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CHEMICAL ECOLOGY OF LOCUSTS AND RELATED ACRIDIDS

Ahmed Hassanali,¹ Peter G.N. Njagi,¹ and Magzoub Omer Bashir²

¹International Center of Insect Physiology and Ecology (ICIPE), Behavioural and Chemical Ecology Department, P.O. Box 30772, GPO-00100, Nairobi, Kenya; email: ahassanali@icipe.org; pnjagi@icipe.org

²ICIPE Field Station, P.O. Box 1213, Port Sudan, Sudan; email: yamagzoub@yahoo.com

ABSTRACT

The results and insights from recent research on the chemical ecology of polymorphic acridids are reviewed. Many of the new findings come from studies on the desert locust, *Schistocerca gregaria*, which has continued to be the primary research insect in most laboratories. Earlier confusion between stimuli associated with phase change and social cohesion has been resolved. The roles of chemotactile and olfactory cues together with tactile and visual stimuli in key locust processes, comprising gregarization, social cohesion, synchronous maturation, mating, oviposition, and maternal transfer of gregarious character, are better understood. Some of the key pheromones of the gregarious phase have been characterized. Chemical communication is also shown to be important in the life style of the solitary phase. The behavioral pattern and responses of this phase reflect a strong propensity of the species to exploit opportunities under appropriate conditions to form or join the crowd and to gregarize. Outstanding questions are highlighted.

INTRODUCTION

Many species of acridids manifest varying levels of crowding behavior, ranging from loose assemblages mediated by acoustic and/or visual cues, through temporary aggregations under certain situations in the life cycles of some grasshoppers, to pronounced gregarious character typical of polymorphic species (4, 107). The last group is represented mainly by locusts, a phylogenetically heterogeneous group of acridids that can transform reversibly in a graded manner between two extreme phases, solitaria and gregaria, that differ in physiology, biochemistry, behavior, morphology, and pigmentation (17, 84). Phase dynamics are based on the degree of acridid crowding and its duration within a given and successive generation. At low densities, insects occur as widely dispersed, solitary individuals that are relatively inactive and cryptically colored, and that avoid one another. Gregarization is associated with an increase in overall numbers resulting from improved rains and vegetation and with forced crowding promoted by specific environmental and biotic conditions, including convergent winds, favorable microclimates and habitat topologies, and patchy distribution of food plants and oviposition sites (9, 10, 16, 20, 22, 51, 88, 93, 107). Phase-related traits such as aggregation behavior (27, 92) and pheromone expression (19) change rapidly with density. Others, such as morphometrics, take several generations (18, 84).

Previous work on the desert locust, *Schistocerca gregaria* (Forskål), and the African migratory locust, *Locust migratoria migratorioides* (Reiche and Fairmaire), had implicated a number of pheromonal and interspecific chemical signals in their phase dynamics. Much of this work, including early attempts to characterize the mediating signals, has been reviewed by Whitman (108), Loher (56), and Byer (11). Results of more recent studies were summarized by Hassanali & Torto (41). A different perspective of the results is provided by Ferenz & Siedelmann (32). In this review, we give an overview of the progress made to date in elucidating the complex chemical ecology of these acridids. Many new findings come from studies on the desert locust, which has continued to be the primary research insect in most studies. We stress insights that shed further light on the mechanisms that underlie the remarkable ability of this insect to gregarize and on the primer and/or mediating roles of semiochemicals in the process. We point out gaps in our knowledge and unresolved questions. Last, the implications of the new findings and insights garnered from this insect for possible lines of research on other acridids are also highlighted.

PRINCIPAL ACRIDID CHEMICAL SIGNALS

Some of the earliest examples of semiochemical-mediated activities reported for any insect include the induction of maturation of sexually immature solitary adult *S. gregaria* by volatile emissions associated with bud burst of certain desert shrubs at the beginning of the wet season (6, 13, 62) and the maturation-accelerating effect of the gregarious-phase males of the same insect on conspecific young adults (55, 59, 72). Since then, chemical communication has been implicated or shown to play an important role in other processes in the life history of both phases of polymorphic and aggregating acridids. A summary of these is presented in Table 1.

Primary phase	Acridid process	Species studied	Signal source(s)	Nature and function(s) of the signal
Solitaria	Maturation	<i>S. gregaria</i>	Food and other desert plants at the onset of seasonal rains	Specific secondary metabolites and volatile kairomones that prime maturation of scattered solitary adults (6, 13, 28).
	Mating	<i>S. gregaria</i> and some grasshoppers	Reproductively active females	Sex pheromone that attracts males of both phases in <i>S. gregaria</i> (30, 45).
	Oviposition	<i>S. gregaria</i>	Specific nymphal food plants	Kairomones(?) promote clustered oviposition close to the plants (7).
Solitaria and gregaria	Gregarization	<i>S. gregaria</i> L. m. <i>migratorioides</i> <i>Locustana pardalina</i>	Adults/nymphs	With tactile and visual cues, the close range/contact chemotactile signal may prime transformation to and sustain the gregarious phase (18, 19, 43, 44, 90, 99).
Gregaria	Aggregation (cohesion)	<i>S. gregaria</i> L. m. <i>migratorioides</i>	Gregarious nymphs, fledglings, older adult males	Volatile pheromones that mediate cohesive behavior of the respective gregarious stages, and recruitment of corresponding solitary stages (67, 79, 80, 104, 105).
	Maturation synchronization	<i>S. gregaria</i> L. m. <i>migratorioides</i>	Gregarious nymphs and adult males	Sequential retardation (nymphal pheromone) and acceleration (adult pheromone) of maturation of early and late fledglers, respectively, resulting in synchronous maturation in the population (5, 59, 72, 78).
	Mating	<i>S. gregaria</i> L. m. <i>migratorioides</i>	Contact signals in females(?); volatile signal in males	Specific cuticular constituents may promote conspecific recognition of females by males; male homosexual encounters inhibited by the aggregation pheromone acting parsimoniously (2, 14, 32, 75, 96).
	Communal oviposition, maternal transfer of gregarious traits	<i>S. gregaria</i> L. m. <i>migratorioides</i> <i>Zonocerus variegatus</i>	Ovipositing gregarizing/gregarious females	Volatile signals that attract both phases of acridids to common egg-laying sites (87, 94, 103); parsimonious function of one of the volatile oviposition signals that primes embryonic development of eggs to the gregarious phase (8, 38, 54, 61, 64).

Table 1 Principal processes in polymorphic acridids mediated by semiochemicals

CHEMICAL COMMUNICATION IN SOLITARIA

The solitarious phase of many polymorphic acridids recedes from the insects' invasion areas into habitats that are associated with periods of dry and hot or cold weather. Under these conditions, young solitarious adults may go through varying states of reproductive diapause (85). Suitably timed and synchronized maturation is an important part of the reproductive strategy in the solitary phase of these insects. Moreover, effective mechanisms for locating mates at low densities and suitable food plants for the progeny in patchy environments are important. Chemical communication may play a critical role in these processes. In addition, in a gregarizing population, solitarious acridids interact with behaviorally gregarious counterparts and members of one phase may encounter the pheromonal signals of the other. Interphase responses in these situations reflect a strong propensity of these insects to exploit opportunities to recruit into or join the crowd, and thus to facilitate the spread of gregarious characters across the population. These are highlighted in appropriate sections of the review.

Maturation

Sexual maturation in the solitarious desert locust coincides with the bud burst of certain desert shrubs just before the onset of rainy seasons one or two weeks before the appearance of the annual vegetation (12, 13, 62). The shrubs include species of *Boswellia* and *Commiphora* with resinous buds that have been sources of the biblical frankincense and myrrh. Several interesting observations implicating plant secondary metabolites in locust maturation have been described. First, studies involving laboratory manipulations of humidity, photoperiod, and temperature failed to demonstrate a clear correlation between these environmental variables and the onset of maturation (75). However, exposure of immature locusts to aromatic emissions of the floral parts and commercial articles derived from *Commiphora* shrubs accelerated their maturation (28). Locusts reared on a diet derived from senescent plants remained sexually immature even if leafing twigs of *Commiphora* species were introduced into the diet (48). However, if senescent diet was supplemented with gibberellin A₃ and eugenol, the insects matured normally (28). One follow-up study has been described (6). The composition and gas chromatography-electroantennography (GC-EAD) profiles of the essential oils of the desert shrub *Commiphora quadricincta* collected before and after winter rains in the Red Sea area of the Sudan were compared. The oil collected before the rains was richer in terpenoids, particularly the more volatile monoterpenes, with almost twice as many electrophysiologically active constituents compared with oil collected after the rains. Of particular significance was the finding that immature adults of both sexes of *S. gregaria* exposed to vapor from oil collected before the rains matured faster (earlier yellowing and copulation activity in males, earlier ovulation and oviposition in females) than those exposed to the oil obtained after the rains.

These findings give credence to the suggestion that widely scattered solitary adults of *S. gregaria* and other acridids may use changing physiology of food and nonfood plants as sources of dependable cues to synchronize their reproductive activities with oncoming rains (6, 13). More comprehensive studies on such plant-insect relationships in acridid primary breeding areas are needed to clarify mechanisms that underlie the induction and termination of reproductive diapause in these insects.

Mate Location and Recognition

In many grasshopper families, complex visual and acoustic signals play key roles in mate location, recognition, and courtship (31, 49, 82). However, even in these acridids, close-range

sex and species recognition may be mediated by pheromonal signals of low volatility (108). In many others, long-range volatile and/or contact nonvolatile signals may be involved, although, with a few exceptions (98), evidence for these is largely anecdotal (108). Reproductively active polymorphic acridids in their solitary phase can occur at low population densities ($<5 \text{ ha}^{-1}$ in *S. gregaria*; 107). Although patchy distribution of preferred host plants may contribute to bringing the insects together, long-range pheromonal communication may be critical in mate location (11, 41). A detailed wind tunnel study of solitary-reared desert locusts demonstrated that mature solitarious males are attracted upwind to hidden solitarious females (45). Suppression of acoustic signals by gluing females' wings did not significantly affect the male responses, indicating that these were due largely to a pheromonal signal. Another study (30) compared the responses of solitary-reared adult males and those that were similarly reared but crowded for varying periods with solitary- and crowd-reared females. Solitary-reared females were more attractive to both types of males than their crowd-reared counterparts. Solitary-reared males that experienced varying periods of crowding were significantly more attracted to solitary-reared females than their uncrowded counterparts. These results demonstrate a possible means of recruiting solitary locusts into a gregarizing population. A combination of visual and olfactory cues was most effective in attracting males. Efforts to identify the pheromone have implicated long-range attractive and short-range arrestant constituents (41). These are yet to be fully characterized.

Oviposition

A rich literature exists on acridid oviposition, including selection of oviposition substrates and sites, habitat location, and egg-laying behavior (100). These insects vary from generalists that accept a range of substrate factors, such as texture or temperature, to specialists that may have specific requirements for substrate moisture or plants (100). Oviposition studies in polymorphic acridids appear to have focused on the gregarious phase, which show communal egg-laying behavior, but, with one recent exception (7), no comparative studies of the phases have been carried out.

The study was based on detailed field surveys during successive solitary desert locust breeding seasons at different sites around Port Sudan in the Red Sea area. Interestingly, 98% of the egg pods were found near *Heliotropium* spp. (66%) and bulrush millet (*Pennisetum americanum*) (32%), with the rest of about 50 plant species accounting for only 2% of the egg pods deposited. Follow-up field cage experiments confirmed that, in the absence of egg pods derived from gregarious locusts, solitary females preferred to oviposit adjacent to these plants (unlike gregarious females, which preferred moist sand without any plants). However, when present, gregaria egg pods were preferred, as was the case for gregarious females. Post-hatching surveys in the field found most solitarious nymphs (86%) feeding on the two plants. These observations provide some useful insights into the mechanism associated with the initial clustering of otherwise non-aggregating solitary hoppers in patchy environments and of the genesis of gregarizing nuclei of hoppers (7, 10, 16, 21). They also point toward the need for detailed studies on insect-plant relationships and on the mediating chemical signals in primary breeding and outbreak areas to help shed light on the critical mechanisms that underlie population and phase dynamics of these insects.

CROWDING AND GREGARIZATION

Forced crowding of solitarious nymphal and adult locusts leads to rapid development of some gregarious characters (27, 93). The effect of crowding and isolation of *S. gregaria* was studied by quantitative behavior techniques (8, 91). Crowding at nymphal or adult stages led to rapid

(within 1 to 4 h) acquisition of gregarious behavior; isolation of crowd-reared insects led to loss of this behavior. In other studies, the effects of shifting *S. gregaria* adult members of a solitary-reared colony to crowd-rearing conditions and vice-versa were monitored by GC analyses of the pheromone emission from the males (19, 97). Crowding of solitaria resulted in the production of the pheromone within days. Interestingly, even pairing of two solitarious insects led to detectable production of the pheromone (19), indicating that even confining two insects together can provide the essential stimuli for inducing the onset of phase change. Conversely, adult males resulting from shifting gregarious insects to solitary conditions rapidly lost their ability to produce the pheromone component.

Although phase change is predicated on locust density, a number of mediating factors have been implicated in priming phase transformation, including visual (29), tactile (15, 26, 27), and pheromonal (35, 68). In addition, dietary factors (48) and previous phase history of the locust (65) can also influence phase change. Earlier proposals on the possible role of olfactory signals in priming locust gregarization were based on observations that hoppers isolated from gregarious colonies of *S. gregaria*, *L. m. migratorioides*, and *Locustana pardalina* (Walker), but kept in the same room with corresponding crowded hoppers, continued to retain the pigmentary, morphometric, and cohesive traits of the gregarious insects (36, 68). The source of the olfactory signal was traced to hopper feces of both phases, but not that of the adults (71). Chemical examination of the feces of the migratory locust led to the identification of 5-ethylguaiaicol (called locustol) as the major component of the gregarization pheromone. However, analyses in different laboratories (33, 34, 81, 95, 104, 105) have failed to detect the compound in any of the airborne volatiles of locusts or their feces. And, in several different studies, locustol did not induce key traits, such as grouping behavior (36) and morphological characteristics typical of gregarious phase (70, 71). In any case, because solitarious stages do not emit aggregation pheromones of their gregarious counterparts, it is unlikely that these would be involved in priming phase transformation of the solitaria to the gregaria (41).

More recent studies have explored possible roles of both nonsemiochemical (visual, tactile) and semiochemical (olfactory, chemotactile) stimuli in priming gregarization of solitarious locusts (18, 44, 90). In one study, solitarious *S. gregaria* nymphs or fledglings were exposed to volatiles from crowd-reared nymphs without visual and physical contact, but no evidence of phase change was observed, although some melanization occurred (18). In another study, second-instar *S. gregaria* solitarious individuals were observed in a chamber with and without visual and/or olfactory cues (44). In addition, the effects of nymphal fecal volatiles and extracts, and nymphal cuticular extracts, on solitarious nymphs were compared. Phase change was monitored by two behavioral indices based on nymphal activity and association. Visual stimuli alone were not effective, nor were fecal volatile components, their extracts, or visual cues in combination with nymphal volatiles. On the other hand, cuticular dichloromethane extracts significantly affected behavioral phase transition. Antennectomy of crowd-reared locusts induced solitarization. Hind tarsal amputation had no such effect, indicating that antennal chemoreception is critical for sustaining the gregarious phase. In a follow-up study (43), phase change was specifically induced by the hydrocarbon fraction of the cuticular extract. The hydrocarbon blend induced a rapid and transient increase in the concentration of inositol triphosphate (IT₃) in antennal preparations from crowded nymphs, which suggests interactions of specific hydrocarbon constituents with antennal chemosensory cells (43). A third set of studies included the effect of tactile stimuli together with visual and olfactory stimuli presented singly and in combination (90). Olfactory stimuli alone were ineffective, while visual stimulation alone was weakly gregarizing after prolonged exposure. A combination of the two caused only partial behavioral change. However, tactile stimulation provided by gently moving paper balls, whether presented alone or in combination with the other stimuli, was most effective in causing behavioral transformation of test insects toward the gregarious phase (39, 90). The site of mechanosensory input that elicits phase change was

identified by repeated localized touch of different body parts of solitary nymphs over four-hour periods and then monitoring the behavior of the insects (99). A significant switch to grouping behavior occurred when the outer face of a hind femur was stimulated but not when 10 other body sites were similarly stimulated.

In summary, studies have identified a contact pheromone and a site-specific mechanotactile stimulus as the principal causes of phase shift of solitary locusts. The combined effects of these two stimuli and their relative contribution toward initiating and sustaining the gregarious phase remain to be elucidated. However, once phase shift has occurred, olfactory signals may also contribute to the primer stimuli to sustain the gregarious phase, in addition to their primary roles as mediators of behavioral cohesion. This would account for earlier observations on delayed solitarization of hoppers of different locust species that were isolated from parent colonies but kept in the same rooms as their crowd-reared counterparts (36, 68). Indeed, in a study on the rates of solitarization of isolated crowd-reared nymphs and adults (monitored by pheromone titers and grouping assays), insects that had olfactory contact solitarized significantly more slowly than those that were isolated in the complete absence of these volatile signals (60).

PHEROMONAL EFFECTS IN GREGARIA

Once gregarious, many polymorphic species exhibit several characteristic behavioral and physiological traits. The most studied pheromonal effects comprise those associated with social cohesion, synchronous maturation, communal oviposition, and maternal transfer of phase traits to the progeny. In addition, the possible role of contact pheromones in mate recognition has been considered (33), and a study has demonstrated pheromonal mediation to reduce male-male contact in *S. gregaria* (96). The status of our knowledge of these effects and the nature of mediating pheromones are outlined below.

Aggregation (Cohesion)

Much of the earlier work on *S. gregaria* and *L. m. migratorioides* appeared to confuse primer effects (outlined above) that initiate the physiological transformation (and associated behavioral, biochemical, and morphological changes) of the solitary insects to the gregarious phase, with releaser effects that mediate the resultant behavioral aggregation of gregarious locusts. Moreover, experimental methodologies designed to demonstrate an olfactory signal in locust aggregation were based on the assumption of an anemotactic attraction mechanism. Studies undertaken by Fuzeau-Braesch et al. (34) showed that blends of specific constituents identified from volatiles collected from air surrounding crowd-reared *S. gregaria* and *L. m. migratorioides* were unattractive to the insects. However, they elicited significant clumping behavior of the locusts and were considered to function as a cohesion pheromone.

More behavioral studies were undertaken in an olfactometer that was designed to measure such cohesive responses of locusts to potential sources of aggregating signals (80). The olfactometer was an enclosed, single-chamber arena with two columns of air rising from the bottom, one with clean air and the other with air enriched with test volatiles associated with gregarious desert locusts or test synthetic blends (79, 81, 104, 105). The responses of different stages of *S. gregaria* in the olfactometer were studied by releasing the insects in groups as well as individually (80). The results showed that nymphal and adult locusts made clear choices between treated and untreated sides of the arena when they encountered a relevant signal, with aggregation indices between 70% and 80% in favor of the treated side. Of special

interest was the finding that there was a clear stage differentiation in the responses of nymphal (second- to fifth-instar) and adult stages, with nymphs preferring the air column enriched with nymphal airborne volatiles and adults of all age groups preferring volatiles emitted by older males (80), indicating the operation of distinct aggregation pheromone systems for the two stages. Of particular significance was the finding that the aggregating effects of the pheromones were independent of whether the insects were released in groups or individually, indicating that nonolfactory cues are not important mediating components of the grouping response (80), contrary to previous speculations (34, 37).

Analyses (GC-EAD and GC-MS) of the volatile emissions from live fifth-instar *S. gregaria* led to the identification of C₆ and C₈-C₁₀ straight chain aldehydes and carboxylic fatty acids, together with smaller amounts of phenol, guaiacol, and indole (Figure 1), as the major electrophysiologically active constituents (41, 104). The benzene compounds are also the major volatile constituents of nymphal and fledgling feces (41, 81). The second- to fifth-instar nymphs share a common pheromone that is produced by both sexes (79–81). In laboratory assays, synthetic blends of the eight aliphatic compounds and the two phenolic compounds promoted nymphal aggregations to the same degree as the natural volatiles from live nymphs (104). First-instar gregarious nymphs appear to rely on a different set of signals for social cohesion. Its pheromone has not yet been characterized.

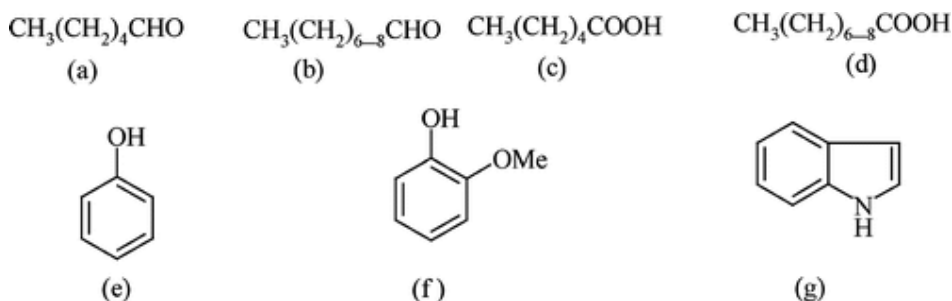


Figure 1 Major constituents of gregarious *S. gregaria* nymphal second- to fifth-instar aggregation pheromone: (a) hexanal; (b) octanal, nonanal, decanal; (c) hexanoic acid; (d) octanoic, nonanoic, decanoic acids; (e) phenol; (f) guaiacol; (g) indole.

Newly fledged adults do not emit behaviorally or analytically detectable amounts of the adult pheromone (19, 97, 105). They are also indifferent to the nymphal pheromone. However, they aggregate strongly in response to volatiles of their own feces and those of nymphs, which comprise phenol, guaiacol, and indole (41, 81). Field observations indicate a close association between fledglings and hoppers and, associated with them, large amounts of fecal droppings (81, 107). Thus, nymphal and fledgling volatiles may act as a transient aggregation signal for the young adults until they start to produce the adult pheromone (81).

Analyses of airborne volatiles of older adults (from about 10 to 12 days after fledging) showed in males the presence of six electrophysiologically active benzene compounds, anisole, veratrole, benzaldehyde, guaiacol, phenylacetonitrile, and phenol (18, 105) (Figure 2). Phenylacetonitrile was the dominant component, accounting for ~80% of emissions of the older and mature males. While phenols are products of locust gut bacterial activity (23),

phenylacetonitrile and benzaldehyde are biosynthetic products of phenylalanine produced in the epidermal cells of wings and legs of the desert locust (97a). Females produced only traces of guaiacol and phenol, consistent with behavioral assays that showed that females do not elicit significant clumping responses from conspecific adults of either sex (79, 105). Of the six compounds, anisole and veratrole did not elicit significant aggregation. Of the rest, phenylacetonitrile was the most active. Interestingly, single-cell recordings from antennal olfactory receptor neurons and antennal lobe interneurons showed the presence of groups of neurons that were specifically excited by the six compounds, and others that were identified as blend specialists responding to specific mixtures of the pheromone components (3, 40). The significance of the two groups of neurons remains to be elucidated.

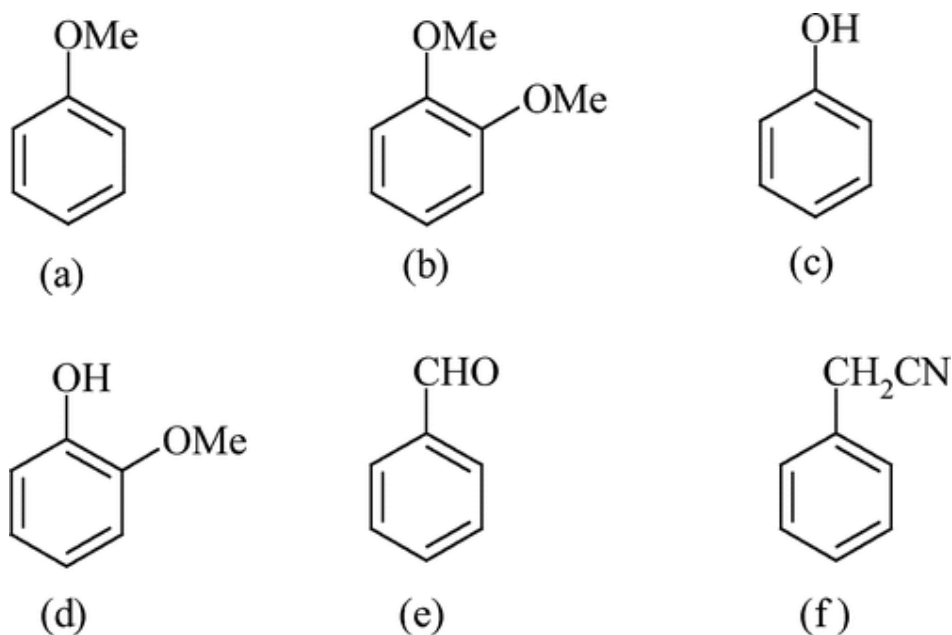


Figure 2 Major constituents of the pheromone produced by gregarious *S. gregaria* adult males: (a) anisole, (b) veratrole, (c) phenol, (d) guaiacol, (e) benzaldehyde, (f) phenylacetonitrile.

The significance of the evolution of distinct sets of aggregative signals for different stages of *S. gregaria* is unclear. Perhaps the need to separate adults from hoppers is related to patchy food resources in the primary breeding areas and the need to minimize competition between these stages (80, 106). The biological rationale for pheromonal differentiation between the first instar and other nymphal stages is less clear and further field observations and physiological studies are needed to shed some light on the question.

With the exception of one study (66) on *L. m. migratorioides*, there are no reports on studies on the aggregation pheromone biology of other locusts and aggregating grasshopper species. Unlike *S. gregaria*, *L. m. migratorioides* shows a less distinct pattern of stage and sex differentiation in its aggregation behavior. Thus, whereas fifth-instar nymphs do not respond to the adult pheromone, adults respond significantly to pheromone of nymphs. Moreover, both adult sexes induce aggregation from conspecifics and emit the pheromone, which is dominated by aliphatic aldehydes and alcohols. Of interest is the finding that the nymphal stages of the two species share a series of common constituents, including the acids and phenols. Aggregation assays of corresponding stages of the two species showed relatively

strong interaction between nymphal stages and account for frequent occurrence of mixed hopper bands in the field (24, 50).

Aggregation Pheromones and Recruitment of Solitaria

Normally, solitarious desert locusts actively avoid one another (26, 92, 93). Airborne volatiles of solitary-reared adult males are qualitatively and quantitatively different from those of gregarious counterparts, with some of the key components of the aggregation pheromone missing or present only in trace amounts (67, 104). However, studies on their EAG responses to the four behaviorally active constituents of the gregarious-phase aggregation pheromone show a pattern of response, including threshold levels, comparable to those of the gregarious counterparts (67). Of particular significance was the finding that, in behavioral assays involving volatiles derived from adult gregarious males, different pheromone components, and different combinations of these compounds, the responses of the solitarious insects were comparable to those of the gregarious counterparts. These findings suggest that solitarious adults that encounter pheromone-emitting groups of gregarizing adults would be arrested and recruited into the groups and, if contact with such groups were sufficiently prolonged, the new recruits would rapidly acquire gregarious characteristics (8, 27, 92). A parallel recruitment mechanism is believed to operate in nymphal stages (67), and such recruitment processes may constitute an important mechanism of spread of the gregarious character across the population (41).

Maturation Synchronization

Maturation synchrony constitutes an important attribute of the gregarious-phase polymorphic acridids. It ensures more or less concurrent mating of the sexes and communal oviposition by the gravid females, which results in spatial and temporal cohesiveness of the progeny critical for sustaining the gregarious phase (58, 72, 75, 86). In addition to interspecific signals that may affect primarily reproductively inactive solitarious adults (referred to above), pheromonal signals play an important role in synchronizing sexual maturation of gregarizing and gregarious populations of *S. gregaria* and *L. m. migratorioides* (72, 73, 75, 78, 89). Two sets of olfactory signals are involved: a maturation-retarding signal associated with nymphal stages of the insects (72, 73, 75, 78, 89), and a maturation-accelerating signal associated with older and mature adults (2, 55, 72, 73). The former delays the maturation of early fledgers, and the latter accelerates that of late fledgers. These sequential exposures to inhibitory and acceleratory signals promote maturation synchrony in locust populations (58, 89).

Assad et al. (6) investigated the nature of the maturation-retarding signal associated with the desert locust using two-story aluminum cages, which exposed recipient insects in the bottom chamber to test volatiles from the upper chamber. The effects of the presence of male or female fifth-instar *S. gregaria* on the maturation of immature adults were compared with exposure of the latter to volatiles from fifth instars, their feces, and synthetic blends of the nymphal aggregation pheromone. Maturation was monitored by integumental yellowing, copulation activity, pheromone titers (in males), ovulation (monitored by oocyte length), and oviposition time (5). The results showed that maturation-retarding effects of nymphs on groups of immature adults are attributable wholly to their aggregation pheromone. None of the different groups of constituents (aldehydes, acids, or benzene compounds) on their own had significant effects on maturation. Thus, the nymphal pheromone plays a dual role, as the nymphal aggregant (a releaser effect) and as an adult maturation retardant (a primer effect). Significantly, the close association between young adults and nymphs observed in the field when the latter are fledging (107) is facilitated by the delay in the production of the adult pheromone. During this period (as pointed out above), the young adults rely on their own

fecal volatiles and those of the nymphs (which are compositionally identical) to stay cohesive (79).

Two recent studies from different laboratories on the maturation-accelerating effects of gregarious mature male *S. gregaria* and their pheromonal candidates have been described. In both studies, the maturation rates of immature males in contact with mature males or their pentane or hexane extracts were significantly faster than those of unexposed immature males (59, 95). Exposure of up to 8 days was necessary for maturation effects to be observed (59). In females, maturation acceleration was reflected in earlier increases in hemolymph vitellogenin titers (57). The results from the two laboratories on the effects of mature male volatiles on maturation were somewhat different. Mahamat et al. (58, 59) found that mature gregarious males and their trapped volatiles dispensed from polyethylene glycol placed in the upper chamber of two-story aluminum cages were equally effective in hastening the maturation of groups of immature males in the lower chamber. In follow-up tests, different blends of five chromatographically prominent constituents of mature male emission (anisole, benzaldehyde, veratrole, phenylacetonitrile, and 4-vinylveratrole) were monitored with respect to integumental yellowing and copulation activity. Insects exposed to the full blend and one without veratrole (four components) mated at approximately the same time as those exposed to volatiles from live mature males. However, the synthetic blend was slightly but significantly less effective in accelerating yellowing, indicating that other minor constituents of the pheromone emission contribute to this process (58). Other four-component blends showed varying levels of maturation acceleration; blends without phenylacetonitrile or benzaldehyde were least potent, indicating the greater contribution of these constituents to the maturation-accelerating property of mature male volatiles.

Schmidt & Albütz (95) found that single immature males enclosed in wire boxes placed with mature males and females did not exhibit earlier integumental yellowing. However, pairs of immature males placed in direct contact with mature males showed accelerated maturation. These authors concluded that direct contact with mature males was important for manifestation of the effect. An alternative explanation that reconciles results from the two laboratories, as well as previous demonstrations of involvement of an olfactory signal, is that the volatile adult pheromone functions in the presence of other chemotactile signals available in groups of adults, mature or immature. Further experimentation with exposure of individuals and groups of immature males and females to the volatile signal with and without low-volatility constituents of locusts is needed to confirm this. No similar studies have been reported on other polymorphic acridids, although maturation effects for *L. m. migratorioides* and *Schistocerca cancellata* that implicate the mediation of pheromones have been reported (1, 2, 42).

Mating

High population densities in the gregarious phase reduce mate-finding and recognition to a close-range problem. In the desert locust, for example, there may be as many as 15×10^3 individuals ha^{-1} (25). Crowd-reared female *S. gregaria* are relatively passive and display no courtship behavior (2, 75, 102), whereas males are relatively aggressive and appear to recognize females (45, 75). Thus, short-range or contact pheromonal signals may play an important but unrecognized role in both polymorphic and nonpolymorphic acridids (108). Studies to establish and characterize the role of such signals have not been reported.

High population densities may also present the problem of homosexual encounters between nonmating males and competitive interactions between unpaired males and male-female pairs, and the need for male-male recognition signals. Francke & Schmidt (33) investigated high-boiling constituents of pentane body washings of crowd-reared *S. gregaria* adult males. In

addition to the major hydrocarbon constituents, long-chain 2-methyl ketones with 3-methyl substituents were located in GC-MS investigations. One of these (3,7-dimethylpeptacosan-2-one) bears a striking resemblance to the sex pheromone of the German cockroach, *Blattella germanica*. No follow-up studies on the effects of these constituents on male (or female) mate selection behavior have been described, but their presence is suggestive of a possible role in such a process.

In recent studies, Ferenz and coworkers (32, 96) have explored a different role for the major component of the male-produced aggregation pheromone of the desert locust. In mating experiments, they found that crowd-reared males jumped on or made pairing attempts with solitary-reared males, but not with gregarious male counterparts nor with gregarious male-female mating pairs. When solitarious males or gregarious females were treated with phenylacetonitrile, no pairing attempts by crowd-reared males were observed (96). The authors concluded that phenylacetonitrile was a repellent agent that functioned as a courtship-inhibiting pheromone that prevents male-male pairing, and proposed that this was the exclusive function of the male-produced pheromone (32, 96). However, need the different demonstrated functions of the pheromone be mutually exclusive? Indeed, if phenylacetonitrile was a repellent with a simple dose-response relationship, how do we account for the cohesive behavior of mature males and females, and of males alone? Results described by Obeng-Ofori et al. (80) have shown that gregarious adults (males and females, immature and mature) that were released in the two-choice arena, whether in groups or individually, preferred to be within the air column enriched with the pheromone (or specific constituents such as phenylacetonitrile). If tactile/chemotactile effects were responsible for behavioral cohesion (32, 96), in addition to their roles in priming gregarization, how does one account for the same level of preference for the pheromone-enriched air column whether the insects were released individually (no tactile/chemotactile or visual cues) or in groups (all cues present)? Moreover, pheromone production starts well before (10 to 12 days) maturation (19, 95), which is inconsistent with its exclusive function as a sex recognition signal. Both functions of the adult pheromone are possible if male-male avoidance occurs at relatively high concentrations near the source, and a cohesive effect at lower concentrations away from the source. Experimental confirmation of this will provide an interesting example of multiple parsimonious roles of the adult male-produced pheromone, comprising behavioral cohesion, maturation acceleration, and homosexual male-male recognition.

Oviposition and Phase Transmission

Oviposition in gregarious-phase acridids constitutes the principal means of transmitting gregarious traits to the progeny and facilitating accumulation of these traits across generations. This occurs through two augmentative mechanisms. One relates to group oviposition behavior, which ensures high egg pod densities at oviposition sites and resultant spatial cohesiveness of the progeny (74, 77, 86, 93, 101). The second is associated with factors demonstrated in *S. gregaria* and *L. m. migratorioides* that predispose developing embryos (of either phase) toward the gregarious phase (8, 46, 47, 54, 64). These factors are produced by ovipositing gregarious or gregarizing females, including those that experience crowding at mating or oviposition. Gravid solitarious females also respond strongly to the presence of egg pods of their gregarious counterparts, preferring to lay their eggs adjacent to these rather than near their preferred desert plants (7). This behavioral switch constitutes another mechanism of recruiting solitarious individuals into gregarizing populations.

Gravid gregarious desert locusts have been observed to oviposit in open ground away from vegetation and to avoid ovipositing near certain plants, in spite of being attracted to feed on these when hungry (76, 86). Plant repellents and visual effects were implicated in this behavior, but no follow-up studies have been reported. A similar behavior has been reported

for red locusts (*Nomadacris septemfasciata* Serville) that move away from vegetation to oviposit in the bare soil of recently burned grassland (109). In general, females prefer to lay eggs where others are ovipositing, even though environmentally suitable alternatives may be present (86, 101, 107). Several stimuli appear to mediate communal oviposition, including tactile (26, 27), visual (29), and pheromonal, both olfactory and chemotactile (35, 68, 69, 94). Because males remain on females for varying periods after copulation (107), communal ovipositing sites of acridids are generally mixed-sex aggregations (63, 86). It is thus possible that the male-produced aggregation pheromone also plays a role in group oviposition (94). Unfortunately, no field and laboratory studies designed to elucidate the roles and relative contributions of these stimuli have been reported. However, significant progress has been made in identifying some of the semiochemical signals that mediate group oviposition in *S. gregaria*. Saini et al. (94) compared the effect of the egg pods, froth material, and eggs on oviposition choices of gregarious females. Attraction was associated with the presence of froth. Sand in which females had laid eggs previously also elicits enhanced oviposition. Extracts of the froth obtained by sequential extraction with solvents of increasing polarity (hexane, ethyl acetate, and methanol) elicited different levels of egg laying. Hexane extract was the most potent, followed by the methanolic extract, which suggests the mediation of volatile constituents of low polarity and nonvolatile, polar components. Volatiles trapped from the froth evoked strong oviposition. Ovipositing females were frequently seen touching sand contaminated with froth materials with their antennae and palpi, which suggests a search for additional signals or continued processing of the ones first encountered (94). A similar behavior has been reported for *L. m. migratorioides*, which may even ingest contaminated sand prior to laying eggs (52–54).

Examination of volatiles trapped from egg froth of crowd-reared *S. gregaria* by GC-EAD and GC-MS led to the identification of two candidate pheromone constituents, acetophenone and veratrole, each of which induces oviposition (87). The more polar constituents associated with methanol extract remain to be investigated. The possibility of additional constituents specifically associated with sand following oviposition by *S. gregaria* was explored by Torto et al. (103). Trapped volatiles from moistened contaminated sand enhanced oviposition by *S. gregaria*. GC-EAD and GC-MS analyses of the volatile collection revealed the presence of three EAG-active unsaturated ketones, (*Z*)-6-octen-2-one, (*E,E*)-3,5-octadien-2-one, and its (*E,Z*) isomer (Figure 3). The relative amounts of the three constituents increased with consecutive ovipositions. Comparative analysis of volatiles derived from eggs and froth showed detectable amounts of the three ketones in the former but much less in the latter, which suggests that the ketone blend is probably secreted directly into the sand at the onset of oviposition.

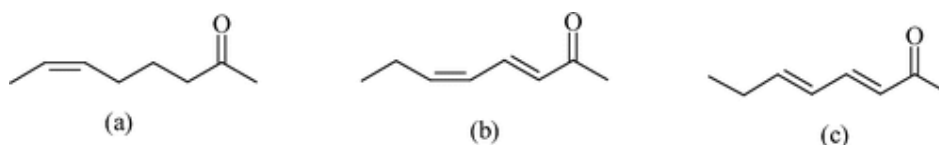


Figure 3 Unsaturated ketones secreted into the sand by gregarious *S. gregaria* females during oviposition: (a) (*Z*)-6-octen-2-one, (b) (*E,Z*)-3,5-octadien-2-one, (c) (*E,E*)-3,5-octadien-2-one.

The identity and source of the gregarizing factor associated with ovipositing gregarious and gregarizing females were investigated in two different laboratories. McCaffery et al. (64)

considered the soil previously laid into by gregarious ovipositing *S. gregaria* females and foam plugs as possible sources of the primer pheromone. A soilborne factor was ruled out because egg pods of solitary females laid into sand previously used for oviposition by gregarious females yielded hatchlings that did not show any gregarious traits. There was, however, evidence of gregarization in hatchlings derived from solitary eggs incubated with froth from egg pods laid by gregarious females. Saline aqueous extracts of the froth were also effective in inducing shifts toward the gregarious phase. Ultrafiltration at 3 kDa provided a filtrate that essentially retained the activity of the original aqueous extract. The authors proposed that the pheromone was a polar substance of low molecular weight (<3 kDa) associated with the egg pod. Malual et al. (61) considered the possibility of dual functions for the blend of C-8 unsaturated ketones, as a releaser and a primer signal. These ketones adhered strongly to dry soil and could be desorbed only at relatively high humidities (61, 103). Hatchlings derived from the eggs of solitary females that were incubated in moistened sand previously used for egg-laying by gregarious females exhibited gregarious behaviors, which increased in a dose-response fashion. Washing the sand with an organic solvent, or flushing it with nitrogen gas, led to substantial loss of its gregarizing effect, consistent with medium polarity and volatility of the ketones. The ketones were also detected in the accessory glands of gregarious gravid *S. gregaria* females (61) shown previously to be the likely source of the gregarizing factor (38). Thus, the ketonic blend's role as an oviposition aggregant and as a gregarizing factor for developing embryos is strong, but this remains to be confirmed with authentic synthetic compounds.

CONCLUSIONS AND FUTURE RESEARCH

Although some of the earliest examples of semiochemical activities in insects came from studies on the desert locust and the African migratory locust, chemical communication in Acrididae as a whole has received limited attention to date. This may be due in part to the assumption that members of this family rely primarily on nonchemical signals (visual, acoustic, and tactile) in their communication systems. However, research on the desert locust, spurred by the 1985–1989 plague and major subsequent outbreaks in the early 1990s, demonstrated that we have just begun to unravel the rich and complex chemical communication systems of these insects. In this review we have summarized the important roles chemical signals play in the behavioral patterns and responses of the two phases of *S. gregaria*. We have highlighted new insights garnered on the predisposition of the species to exploit opportunities under appropriate conditions to congregate and gregarize. The studies on this species and the results obtained provide a useful model for similar studies on other polymorphic and aggregating grasshoppers.

However, much remains to be done on the desert locust. The role and identity of semiochemicals in the solitary phase, particularly in plant-locust relationships in the recession and breeding areas, remain to be elucidated. A better understanding of reproductive diapause and its termination, mating, and oviposition patterns in solitaria in relation to weather and vegetation patterns would provide the groundwork for developing population and gregarization models and for predicting potential outbreaks.

In the gregarious phase, the role of the pheromone system mediating social cohesion, maturation acceleration, and male-male recognition needs to be clearly defined and differences in the results obtained in different laboratories reconciled. The primer gregarization pheromone(s) associated with phase shifts during crowding in nymphal and adult stages remains to be elucidated and the relative roles of pheromonal and tactile stimuli

in priming gregarization clarified. In oviposition, the roles that different stimuli play in communal egg-laying behavior and the contribution of different pheromonal signals need further research, and the releaser and primer effects of the ketonic blend need to be confirmed.

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