

Gillett (1988) ignores the 'solitarization' pheromone in her recent work entitled 'Solitarization in the desert locust'. In this paper the gregarization pheromone seems to have a greater effect on the loss of gregarious behaviour than on its development. Gregarization and the willingness to form groups take place rapidly within hours while

the loss of grouping behaviour when isolated occurs gradually over about 10 days. Gillett (1983) found no effect of locustol in hexane on filter paper on the grouping behaviour and coloration of second-instar *Schistocerca gregaria*, while an effect was found for exposure to faeces. These results do not support locustol as the gregarization pheromone, although insufficient release or exposure time could account for the inactivity.

(*a*) Isolation of pheromone

Fuzeau-Braesch *et al.* (1988) considered that isolation of the gregarization pheromone from air surrounding crowded locusts (and faeces) would be more appropriate than isolation from faeces, since locusts were actually responding to volatiles. The relative proportions of candidate pheromone components could be quantified without the contamination from inappropriate non-volatile constituents in the faeces. Also, no assumptions as to the source of pheromone, whether faeces of integument, would be needed. Their collection of volatiles was inefficient, however, since they were collected in condensed water vapour in an ice bath. It can be assumed that nonpolar and volatile compounds would be incompletely collected. They did collect phenol, guaiacol and veratrole (Fig. 2) from both *Locusta migratoria* and *Schistocerca gregaria*, so it is likely that locustol also should have been collected. However, they report that locustol could not be identified by GC–MS. They wonder if locustol could exist only in faeces or be hydrolysed from a precursor through extraction by steam with the methods used by Nolte *et al.* (1973).

Fuzeau-Braesch *et al.* (1988) conclude that phenol or guaiacol (isomers not determined) alone or in mixture with veratrole act as a 'cohesion pheromone'. Thus these compounds mimic, at least partly, the behavioural grouping effect of the gregarization pheromone. However, there are several problems with their bioassay as well as conflicts with earlier work. This work has shown consistently that adults are not effective in causing gregarization while only nymphs are bioactive (Nolte *et al.*, 1970, 1973; Nolte, 1976; Gillett & Phillips, 1977; Gillett, 1983). On the other hand, Fuzeau-Braesch *et al.* (1988) report that in *Schistocerca gregaria* 'where all ages provide enough substance for easy calculation' it seems that young immature adults have a lower concentration of volatile products. Since they inspected fifth-instar nymphs as well as copulating (mature) adults and egg-laying adults, these findings contradict the earlier work.

Fuzeau-Braesch *et al.* (1988) used a bioassay that counted the number of locusts clumping in each of four arms of the centre of a cross-shaped arena. Phenol, guaiacol and veratrole (Fig. 2) were released from one arm (no. 4) and air flowed from arms 2, 3 and 4 to 1, where locusts were released. The first problem is the use of Chi squared to show a difference in distribution among arms between treatment and control. Since there is little reason to suppose that a pheromone would cause a different distribution among the arms but only in clumping in the centre (as they hypothesize) it is probably wrong to make such a comparison. For example, phenol caused 42 of 200 to group in the middle compared to 28 for the control ($P < 0.01$). The supposedly significant result is due to a comparison of all four arms and centre, while a comparison of just the centre shows no significant difference ($P = 0.07$). According to Fuzeau-Braesch *et al.* (1988), of their 13 tests (tables 4 and 5) 12 are significant, but if one compares only the centre

areas, 9 of the tests are significantly different. Unless an error in printing the value for guaiacol occurred, the compound appears surprisingly to have induced significantly less grouping than the control in *Locusta migratoria*. Also the controls for *L. migratoria* varied from 16 to 52 in the centre while treatments varied from 34 to 57. Unfortunately, locustol was not tested. Another problem is that these compounds were chosen based on their dominance in the extract. Minor components and one unidentified major component were not tested, so their importance could have been missed. Neither additive- nor subtractive-combination bioassays were attempted that could have rigorously tested for synergists (Byers *et al.*, 1990). In spite of the statistical criticism for individual experiments, it does seem that an immediate pheromone effect on grouping can be shown in their bioassay.

(3) *Source and biosynthesis*

Locustol is postulated to be synthesized from guaiacol, a degradation product of lignin that is ingested in grass or shrubs (Nolte *et al.*, 1973). Nolte (1977) fed crowded *Locusta migratoria* hoppers a trisulpha antibiotic (sulphamethazine, sulphathiazole and sulphapyridine) that presumably reduced the bacterial flora of the gut. These locusts had a significantly lower chiasma frequency than crowded controls, indicating that microorganisms may synthesize locustol. Charnley, Hunt & Dillon (1985) were able to rear *Schistocerca gregaria* axenically from sterilized eggs about as successfully as a stock culture. They found that axenic locusts took twice as long to complete the last instar as groups of controls (in the stock culture room) or groups of locusts that began axenically but were exposed to unfiltered air throughout life. This finding is not supported by other workers (Nolte, 1976; Gillett & Phillips, 1977), who found that the gregarization pheromone from crowded locusts caused a synchronization of moulting time (relatively shorter last instar). Charnley *et al.* (1985) also reported that axenic females were more typical of the solitary form than controls or the unfiltered air controls, supporting the idea that bacteria may synthesize locustol (or other active component). However, a serious criticism of this work is their admission that the crowded control group was reared in the same room as the stock culture and thus 'may have been exposed to a greater concentration of locustol' than the crowded axenic locusts 'which were produced in relative isolation' in another room. Further work is necessary to elucidate the role of the purported bacteria in synthesis of locustol and other possible pheromone components.

(4) *Reception*

Two theories concern the site of sensory or physiological reaction to the gregarization pheromone or to locustol: (1) the inhalation of locustol and induction of higher cAMP levels; (2) antennal reception of locustol and brain mediation. Nolte (1974, 1976) postulated that locustol is inhaled through the spiracles and ultimately may reach high enough concentrations in the haemolymph to evoke behavioural and physiological reactions. The first theory developed when noradrenaline (norepinephrine) was injected into fourth- and fifth-instar larvae of *Locusta migratoria* and raised the chiasma frequency (Nolte, 1968). Other chemicals related to melanin, e.g. dopa, dopamine and protocatechuic acid, also raised the chiasma frequency in albino but not in normal solitaries. As discussed earlier, chiasma frequencies may be directly affected by melanin and colour changes and thus only correlated with the gregarization pheromone.

Solitary nymphs were injected with norepinephrine or locustol once at the beginning of the fourth instar and once at the beginning of the fifth (Nolte, 1977). The mean chiasma frequency was raised from 10·5 (100%) to 12·4 (118%) by locustol injection and similarly by norepinephrine. F/C ratios were also significantly affected. The combination of locustol and norepinephrine had no effect compared to the control and was interpreted as indicating that the compounds were competitive (and mimics), which Nolte said was not surprising as their chemical structures are similar (norepinephrine is a catecholamine while locustol is a substituted catechol). However, why should mimics or competitors, which alone are active, not be active together?

Higher levels of cAMP were found in testes of adults that were crowded (locustol presumed present) than in those of solitary adults (Nolte, 1977). This result, however, could mean either that locustol 'caused' cAMP increases (as Nolte supposes) or that cAMP is the 'result' of phase changes. Nolte then injected hoppers as above with cAMP and found an increase in chiasma frequencies as well as a change in F/C ratio, but little effect was found on duration of the fifth instar. This result was interpreted as evidence that locustol induced cAMP, which then caused the phase transformation to gregaria. However, cAMP could still cause transformation when cAMP levels are artificially increased by injection, but under natural conditions higher cAMP levels may result from phase transformation. It would be interesting to determine the cAMP levels in locusts injected with locustol, exposed to locustol vapours, and untreated.

The involvement of cAMP and locustol in gregarization may be still more complicated when one considers the role of octopamine and stress during crowding of locusts. Stress from mechanical, heat or chemical injury causes the levels of the neurohormone, octopamine, to increase in locusts (Davenport & Evans, 1984). One probable function of octopamine is to boost the rate of glycolysis to prepare for strenuous demands of flight or defence. Injection of octopamine into locusts also induces higher concentrations of cAMP in the haemolymph (Worm, 1980; Evans, 1985). Crowding may cause social conflicts and stress which would raise the octopamine and cAMP levels to somehow promote gregarization. Further work is necessary to elucidate the possible interactions of pheromone, octopamine and cAMP in phase transformation.

The second theory is that the gregarization pheromone (locustol) is perceived by antennal receptors (Mordue, 1977; Gillett, 1983). Removal of antennae from crowded *Schistocerca gregaria* early in the third or fourth instar resulted in fifth-instar nymphs with green colour (mesobiliverdin) typical of solitary forms. The first quantitative study of colour was done by extracting haemolymph and measuring the absorption at 650 nm (Mordue, 1977). When hind tarsi were removed or other physical damage done as a control, no such effect in coloration occurred. Corpora allata from mature adults of *Locusta migratoria* were implanted into fourth-instar *S. gregaria* and caused haemolymph mesobiliverdin levels to increase after 6 days. Mordue proposed that the antennae perceive the gregarization pheromone and inhibit the corpora allata from releasing a hormone (juvenile hormone?) that induces the darker coloration and gregarious phase changes.

The injection of haemolymph from gregarious *Schistocerca gregaria* hoppers into solitary ones caused them to develop gregarious coloration, while injection of Ringer's solution or 'solitary' haemolymph had no effect (Nickerson, 1956). The basic nature of this effect has not yet been explained. Studies of juvenile hormone titres and the role

of phase polymorphism in locusts have been recently reviewed by Dale and Tobe (1990). They conclude that 'no very startling evidence has yet been yielded by the comparative study of the action of endocrine agents in locusts of different phases'.

Gillett (1983) used second-instar nymphs of *S. gregaria* and removed their antennae while they were reared crowded (pheromone) or isolated, with or without nymphal faeces (pheromone). By the third instar, isolated nymphs without antennae reared with nymphal faeces were less gregarious in behaviour and were differently coloured than controls with antennae, which were more gregarious in the presence of pheromone from faeces. When isolated without faeces the removal of antennae had no effect, since no pheromone was present. Crowded nymphs without antennae did however show more grouping, possibly due to social learning, but they were less likely to touch and had different coloration than crowded intact nymphs. These results generally support the view of Mordue (1977) that the antennae perceive the pheromone. However, Nolte's theories arose while working with *Locusta migratoria*, while Gillett and Mordue experimented with *S. gregaria*.

A striking finding is that solitarious fifth-instar and adult *Locusta migratoria* have more olfactory sensilla on the antennae than do comparable gregarious-phase insects (Greenwood & Chapman, 1984). In contrast, the numbers of trichoid and coeleconic sensilla were not significantly different between the two phases. Greenwood & Chapman (1984) speculate that the differences in olfactory sensilla may have evolved because individuals in groups (gregarious phase) require less sensitivity to environmental stimuli due to the socially reinforcing behaviour of others. One can also speculate that solitary individuals require more receptors in order to respond to the gregarization pheromone.

(5) *Ecology*

What is the advantage or purpose, from an individual's point of view, of the gregarization effect from the group? Why is the morphological transformation adaptive? Obviously some physiological changes are advantageous in preparation for migration. The ability to fly longer and more powerfully has been documented in gregarious forms (Michel, 1980; Nolte, 1977). In pheromone communication it is proposed that both parties, sender and receiver, benefit (Burghardt, 1970). The advantage for individuals producing pheromone is that all available locusts are 'recruited' to the migratory condition. The receivers benefit as they should need to join the migration swarm. Both sender and receiver benefit if the fifth-instar length is reduced and moulting is synchronized so that all individuals are able to leave in the swarm.

The elevated chiasma frequencies in gregarious-phase individuals have been attributed by Nolte (1973) to a beneficial increase in genetic recombination. Thus 'the offspring of migrations to new territories' will provide 'genotypes which might be found to be suitable for new adaptive requirements'. In other words a solitary individual is likely to be rather well adapted to the local environment, where it has reproduced for several generations. But when preparing to migrate it is advantageous to prepare sperm (and eggs if a female) that are even more genetically variable than usual, since it is not possible to predict which of the many possible habitats the migrant will settle in. With a larger ability to produce variable gametes it is more likely, in theory, to produce a few progeny best adapted to the unique requirements of the newly

colonized land. One would predict that female oocytes also would show chiasma increases on exposure to the gregarization pheromone. If this genetic recombination hypothesis is correct, then it could be expected that nearly all long-range dispersing insects exhibit increased chiasma frequencies in the generation that founds colonies in new breeding habitats.

Mordue (1977) describes the colour of gregarious *Schistocerca gregaria* as having an 'orange, pink and yellow background superimposed with a well-developed black pattern', while solitary forms at endemic population levels are 'cryptic', with green cuticle and haemolymph and no black pattern (Ellis, 1951). Kennedy (1962) and Lea (1962) have suggested the coloration of the gregarious form is aposematic (bright warning colours indicating a poisonous insect). Gillett (1973) criticizes this hypothesis since the nymphs are palatable to birds, insects, reptiles, spiders, amphibians and many mammals, including humans (Ashall & Ellis, 1961; Roffey & Popov, 1968; Stower & Greathead, 1969; Shurney & Zottola, 1976). Experiments with albino nymphs and normal *S. gregaria* showed no preferential grouping with either colour form, indicating that visual stimuli regarding colour patterns were not important in forming aggregations (Gillett, 1973). This led her to conclude that the colour pattern is not aposematic or Batesian mimicry (not poisonous but colour/form mimicking a poisonous species), since the ratio of mimics to models in locust swarms must greatly exceed 4 to 1. Brower (1960) found mimics derive some protection from birds if the mimics outnumber their models by a ratio of up to 4:1. Gillett further argued that for locusts to derive a benefit any models would need to occur over a wide range of habitats of migrating locusts, and no such model has been proposed.

However, one can suppose that the gregarious coloration is advantageous to locusts as a form of non-specific Batesian mimicry. All can agree that there are many brightly coloured insects that are poisonous, such as wasps and bees in a broad diversity of habitats. A locust swarm is ephemeral in space and time, and habituation by local predators might not occur for some time after a swarm arrived. The very nature of a swarm of 'aggressive' and 'aposematic' insects buzzing loudly could frighten many predators away from the area.

Individual locusts when flying in proximity to others do have a common orientation that can be at almost any angle to the wind, but the swarm usually migrates downwind (Waloff, 1972; Riley, 1975; Riley & Reynolds, 1983; Baker *et al.*, 1984; Rainey, 1989; Farrow, 1990). Individual locusts (probably *Locusta migratoria*) in a swarm at night were seen by radar to be flying with a similar body orientation (Riley, 1975). Observations of locust swarms have stated that the orientation of individuals at the swarm periphery was deflected inward toward the centre of mass (Rainey & Sayer, 1953; Haskell, 1957). The turning back into the swarm was reported by Haskell (1957) to range from 2 to 23 m outside the swarm, and from 20 to 80 m by Waloff (1972). The swarm cohesion is believed to be maintained by visual cues and at closer range also by acoustic stimuli at 4–8 m range (Haskell, 1957). Locust swarms may migrate slowly and even appear stationary for many hours (Rainey, 1989), and individuals may spend up to 90% of their time on the ground (Farrow, 1990). Waloff (1972) has questioned whether a swarm cohesion pheromone might exist.

What is the advantage of swarming as opposed to migrating singly? As mentioned above, a swarm of seemingly aposematic insects might be more threatening than just

one such insect. If it is assumed that locusts derive a benefit from migration in a certain direction as do birds, then one theory is that a single animal is more likely to be inaccurate in orienting in a preferred direction than is a flock or swarm that uses the mean direction (Hamilton, 1967; Wallraff, 1978). However, although locusts probably migrate using a mean direction of many individuals' responses held together by acoustic responses (Michel, 1971; Yinon, Shulov & Tsvilich, 1971) there is no evidence for orientation to compass or sun direction (Baker, Gewecke & Cooter, 1984).

It might also be that individuals derive benefits by flying in a concentrated mass so that territorial predators are locally satiated and the probability of an individual's capture is thus reduced. Another theory is that the swarming individuals 'confuse' a predator and make it less likely that any particular individual is captured (Bertram, 1978). Finally, if a long-range sex pheromone is lacking (as appears the case) then locusts that could remain in groups during and after migration would have advantages in finding mates. Field observations and experiments are necessary to investigate these hypotheses.

III. ADULT MATURATION PHEROMONE

A maturation pheromone was demonstrated for *Schistocerca gregaria* by Norris (1954). Immature males change from pinkish-brown to uniformly yellow as they become sexually mature. Mature yellow males when placed with immature males and females accelerate the latter's maturation process. Loher (1958) then reported that parts of mature males or oil extracts held in front of antennae of immature adults of either sex released a 'vibration reaction', the 'antennae begin to move in a non-directional manner, and this is followed by strong agitation of the two pairs of palpi', then 'the hind femora begin to vibrate rapidly'. The vibration reaction was reported to contain no acoustical component. Few data were reported until the full report by Loher (1960), which found a correlation between the olfactory vibration stimulus and the maturation pheromone.

(1) *Vibration reaction*

The vibration reaction was observed often in immature locusts of either sex when a yellow mature male approached (Loher, 1960). Covering the eyes and ocelli with black varnish did not prevent the vibration reaction when a mature male was placed within 1 cm of the blindfolded locust. Visual stimuli alone from mature males placed in transparent airtight glass tubes were not effective in releasing the vibration reaction. Air passed over mature males and then through a tube to the antennae of immatures caused the vibration reaction, while pure air puffs were ineffective. Mineral oil extracts of mature males placed on cotton-wool and offered to immature locusts elicited the vibration fairly consistently in over 1000 tests while control oil gave no reaction. Only the oil extracts of mature males were effective; young or mature female or young males did not elicit the vibration reaction. However, Amerasinghe (1978*a*) was unable to invoke the vibration response reliably with mature male extract in his strain of *Schistocerca gregaria*. Instead he describes a 'freezing' or avoidance reaction, if a response occurs at all.

(2) *Reception*

The antennae appear to be the receptors for the vibration stimulus, since removal of antennae from 50 males and 20 females prevented the vibration response to active

extracts in all cases (Loher, 1960). On the other hand, removal of palpi from 20 males still allowed the response in every case when offered a yellow male. Even dilution by 5000 of an extract from one mature male gave a vibration reaction in 18 of 31 males, while oil alone gave no such reaction. Loher (1960) found that diethyl ether was efficient in extracting the stimulus from locust males, but that after the solvent evaporated the stimulus remained on cotton-wool for a 'short time', indicating a significant degree of volatility. Mineral oil was found to be a convenient way of retarding the volatility of the active substance for longer-term experiments on sexual maturation. It should be emphasized that the chemical stimulus for the vibration reaction may not necessarily be the same as that promoting yellowing or sexual maturation. Amerasinghe (1978*a*) found ether extracts of mature males induced sexual maturation (willingness to mate), but these were inconsistent compared to living mature males in causing the yellowing process. A pheromone isolation strategy based on the vibration reaction would provide a convenient and consistent bioassay, but this bioassay may not be relevant to sexual maturation. A substance could be isolated that evokes vibration, and nothing more.

Short exposure of sexually immature males to within 1 cm (but not touching) of mature males each day for 20–30 days caused most test males to copulate with females, while control males did not copulate (Loher, 1960). Also the yellow coloration of the treated males was more pronounced than in the controls. A similar test with oil extract of mature males on cotton-wool caused test males to accelerate the yellowing process compared to the control group. Males of *Locusta migratoria* did not appear to cause sexual maturation in *Schistocerca gregaria*. It was not possible to determine if the maturation pheromone is received by the antennae, since their amputation, or other body damage, caused an acceleration of maturation.

(3) *Source and physiological regulation*

Loher (1960) also found differences in the *Schistocerca gregaria* epidermis between mature males and young males or females that were correlated with the presence of the maturation pheromone. Mature males have an epidermis about three times as thick as that of immature males. The many vacuolated epidermal cells of mature males are presumed to hold the maturation pheromone. Gregarious-form females, either young or mature, had an epidermis similar to young males. Mature males of *S. gregaria* in the solitary phase and mature *Locusta migratoria* males have a thicker epidermis, but the cells are not vacuolated. These findings have been confirmed for *S. gregaria* (Thomas, 1970; Strong, 1970, 1971).

The glandular cells (vacuolated cells) are more numerous and more widespread in crowded males than in isolated males (Thomas, 1970). Thus one can postulate that production of the maturation pheromone is stimulated by the gregarization pheromone. Strong (1970) also reported vacuolated cells in gregarious mature males of *Schistocerca gregaria* and states that, contrary to the earlier belief that the vacuolated cells arise from the original epidermis, the vacuolated cells grow as additional cells. Coiled ducts have been found that appear to connect the vacuolated cells with the outer surface, presumably for release of the maturation pheromone (Thomas, 1970; Strong, 1971; Kendall, 1972). Mature males have an aromatic smell (Norris, 1954), but attempts to identify the responsible chemicals, or the pheromone, have been inconclusive. Blight (1969) collected air from locusts and identified an unusual amine, 1-pyrroline,

associated only with mature males. Further tests were proposed by Blight (1969) in order to determine the role of the sex – specific volatile, but have apparently never been published.

Loher (1960) studied the role of the corpora allata in sexual maturation. He first removed gonads and accessory glands, but this had no effect upon maturation. The histological sectioning of the corpora allata, however, revealed that in mature males these glands were active and produced 'abundant secretion'. Removal of corpora allata from immature males that were reared 'crowded' inhibited accessory gland development, as well as the normal change to yellow colour and normal sexual behaviour. These allatectomized males also appeared to lack the maturation pheromone, since they could not evoke the vibration response in other locusts. Most importantly, the epidermis of allatectomized males was indistinguishable from that of young immature males. These changes could be substantially reproduced even with already mature males, which subsequently lost coloration and vacuolated cells and were unable to release the vibration response. This indicates that a continuous supply of hormone is required to preserve sexual maturation.

Loher (1960) implanted corpora allata into previously allatectomized males that had lost coloration and glandular epidermal cells as well as sexual capacity. After implantation, the males became yellow, copulated freely, and produced epidermal secretion from the vacuolated cells. However, the males with implanted corpora allata needed the presence of other males to provide a source of maturation pheromone. It is not clear how important the maturation pheromone is compared to the gregarization pheromone in this case. The effects of removal and implantation of corpora allata were confirmed by several workers (Pener, 1965, 1967*a*, *b*; Odhiambo, 1966). However, Cassier & Delorme-Joule (1976) are in conflict with the studies on one point. They report that corpora allata are more active in hormone secretion in solitary males than in crowded males. They propose that ecdysone promotes gregarious development, while the presence of ecdysone and juvenile hormone induces solitary-type development.

Amerasinghe (1978*b*) assumes that the corpora allata secrete one or more juvenile hormones (J.H.) as 'this is well established'. Injection of J.H. I (3,11-dimethyl-10-epoxy-7-ethyl-*trans*, *trans*-2,6-tridecadienoic acid, methyl ester) and J.H. III (10-epoxy-3,7,11-trimethyl-2,6-*trans*-dodecadienoic acid, methyl ester) into crowded allatectomized males stimulated yellowing, with J.H. I being more effective. As found also for corpora allata, the juvenile hormones are not effective in restoring sexual maturation when insects are kept isolated (Loher, 1960; Amerasinghe, 1978*b*). The male-specific maturation pheromone was produced by J.H. injection in allatectomized males. However, the effect of females or immature males on J.H.-treated allatectomized males was not determined (Amerasinghe, 1978*b*), which might have proved whether the effects were due to the maturation or to the gregarization pheromone. Amerasinghe (1978*b*) refers to his Ph.D. thesis, in which extracts of the maturation pheromone were not effective in accelerating maturation in isolated locusts, indicating that the gregarization pheromone is necessary. Only J.H. III has been found in *Schistocerca gregaria*, and the doses of hormones were far in excess of natural estimates, although such doses may be necessary due to excretion and the requirement for physiological action over a longer period of time (Amerasinghe, 1978*b*).

A maturation pheromone has also been found in male *Locusta migratoria* (Norris, 1964). The time from moulting to first copulation was noted for each male in groups of 10 pairs that had two mature males or not. The immature males in groups without maturation pheromone from mature males took significantly longer to attain sexual maturity (about 21 days compared with 14 days). Little else has been done to elucidate this phenomenon. Since crowding promotes maturation in *Schistocerca gregaria* but retards it in *L. migratoria* (Norris, 1964) it seems that the gregarization pheromone is also involved, a fact ignored previously.

Norris (1962, 1964) also proposes that in both species a pheromone inhibiting male maturation is released by young nymphs while a maturation pheromone is released by mature adults – thus maturation of the group is synchronized. There is some evidence that adult males crowded with young nymphs took longer to mature sexually than those reared isolated (Norris, 1962). The effect may not be due to an anti-maturation pheromone but simply to effects of crowding on feeding behaviour or even due to the gregarization pheromone. The use of extracts of nymphs presented to isolated immature adult males might settle the question of the existence of the anti-maturation pheromone.

(4) *Ecology*

The benefits for mature individuals from releasing a maturation pheromone, if they are gregarious, that promotes groups maturation are the same as discussed for the gregarization pheromone in terms of migrant recruitment. Similarly, the receivers should need to mature rapidly if many gregarious mature adults are present and preparing to migrate. The anti-maturation pheromone would benefit receiving adults, who would need to wait until the many nymphs had completed development. It seems important to investigate the maturation of females (Norris, 1954; Highnam & Lusis, 1962) since they should be affected similarly as immature males in regard to maturation pheromone released by males and anti-maturation pheromone released by nymphs.

Carlisle, Ellis & Betts (1965) provide another explanation for the synchronization of adult maturation in *Schistocerca gregaria*. They report extensive data that locust maturation coincides with the bud burst of certain desert shrubs, a week or more before the heavy rains begin and several weeks before the appearance of the annual vegetation. The shrubs included many species of *Boswellia* and *Commiphora*, which have resinous buds that are the source of the biblical frankincense and myrrh. These essential oils contain monoterpenes, among other compounds. Buds of the shrubs when placed in a cage with locusts caused them to mature more rapidly than controls, as evidenced by coloration changes. The monoterpenes, α-pinene and β-pinene, found in myrrh when applied to locusts were effective in promoting and synchronizing maturation (Carlisle *et al.*, 1965). These authors did not consider the possibility of a maturation pheromone, although their work does not rule one out. It is possible that volatile monoterpenes serve as a signal for the induction of maturation pheromone, which then stimulates maturation.

It should also be pointed out that maturation rate is enhanced when locusts are injured or stressed by forced activity (Norris, 1954; Highnam & Haskell, 1964). These confounding effects may have influenced results of earlier studies on maturation pheromone. As mentioned earlier, octopamine and cAMP levels may be increased due

to stress and forced activity (Davenport & Evans, 1984; Evans 1985), and these compounds may have mimicked or interacted with the effects of the maturation pheromone.

IV. OVIPOSITION-STIMULATING PHEROMONE

Oviposition by female *Schistocerca gregaria* is stimulated by copulation (Norris, 1954). Pickford, Ewen & Gillott (1969), working with the migratory grasshopper, *Melanoplus sanguinipes*, showed that an egg-laying stimulant was produced by the male accessory reproductive glands. In *S. gregaria*, Leahy (1973) implanted male accessory glands in virgin females and found their oviposition rate could be increased. Lange & Loughton (1985) showed that injection of mature male accessory gland extracts of *Locusta migratoria* stimulated an increase in the oviposition rate of virgin females comparable to that of mated females.

The accessory gland is composed of 16 pairs of tubules, of which tubule 1 is called the opalescent gland (Odhiambo, 1969). Only the opalescent gland or the spermatophore (sperm packet) were active in stimulating oviposition, therefore a substance is transferred to the female through the spermatophore during mating (Lange & Loughton, 1985). The pheromone appears to be proteinaceous, with a molecular weight of 13000 as determined by Sephadex gel filtration. The molecule contains large amounts of lysine and may interact with the corpus cardiacum, since injection of only 4% of this body into virgin females stimulated oviposition (Lange & Loughton, 1985). Earlier, Okelo (1971) with *Schistocerca gregaria* showed that oviposition is stimulated by a blood-borne factor, since egg-laying was induced in females injected with haemolymph from ovipositing females.

V. OVIPOSITION-AGGREGATING PHEROMONE

Females of *Schistocerca gregaria* tend to lay their egg-pods in areas where other females are ovipositing even though other areas may have had environmental factors that appeared suitable (Popov, 1958; Stower *et al.*, 1958). Norris (1963) explored this phenomenon in the laboratory. She found that females oviposited more in sandy areas with living decoys (locusts of either sex tethered with fine wire) than in areas without decoys. The ovipositional preference for areas among decoys occurred in both light and dark. Paper decoys were ineffective unless the paper was taken from cultures of locusts. Mature males of *Locusta migratoria* were effective as decoys only when alive, and could not compete with locusts of *S. gregaria*. When used as decoys, freshly killed *S. gregaria* were as effective as living locusts in the dark. Ether extracts of mature adults usually were effective in the oviposition bioassay, but no further progress in isolation has been made. These results indicate a species-specific pheromone present on the body of both males and females of *S. gregaria*. The effect from living decoys in the dark was even able to overcome the female's usual preference for moister sand in which to oviposit. Many insects have been shown to possess oviposition-stimulating or deterring pheromones, but very few chemicals have been identified until recently (Hurter *et al.*, 1987; Ali & Morgan, 1990; Prokopy, 1981).

(1) *Reception and source*

Removal of the antennae of females only diminished slightly the responses to dead decoys in the dark. The lower locomotory activity of antennectomized females was

believed to lessen their chances of coming within effective range of the decoys. However, removal of the antennae greatly diminished response to decoys screened within cages (Norris, 1963, 1970). Norris (1970) supposes that chemotactile receptors on other parts of the body in addition to the antennae and possibly the palpi are able to function sufficiently well to promote oviposition. Chemoreceptors on the dorsal and ventral valves of the ovipositor have been described for *Schistocerca gregaria* by Thomas (1965). Contact chemoreceptors of locusts also occur on the tarsi, mouthparts and antennae (Chapman 1982; Blaney & Simmonds, 1990).

In other experiments Norris (1963) demonstrated that isolated females were not able to respond to the oviposition-aggregating pheromone released by live decoys in the dark. Since the other tests used locusts reared in groups, this implies that the gregarization pheromone must predispose females to respond to the oviposition-aggregating pheromone. In a subsequent report, Norris (1970) tested dead locust decoys that had been reared isolated and found they had less oviposition-aggregating pheromone than dead decoys reared crowded. However, the isolated decoys when compared with *Locusta migratoria* decoys were more stimulatory to ovipositing females. Heads, thoraxes and abdomens were all effective in eliciting oviposition females. Observations of females searching for oviposition sites have been described by Norris (1963); 'the females seemed to enter the decoy group accidentally as a result of random wandering' and any attraction was exerted only at a distance of a few inches at most. There is no mention of females touching the decoys with their antennae. *L. migratoria* females in the dark also appear to respond to decoys of their own species preferentially over *S. gregaria*; however, the response to oviposition-aggregation pheromone seems weaker than those normally found for *S. gregaria* (Norris, 1970).

An interesting comment by Norris (1970) is that 'response to extracts had been deteriorating since the first experiments were carried out, and the possibility has to be considered that there had over the years been unconscious selection against responsiveness in the locust stocks at the Anti-Locust Research Centre'. In fact, the artificial breeding of locusts in groups much smaller than natural populations should lead to genetic drift as well as loss of heterogeneity (once a gene is lost due to chance it cannot be reintroduced as in natural populations by immigration). It is also possible that artificial selection for traits adapted to the conditions in the laboratory resulted in unfortunate changes in genetic frequencies of natural traits of interest by means of genetic linkages. This is a common, and largely unaddressed, problem with insect cultures that may be more significant than realized. In general, laboratory stocks should be replaced (not added to) with field collections after several generations. The number of recommended generations is difficult to estimate, however, since it depends on the strengths of the artificial selection pressures (which are unknown) and on the size of the laboratory population.

In contrast to *Schistocerca gregaria*, *Locusta migratoria* females of both phases were attracted over a distance of 0·5 m to sand into which gregarious females had laid egg-pods (Lauga & Hatte, 1977). The females were reported to ingest sand. An accumulation of an oviposition-aggregation pheromone occurred as the attractiveness of the sand increased with more frequent use for oviposition. The attractiveness lasted for up to 6 months. Lauga & Hatte (1978) found that when solitary females were given attractive sand, the number of egg-pods increased as in gregarious females, as well as the weight

per egg. The active sand caused females to lay eggs that hatched in a more gregarious form than if laid in clean sand. The antennae and palpi may detect the pheromone. it is not known if the aggregating pheromone consists of the same components as the primer pheromone that alters the physiology of ovulation, leading to egg production of the gregarious type.

(2) *Ecology*

Norris (1963) wondered if the oviposition-aggregating pheromone 'may not always be advantageous', since females could be fooled by decoys into laying eggs in sandy areas of suboptimal moisture where eggs would not hatch. However, tethered decoys are not natural, and it must be assumed that the first females will choose appropriate sandy areas. Also, it may not be possible for females to predict the future moisture conditions at the oviposition site that would depend on future precipitation. The phase of *Schistocerca gregaria* hatchlings is not determined by a pheromone but rather by the moisture content of the sand surrounding egg-pods. Sand of 24% moisture produced mostly black hatchlings of the gregarious form, while sand moisture of only 2% produced solitary-from hatchlings (Hunter-Jones, 1962). Norris (1963) expressed the belief that the habit of gregarious oviposition is adaptive because the young hoppers upon hatching are aggregated so that gregariousness is perpetuated. As discussed earlier, remaining in groups may be beneficial in terms of preparation for migration, avoidance of predators and finding mates.

VI. OTHER POSSIBLE PHEROMONES AND SEMIOCHEMICALS

A swarm of gregarious-phase locusts may contain millions of individuals per km^2 (Singh & Singh, 1977). Solitary-form populations of *Schistocerca gregaria* in India have been estimated at various places to range from 25 to 20000 per km^2 (Harjai, 1974). At high densities it should be easy for males to locate females by random wandering, but at densities of a few tens or hundreds per km^2 it seems that the population would become extinct (maybe it does) unless a long-range sex pheromone is used. However, Haskell, Paskin & Moorhouse (1962) found no evidence of an upwind attraction to locust volatiles under the conditions they employed. According to Whitman (1990) there are only two grasshopper species that have been rigorously shown to possess sexual pheromones. *Hieroglyphus nigrorepletus* males use their antennae in attraction to females over several centimetres distance (Siddiqi & Khan, 1981). In *Taeniopoda eques* a contact sex pheromone from females, detected by the male's antennae, causes males to attempt copulation (Whitman, 1982). No chemical structures have yet been identified.

Many other insects use a long-range pheromone (usually attracting at a metre or more) to find mates or mates at food resources (Baker, 1989; Byers, 1989; Ali & Morgan, 1990). It would be interesting to apply a recent mate-finding rate model (Byers, 1991) to locusts to see if they require a long-range pheromone during the solitary phase. The model uses the parameters of insect density (number per area), apparent detection radius (i.e. attraction to pheromone), time of search, and walking/flying speed to determine mate-finding success.

In groups of locusts a long-range sex pheromone seems unnecessary, although a sex-recognition pheromone is evident. Females of *Schistocerca gregaria* are passive, displaying no calling behaviour, and appear to be forcibly copulated with by males

(Norris, 1964; Amerasinghe 1978*b*; Strong & Amerasinghe, 1977). Males, however, seem to recognize females due to some contact sex pheromone. Norris (1962) reported that when mature males are crowded together without females they sometimes mount backs of males and attempt copulation. Interestingly, isolated and thus more solitary-form males were the ones most frequently selected by gregarious-form males. Apparently the crowded males, who naturally would not be exposed to solitary males, were less able to differentiate solitary males from females, while gregarious males were recognized as males. The absence of male maturation pheromone on bodies of females and solitary-form males could be the cue, or a sex pheromone on females, as they were preferred most. In addition to the maturation pheromone, sexual dimorphism has been observed in cuticular proteins of *Locusta migratoria* (Cassier & Papillon, 1983; Cassier *et al.*, 1980), which indicate that chemical differences are available for sexual discrimination during copulatory attempts. Peschke (1987) showed that cuticular hydrocarbons served as cues for sexual recognition in a rove beetle (Staphylinidae). Few studies have identified the contact pheromones that indicate sex and species other than those with moths (Baker, 1989; Byers, 1989; Ali & Morgan 1990; Peschke, 1987).

Haskell *et al.* (1962) showed that *Schistocerca gregaria* hoppers wandered downwind in a wind tunnel in clean air but immediately orientated and then walked upwind in response to the introduction of grass odours. Kennedy & Moorhouse (1969) showed that the attractive response to odours was anemotaxis, since one antenna, or crossed-over antennae, still allowed upwind response. *Locusta migratoria* has been shown to possess single olfactory receptor cells on the antennae which respond to enantiomers of 4-methyl hexanoic acid, more so to the (−)-isomer, at concentrations of only 2 ng/cm^3 (Kafka *et al.*, 1973). It is not known if these enantiomers are biologically relevant, but it does indicate that receptors exist for enantiomeric discrimination of compounds. Locustol, guaiacol and phenol, purported locust pheromone components, contain no asymmetric carbon atoms and thus do not possess enantiomeric forms (Fig. 2).

Norris (1962) reports that attraction to 'grass odour' can occur on a micro-environmental level, the 'locusts sat or crawled in the vicinity of the food plant for long periods without feeding until one would fortuitously encounter a leaf and begin to feed. Almost at once several others would approach the plant and feed...'. Upwind attraction of *Schistocerca gregaria* to grass, cabbage or privet odours in a laboratory arena has also been reported (Haskell *et al.*, 1962). It may be important to test olfactory responses at appropriate times of the day, since Ellis & Ashall (1957) showed there was a diurnal rhythm of feeding. No plants have been reported to repel locusts from a distance of several centimetres or more. However, vapours of carbon tetrachloride or valeric acid induce anemotaxis downwind (Haskell *et al.*, 1962; Kennedy & Moorhouse, 1969).

The antennae of *Locusta migratoria* have olfactory receptors of two types, A and B (Ameismeier, 1987). Type A has from 20 to 30 neurones (Ameismeier, 1987), suggesting that this receptor probably functions in recognition of plant odours. Type B has only three neurones, more typical of receptors responding to pheromone components. Greenwood & Chapman (1984) did not observe significant differences in the distribution and abundance of olfactory receptors on the antennae between males and females. As mentioned earlier, they did find significantly more of type A and type B receptors on the solitary adult than the gregarious adult. The solitary adult, being at low densities, would require more receptors and sensitivity for locating mates (type B

as proposed here) and possibly also food plants (Type A). Locusts have chemoreceptors on the tarsi, mouthparts and antennae, which serve in the detection of suitable food (Thomas, 1966; Chapman, 1982; Greenwood & Chapman, 1984; Ameismeier, 1987; Blaney & Simmonds, 1990).

Many plant species contain feeding deterrents, including terpenes (limonene, geraniol, citral and azadirachtin), non-protein amino acids and alkaloids (Butterworth & Morgan, 1971; Gill & Lewis, 1971; Navon & Bernays, 1978; Evans & Bell, 1979; Ohabuike, 1979; Mwangi, 1982; Singh, 1983; Monache, Bettolo & Bernays, 1984). Adams & Bernays (1978) found that 14 feeding deterrents when presented individually at lower dosages were not deterrent, but when combined they were deterrent. It is interesting to note that the polyphagous *Schistocerca americana* can acquire taste aversions for palatable plants by learning to associate an illness-inducing injection of nicotine hydrogen tartrate (NHT) (Bernays & Lee, 1988; Lee & Bernays, 1990). However, the food aversion learning was non-existent with preferred foods such as broccoli compared with immediate learning with a less acceptable food (spinach). A potential problem for control applications with deterrents is that central nervous habituation to at least some feeding deterrents can occur in *S. gregaria* (Szentesi & Bernays, 1984), as has been shown in other insects (Chapman, 1974).

Feeding stimulants have been isolated from a host plant of *Schistocerca gregaria* but not identified except for sucrose (Rao & Mehrotra, 1977; Rao, 1982). Of a range of nutrient chemicals only hexose and disaccharide sugars were highly stimulatory, while L-proline and L-serine elicited some feeding response (Cook, 1977). Chemoreception studies of locust mouthparts have shown that most sensilla respond to a wide variety of compounds (Haskell & Schoonhoven, 1968; Blaney, 1975, 1980; Winstanley & Blaney, 1978). Recently it has also been shown that *S. americana* have tarsal receptors sensitive to various chemicals (White & Chapman, 1990). NaCl appeared to be detected generally by tarsal receptors, sucrose weakly, while specific neurons received NHT but not NaCl.

VII. CONTROL

Integrated insect pest management involves the use of more than one and usually several methods designed to reduce damage to plants. One primary strategy that has been employed extensively is the use of general factors that affect insect biology such as neurotransmitters, hormones, and unspecific predators and parasites, to formulate a population control method. The other main strategy has been to investigate the pest species system of interest in order to find uniquely specific components that can be manipulated or weakened, resulting in mortality of the pest population. The problem with the first strategy that uses pesticides, hormones, and general insect enemies is that it has the potential to affect many insects and other organisms in the ecosystem with unknown consequences.

While all knowledge is useful to varying degrees when designing integrated pest-management programmes, it should be considered best to concentrate on species-specific or group-specific physiological, behavioural and ecological aspects that can be interfered with in a manipulative way. For example, releasing a natural or molecular-engineered pathogen into the environment is not manipulative if the pathogen become established. The pathogen is potentially available for colonization of other species without regulation by man. On the other hand, if the pathogen kills the pest and then dies out, this would be considered manipulative, since man has control over the use of

the pathogen. Pesticides are then manipulative, but of course have the disadvantage of upsetting the ecosystem because of their non-specific effects on a wide variety of species. The great advantage of the use of pheromones and other semiochemicals is that they are both manipulative and species-specific. In addition they are generally non-toxic and at the concentrations envisaged for use in control programmes would be expected to have virtually no adverse effect on any other organisms in the ecosystem.

The use of feeding deterrents and stimulants would be manipulative, but deterrents may be distasteful or toxic to humans as well as to locusts. Grainge and Ahmed (1988) have compiled a list (with references) of plants which are noxious to locusts as well as many other insects. *Locusta migratoria* has so far been found to be deterred by 56 plant species, at least 60% containing alkaloids, while *Schistocerca gregaria* is deterred by 19 plant species, also mostly containing alkaloids. One major problem with deterrents is that crop plants must be treated uniformly with a generally non-volatile compound of long persistence; this may be impractical. Feeding stimulants in baits containing biological agents or insecticides are also of limited value unless a long-range attractant can be added. Otherwise, locusts would not find the limited number of baits; or a high density of baits would be required, making the strategy impractical.

Speculation on the use of locust pheromones in integrated control programmes has focused on disrupting the gregarization process during favourable climatic conditions and preventing the damaging swarms of migrating locusts. Thus the gregarization pheromone must somehow be countered. The evidence for a solitarizing pheromone produced by adults (Gillett & Phillips, 1977; Gillett, 1983) is weak and thus not promising. An anti-maturation pheromone produced by very young nymphs as suggested by Norris (1962) also may not exist and is of dubious value. Even if these pheromones are proved and eventually isolated, they probably will not be able to overcome the natural gregarizing pheromone produced by dense populations of locusts. However, more research should be done to see whether these pheromones exist and whether they inhibit the responses to the gregarization and maturation pheromones.

More promising, but little considered until now, is the use of gregarizing pheromone and maturation pheromone to cause low-density populations of solitary form individuals to undergo phase transformation and migrate prematurely. It can be argued that migration by single locust individuals is disadvantageous, since predators may be more effective than when migration is in swarms. Pheromones could also be used during unfavourable conditions for migration. Also it can be hypothesized that pheromone application on locusts at low population levels would cause inopportune migration, and dispersion of individuals so wide that mate finding would be nearly impossible.

Similar reasoning makes a case for the oviposition-aggregating pheromone as being very promising for control. Here two methods can be experimented with once components are isolated and identified. The first strategy would be to add either insecticides or parasites to a sandy area treated with pheromone, thus killing either the adults with a fast-acting insecticide or the eggs/nymphs with a persistent one. Unfortunately, insecticides are often repellent to insects, so this may be a drawback, in addition to the other problems with toxic substances. Nematodes able to kill eggs (Khan, 1979) might be placed with the pheromone. The second strategy would be to spread the oviposition-aggregating pheromone over a wide area to disperse the egg laying so that no groups were formed. The advantages of grouping, discussed

previously, would thus be negated. The oviposition-aggregating pheromone, once identified, could also be used in traps for monitoring populations. Isolation and identification of the known locust pheromones, and possibly some new ones as suggested above, is the prerequisite to further experiments using pheromones in direct control and monitoring population levels.

VIII. CONCLUSIONS

Most research on the various pheromones of locusts has been undertaken in the laboratory, while confirmatory and complementary studies in the field have been lacking. There is strong evidence for a gregarization pheromone that volatilizes from faeces of both sexes in dense populations. The pheromone effects the physiological transformation from solitary forms to gregarious forms which have gregarious behaviour, darker colour and different morphological dimensions. However, reported effects of the gregarization pheromone on chiasma frequencies during meiosis have not been confirmed by independent workers. There has not been a rigorous isolation and identification of the pheromone, despite reports that locustol and various analogues are biologically active. Reported evidence of a counteracting pheromone or solitarization pheromone has not been substantiated. The advantage of a gregarization pheromone to the sender and receiver is that a large group is formed for migration, which presumably is protected from predation and may also orient more accurately than migrating individuals would alone. An adult maturation pheromone affecting immatures of both sexes and produced by adult males, and accumulating on the cuticular surface, has been established, although the responsible chemical compounds are not known. Plant compounds, including monoterpenes, from desert shrubs may induce development of the maturation pheromone in natural populations of locusts. The benefits to individuals in a dense population are that they reach maturity in synchrony and are thus ready to migrate en masse. An oviposition-stimulating pheromone produced by male accessory reproductive glands and transferred during copulation is known, but the amino acid sequence of the protein has not been determined. A volatile oviposition-aggregating pheromone produced by both sexes induces females to oviposit in areas of pheromone release. The responsible semiochemicals have not been identified. An oviposition-aggregating pheromone would benefit individuals by keeping the immature hoppers together from the start, so that if densities were high the gregarization pheromone could exert its beneficial phase-transformation effects in preparation for migration. Other possible pheromones of locusts that would be used in long-range sex attraction and in close-range sex recognition should be looked for. A promising control strategy is the use of the gregarization and maturation pheromones to cause a low-density population to migrate prematurely or at an inopportune time. Using similar reasoning, the oviposition-aggregating pheromone could be used to disperse the oviposition sites to the detriment of the grouping of gregarious phase populations. Alternatively, the pheromone could be used to concentrate the locusts where one or more pathogens or insect enemies could cause high mortality.

IX. SUMMARY

Modern studies of chemical ecology and behaviour of the locusts *Schistocerca gregaria* and *Locusta migratoria* in the laboratory need to be more closely coupled with field experiments and observations. The life history relating to oviposition, trans-

formation to gregarious phases, and adult maturation mediated by pheromones is reviewed. The principles of pheromone isolation and identification are discussed. The long-term effects of the gregarization pheromone on the physiology are presented, with discussion of morphological changes, chiasma frequency increases, and synchronization of moulting induced by the pheromone. Isolation of the purported gregarization pheromone, locustol, from faeces is discussed in regard to inconsistent effects. Other more immediate effects of the pheromone on the social (gregarious) behaviour and the isolation of possible pheromone components different from but related to locustol are presented. It is stressed that more rigorous isolation studies should be undertaken to resolve conflicting reports and methodological problems. The possibility of an anti-gregarization pheromone or solitarizing pheromone is discounted. The source and biosynthesis of locustol (or gregarization pheromone) from degradation of lignin by symbiotic bacteria is discussed. Theories of reception of the gregarization pheromone such as inhalation through the spiracles or sensory perception by the antennae are presented. Also an internal mechanism involving cAMP and/or corpora allata may be induced by gregarization pheromone to effect the physiological phase changes. The advantages to an individual of reception of the gregarization pheromone from a group of gregarious and pre-migrating locusts is discussed. Also the possible benefits of gregarious behaviour, phase polymorphism and migration are dealt with.

An adult (sexual) maturation pheromone has long-term effects on reducing the period of maturation, and immediate effects on the behavioural vibration response. The epidermal source of the pheromone and glandular cells responsible for the production of the pheromone are discussed. The reception and internal mechanisms of response via the corpora allata are mentioned. The benefits to individuals of synchronized and rapid adult maturation in a gregarious group are considered.

An oviposition-stimulating pheromone produced by the male accessory reproductive glands appears to be a proteinaceous substance of large molecular weight. On the other hand, an oviposition-aggregating pheromone volatilizes from epidermal areas of either sex and causes higher oviposition rates in the area of release. The behavioural and ecological aspects of this pheromone are discussed. Several other possible pheromones and semiochemicals are discussed, such as a long-range sex pheromone, sex-recognition pheromone, grass odours and feeding stimulants and deterrents. Several possible control strategies using locust pheromones are considered. The general conclusion is that the chemical isolation of the various pheromones is necessary before further progress can be achieved on the source and biosynthesis of pheromone, reception of pheromone, behavioural effects of pheromone, and control measures.

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