Reproductive Behaviour Of The Solitarious Desert Locust, *Schistocerca Gregaria* (Forskål), In Relation To Semiochemical Attributes Of Desert Plants

By

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DECLARATION

I hereby declare that the work embodied in this thesis is a result of my own investigations during the three years research undertaken under supervision at ICIPE, Nairobi, Kenya, has not been submitted before for any degree in any other university.

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TABLE OF CONTENTS

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

LIST OF PLATES

LIST OF APPENDICES

ABREVIATIONS CITED IN THE TEXT

ANOVA	Analysis of Variance
ARPPIS	African Regional Postgraduate Program in Insect Science
ARQU	Animal Rearing Quarantine Unit
BCED	Behavioural and Chemical Ecology Department
CLAA	Centre de Lutte Anti-Acridienne
DRP	Director of Research and Partnership
DSO	Direct Support to Training Institutions in Developing Countries Programme
FCI	Field-collected insects
GC	Gas Chromatograph
GC-MS	Gas Chromatograph-Mass Spectrometer
GTZ	Gesellschaft für Technische Zusammenarbeit
HSD	Honest Significant Difference
ICIPE	International Centre of Insect Physiology and Ecology
IFAD	International Fund for Agriculture Development
LRI	Laboratory-reared insects
LSD	Least Significant Difference
RH	Relative Humidity
SAS	Statistical Analysis System
SNK	Student-Newman-Keuls
χ^2	Chi-square
12L:12D	12 hours light:12 hours dark

ABSTRACT

Sexual attraction in the desert locust, *Schistocerca gregaria* (Forskål), was investigated by monitoring sexual behaviour of solitary-reared, gregarizing and gregarious locusts. Gregarizing males were significantly more attracted to volatiles from solitarious females than the solitarious males, depending on the length time they had been crowded. 24-day-crowded-solitarious males, traversed the longest distance toward the source of stimuli and also showed additional behavioural activities compared to the control, when no solitarious female was kept upwind. Besides, solitarious females despite grouped together did not gregarize and behaved similarly to solitary-reared ones. However, when solitarious females were grouped together from fledging for 24 days in a lower chamber of a bi-chamber cage with soltarious males (kept in the upper chamber) with olfactory and visual contact (but no tactile contact), they showed significantly more attraction to solitary-reared males.

Visual stimulus when provided in addition to olfactory stimulus, have been revealed important role in sexual attraction, as is involving both test and target insects in the sexual behaviour scenario and therefore, the number of test insects reaching the signal source increased significantly when compared to olfaction alone.

On the other hand, diel behavioural activity patterns of adult solitarious desert locust that were collected from the field in Port Sudan were investigated by monitoring walking/running, resting, taking off, and scanning in a wind tunnel. Solitarious locusts that had been propagated in the laboratory for 20 generations were also observed for comparison. In both groups of locusts, insects were significantly more active after sunset and this activity attained peak level at 1-2 hours after dusk. Of the two groups, solitarious locusts collected from the field were significantly more active. In the nocturnal phase, the former traversed distances that were about seven times

those covered by laboratory-reared insects. Overall, the results showed that the repertoire of behavioural activities of solitarious locusts is maintained in laboratory-reared insects, albeit at a lower level. The implications of these observations in the behavioural ecology of the desert locust were discussed.

In the field, (Red sea coast) solitarious locusts feed on a range of desert plants (*Heliotropium spp., Tribulus spp., Schouwia spp.*, ...) whilst in the laboratory, locusts colonies were reared on wheat seedlings and wheat bran. The responsiveness of adult solitarious desert locust to odours from three host plants was evaluated in a two-choice wind tunnel. Solitarious desert locusts collected from the field (Red sea coast) were more attracted to volatiles from potted *H. ovalifolium* and *Pennisetum. typhoides* than to clean air, concurring with previous observations on ovipostion preferences near these plants. Furthermore, feeding choice among 2 annual and 1 perennial *Heliotropium* species growing in the same area showed that the annuals were more preferred than perennials; desert locusts balanced regularly their food intake between the 2 annual plants. This behaviour suggests that they may feed on more than one plant in the field. Locusts reared for many generations on wheat seedlings (*Triticum aesitivum*) were more attracted to its volatiles than to clean air and volatiles from *Heliotropium ovalifolium* ones, a preferred host plant for feeding and oviposition in the field. Oviposition bioassays showed that, solitary-reared female locusts oviposited randomly in untreated sand and sand treated with lower doses of *H. ovalifolium* volatiles. However, at higher doses of the *H. ovalifolium* crude volatiles, locusts oviposited significantly more in the treated sand.

The reproductive status of solitarious females sampled at the end of the summer and onset of winter breeding seasons (at two locations in the coastal plains of Port Sudan that were 300 km apart and separated by a mountain range) was investigated. Results showed that all of the females collected at the onset of the winter season (100%) had laid eggs compared to a group of females

caught at the end of the summer breeding season of which only 58% had laid eggs. Most of the oviposition was in December-January, which coincided with the appearance of the annual desert plants. Hence, the hatching of hoppers was at time when there were plenty of annual desert plants that ensured abundant food and shelter for the new generation. In addition, the time of oviposition, hatching of hoppers, adult emergence and subsequent synchronized maturation showed that within a winter breeding season (5-6 months) only one generation is likely to occur. Furthermore, females collected at the onset of the rainy season were more fecund and they were capable of laying egg pods throughout 5 successive months since their first mating at the beginning of the season.

بسم الله الرحمن الرحيم

ملخص الأطروحة

السلوك التكاثري عند الجراد الصحراوي الإنفرادي *Schistocerca gregaria* (Forskål) بالعلاقة مع كيماويات النباتات الصحراوية

الانجذاب التناسلي لدى الجراد الصحراوي *Schistocerca gregaria* (Forskål) حُقِّقَ بمتابعة سلوك التزاوج للجراد الإنفرادي (solitary-reared) المربى بالمختبر و الجراد الإنفرادي المجبر على التجمع (gregarizing) و كذالك الجراد التجمعي الصحراوي (gregarious) .لقد إتضح من هذه الدراسة أن ذكور الجراد الإنفرادي المجبر على التجمع بالإعتماد على طول مدة التجمع كان معنويًا أكثر إنجذابًا إلى الروائح الطيارة المنبعثة من إناث الجراد الإنفرادي الصحراوي مقارنةً بإنجذاب ذكور الجراد الإنفرادي. أثبتت الدراسة كذالك أن الجراد الإنفرادي المجبر على التجمع لمدة 24 يومًا، قد قطع معنويًا مسافةً أطول نحو مصدر الروائح الطيارة المنبعثة من إناث الجراد الصحراوي الإنفرادي. كما أظهرت أيضًا الأنشطة السلوكية الإضافية بالمقارنة بالتجربة القياسية، (عند عدم وضع أيّ أنثى جراد إنفرادي في مصدر إنبعاث الهواء) . علاوةً على ذلك، إناث الجراد الإنفرادي بالرغم من إجبارهن على التجمع معًا لم ينهجن سلوك التجمع و تصرفن بنفس طريقة إناث الجراد الإنفرادي. لكن عندما جُمِعَتْ إناث الجراد الإنفرادي معًا بعد التفسخ من مرحلة الحوريات لمدة 24 يومًا في قفص ذي طابقين مع ذكور الجراد الإنفرادي و التي كانت في الطابق العلوي من القفص باتصال شمّ مباشر و لكنّ بدون إتصال لمسي، أظهرت إناث الجراد إنجذابًا معنويًا إلى ذكور الجراد الإنفرادي. و من ناحيةٍ أخرى عندما أتيح الحافز المرئيّ بالإضافة لحافز الشمّ, وجد أن ذالك لهَ دورمعنوي في الانجذاب التناسلي, إشتراك كلا الحشرات المستهدفة و الحشرات الهدف في سيناريو السلوك التناسلي و لذلك، وضح أن عدد الحشرات المختبرة قد ازداد معنويًا بوصله إلى مصدر الإشارة بدرجة كبيرة بالمقارنة بعدد الحشرات المختبرة التي وصلت إلى مصدر الإشارة بواسطة الشمّ فقط.

لقد تمت كذالك دراسة الأنشطة السلوكية اليومية للجراد الصحراوي الإنفرادي الذي جمع مسبقا من الحقل في بور تسودان بعد تقييم المشي، الجري، الإستراحة، الإقلاع، و تحريك مقدمة الجسم في نفق هوائي (wind tunnel) . و في تجربة أخرى، و التي أختبر فيها نشاط الجراد الإنفرادي الذي ربي في المختبر لمدة 20 جيل للمقارنة بالتجربة آنفة الذكر، في كلتا التجربتين، أظهر الجراد نشاطاً معنويًا عند غروب الشمس وذالك في كل السلوكيات. و لقد بلغ هذا النشاط ذروته خلال ساعة أو ساعتين بعد الغسق. و لقد وجد أن الجراد الصحراوي الإنفرادي المجمّع من الحقل كان نشاطه معنويًا . أثناء اللّيل، قطع الجراد الإنفرادي المجمّع من الحقل مسافات حوالي سبع مرّات أطول مما قطع الجراد المربّى في المختبر. عمومًا، أظهرت النتائج أن الأنشطة السّلوكيّة لدى الجراد الإنفرادي المجمّع من الحقل بقيت راسخة في سلوك الجراد المربّى في المختبر، ولكن بدرجةٍ أقلّ . عواقب هذه الملاحظة في علم البيئة السّلوكيّ لجراد الصّحراء نُوقِشَتْ.

الجراد الإنفرادي الصّحراوي يتغذى في الحقل، (ساحل البحر الأحمر)على كثير من النباتات الصّحراوية (*Heliotropium spp.*, *Tribulus spp.*, *Schouwia spp.* ...) بينما تمت تغذيت الجراد الإنفرادي المُربّى في المختبر على نبات و نخالة القمح (*Triticum aestivum*) . وجد أن استجابة الجراد الصحراوي الإنفرادي البالغ إلى الرّوائح الطيارة المنبعثة من نبتتين (*Heliotropium ovalifolium*, *Pennisetum typhoides*) مفضلة للجراد قُيِّمَتْ في نفق هوائيّ ذو اختيارين (أحدهما تيار هوائي خالي من الروائح و آخر مشبع بالرّوائح الطيارة المنبعثة من النباتات) وجد أن الجراد الإنفرادي المجموع من الحقل أكثر إنجذابا إلى الرّوائح الطيارة المنبعثة من *H. ovalifolium* و *P. typhoides* مزروعة في أصص بدلا من الإتجاه المعاكس المنبعث منه هواء نظيف، و هذا مطابق لملاحظات سابقة على تفضيل إناث الجراد وضع البيض قرب هذه النباتات. إتضح من هذه التجربة أن التغذية الاختيارية للجراد على نباتين حوليين (*Heliotropium ovalifolium*)و (*H. arabinensis* و نبتة معمرة (*H. lignosum*) في نفس المنطقة (ساحل البحر الأحمر) . أظهرت أن النباتات الحولية كانت مفضلة على النبات المعمّر ولقد إتضح أن الجراد الصّحراوي وازن بانتظام في تغذيته بين النبتتين الحوليتين دون المعمر. الجراد المربى لأجيال عديدة على نبات القمح (*Triticum aesitivum*) كان أكثر انجذبًا إلى الروائح المنبعثة من القمح مقارنةً بالانجذاب نحو الهواء غير المشبع بالروائح الطيارة المنبعثة من *H. ovalifolium* و هي المفضلة أصلاً في التّغذية و وضع البيض عند الجراد الذي يعيش في الحقل. كما أظهرت اختبارات بيولوجيّة للتبييض عند الجراد أن إناث الجراد الصّحراوي الإنفرادي المربّى بالمختبر تضع بيضها بطريقة عشوائيّة في رمل معالج بجرعات أقلّ من روائح

Heliotropium spp و رمل نظيف غير معالج. لكنّ، في جرعات أعلى من روائح النبتة، يختار الجراد بدرجة كبيرة التبييض في الرمل الغير معامل.

في تجربة أخرى، درس الوضع التكاثري لإناث الجراد الصّحراوي الإنفرادي الذي تم جمعه في نهاية مواسم التكاثر الصّيفي و بداية مواسم التكاثر الشّتوي (في منطقتين في السهول الساحليّة لبور تسودان على بعد 300 كيلومتر عن بعضها البعض و تفصلها سلسلة جبلية) . أظهرت النتائج أن كلّ الإناث التي جمعت عند بداية الموسم الشتوي (100 %) قد وضعت البيض بالمقارنة بالإناث المجموعة نهاية موسم تكاثر الصّيف و التي قد وضع منها البيض فقط في حدود 58 % . كان معظم التبييض في شهري ديسمبر و يناير في فترة تتزامن مع ظهور نباتات الصّحراء الحوليّة و يكون إنسلاخ الحوريات متزامنًا مع إكتمال نمو نباتات الصّحراء الحوليّة التي توفر الغذاء و المأوى للجيل الجديد . وإذا أخذ في الاعتبار وقت التبييض و إنسلاخ الحوريات و ظهور الحشرات البالغة و تزامن النضج لاحقاً ، فإنه لا يمكن النمو إلا لجيلٍ واحدٍ خلال موسم تكاثري في هذه المنطقة و الذي يمتد من 5 إلى 6 أشهر .و بناءً على ذلك فقد أثبتت الدراسة أن الإناث في بداية موسم التكاثر أكثر خصوبة و ذالك لوضعهنّ كميات كبيرة من البيض خلال خمسة أشهر من التزاوج.

CHAPTER 1

GENERAL INTRODUCTION

1.1. Introduction

The desert locust, *Schistocerca gregaria*, is the most destructive of all locusts (Steedman, 1988). It can transform reversibly and in a graded manner between two extreme phases, *solitaria* and *gregaria*, which differ in morphology, physiology and behaviour (Uvarov, 1966; Steedman, 1988) and has the largest distribution area extending from west Africa through the Middle East to Southwest Asia (Fig. 1).

Among the two phases (*solitaria* and *gregaria*) of the desert locust, *Schistocerca gregaria* (Forskål), the solitarious locusts are primarily present during long drought periods and are mainly confined in some patchy habitats of the arid areas in the Sahel (Uvarov, 1921; Roffey, 1982). Solitarious locusts are cryptic during the day, they spend more time either resting on the ground or roosting within bushes (Steedman, 1988). Thus, they exhibit very limited flight movements in daytime and only fly when they are disturbed or flushed.

However, there are documented field observations that in warm weather, solitarious desert locusts start flying after dusk and continue being active during the early part of the night (Roffey and Popov, 1968). These regular night flights sometimes culminate into migrations of the solitarious locusts into distant habitats leading to unexpected locust infestations and like their gregarious counterparts in a swarm, it has been suggested that they can fly distances of up to 1000 km (Rao, 1936b; 1942; 1960; Waloff, 1963a; Roffey, 1963).

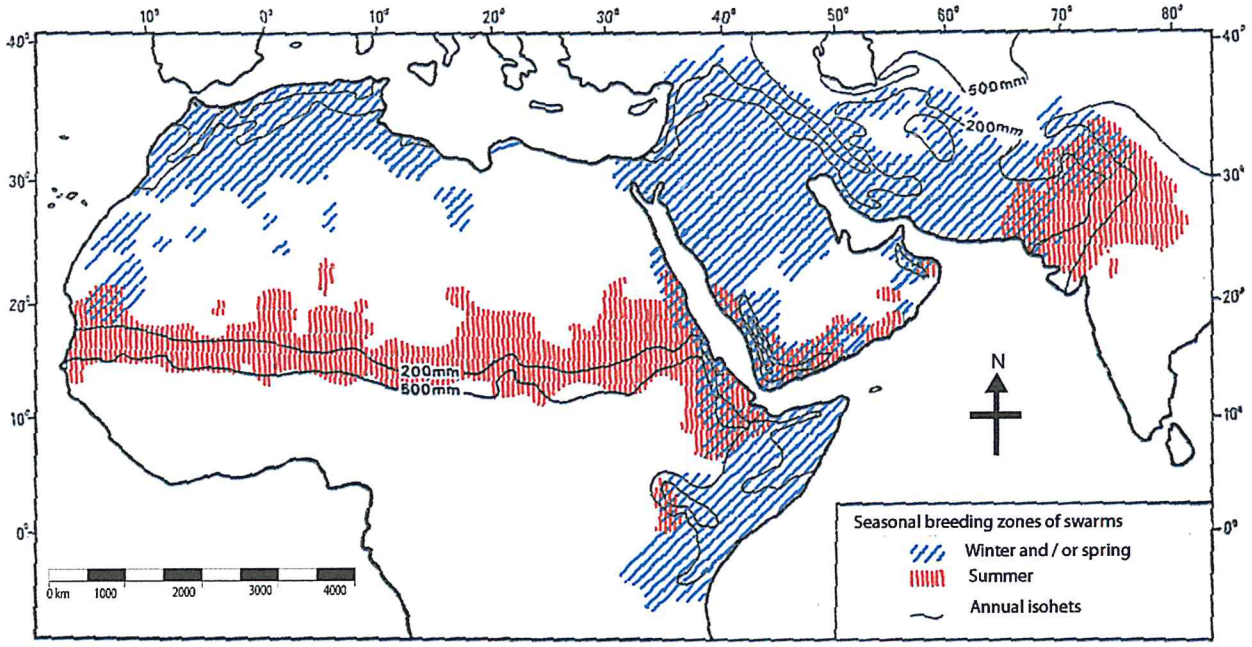


Figure 1. Summer and winter breeding areas of the desert locust, *Schistocerca gregaria* (Forskål) (After Z. Wallof, 1966).

There are also reports on seasonal movements of solitarious locusts between summer breeding areas in the Sahelian zone and winter-spring breeding habitats in the southern and central Sahara (Volkonsky, 1941, 1942; Volkonsky and Volkonsky, 1939, 1940a, 1940b, 1942). Recently, Riley and Reynolds (1995), made an attempt to monitor migrating solitarious individuals flying at high altitudes at night using vertical-looking radar (VLR). From the foregoing records, it is clear that the behavioural activity patterns that are necessary in the understanding of the behavioural ecology of the solitarious desert locust have not been well studied and the available information is very scarce unlike the one on gregarious locusts on which a lot of information is available. Understanding of the periodicity of their behaviour is an important requisite for further studies aimed at elucidating the role played by semiochemicals in the interactions of solitarious locusts with their conspecifics and the host plants. Host plant volatiles have been envisaged to play a significant role in the selection of suitable oviposition sites and congregation of solitarious locusts in the field which are precursors of the initiation of gregarization (Roffey and Popov, 1968; Hassanali and Bashir, 1999: Bashir *et al.*, 2000).

Pheromone communication has been demonstrated in the mating behaviour of many Orthopteroid groups (Whitman, 1982a), but to date, the mediation of sex pheromone has only been demonstrated in a few grasshoppers. According to Whitman (1990) only two grasshopper species have been rigorously shown to possess sexual pheromones. *Hieroglyphus nigrorepletus* males use their antennae in attraction to females over several centimetres distance (Siddiqui and Khan, 1981). In *Taeniopoda eques* a contact sex pheromone from females, detected by the male's antennae, causes males to attempt copulation (Whitman, 1982a). However, the chemical nature of these pheromones has not been elucidated.

The gregarious desert locust, *Schistocerca gregaria,* is termed highly polyphagous (Evans and Bell, 1979) and the hierarchy of its plant preference has been investigated by several authors (Mann and Burns, 1927; Bhatia, 1940; Husain *et al.*, 1946; Alam 1952; Pradhan *et al.*, 1962; Rao and Mehrotra, 1977; Singh and Pant, 1980). In contrast, the solitarious locusts have a selective feeding behaviour, hence, a narrow range of host plants (Bernays and Chapman, 1994). Host plants may contribute much to locust and grasshopper population dynamics through their influence on some key parameters.

Visual cues play an important role in locating of food plant from a distance. However, olfactory cues determine host plant location and acceptance. They also play a major role in other insect behaviours including mating and aggregation (Barrata and Araujo, 2001). These cues are in form of pheromones and plant odours that are transported by the wind in plumes (Barrata and Araujo, 2001). The blend composition of plant odours comprises diverse compounds present in varied concentrations across plant species and across individuals of the same species (Visser, 1986; Städler, 1992; Bernays and Chapman, 1994). Insect host plants produce a wide range of odours which are classified into those occurring in more or less all plants, the green leaf volatiles (GLV) and odours that are more specific to certain plant types such as terpenoids (Hansson *et al.*, 1999). Green leaf volatiles consist of a number of saturated or mono-unsaturated six carbon aldehydes and acetates. These compounds occur in all plants, but in widely varying proportions in different species, and can thus play an important role in host plant location, alone or as a complement to more specific odours (Visser, 1986).

In the solitary phase, the desert locusts are in extremely low densities with the individual insects far separated. Sexual maturity in the solitary locust is associated with the onset of the rainy season (Carlisle *et al.*, 1965, Ellis *et al.* 1965, Assad *et al.*, 1997), and oviposition occurs at sites where soil moisture is adequate and vegetation is sufficient to support the development of their progeny. The

quantitative work done on *Chortoicetes* (Clark, 1947; Key, 1938, 1942, 1943, 1945) and *Nomadacris* (Morant, 1947) leaves little doubt that the *solitaria* habitat provides the most favourable conditions for their growth, survival and reproduction. However, this does not mean that habitats for solitarious locusts are equally favourable for both phases. Only the solitarious phase is otherwise well adapted to that habitat, with its greater longevity and fecundity (Norris, 1950; Hunter-Jones, unpublished). Unlike those of the gregarious phase, encounters between opposite sexes may not be easy (Bashir *et al.* 1993). There might be some strategies that facilitate mate location in the solitarious phase, of which rainfall and consequently patches of annual desert plants may play a significant role.

1.2. Main objectives of the study

1.2.1. General objectives and hypotheses

Field observations in Port Sudan and preliminary laboratory studies suggest that gregarizing males are strongly attracted to solitarious females more than their solitarious male counterparts. This is one of the mechanisms through which solitarious locusts are recruited into gregarizing field populations. The objective was aimed at investigating the reproductive behaviour of solitarious desert locusts as well as their gregarizing counterparts under laboratory conditions with regard to mate location and interaction with host plants. These studies will be supplemented with chemical investigation on plant volatiles collected during different times of the day and their relation to locust physiology, behaviour and reproduction. In this regard, it will be important to provide an understanding of the diurnal and nocturnal activities of the solitarious field populations in order to be able to carry out behavioural experiments at the appropriate time of the day. These will help elucidate the nature of plant-insect relations and the mediating signals

associated with solitarious populations, which will help throw light on some of the mechanisms and strategies that underlie population and phase dynamics of desert locust in its breeding areas.

The hypotheses for the project are:

- Gregarizing desert locust males are more strongly attracted to solitarious females than their solitarious counterparts - this may constitute a basis of a recruitment mechanism into a gregarizing population.
- Documented field observations reported that solitarious locust populations are largely immobile throughout the day and only start flying after sunset.

1.2.2. Specific objectives

The specific objectives of the project are:

I. To investigate mate attraction in solitarious desert locust by monitoring sexual behaviour of solitary-reared and gregarizing (forced-crowding) and gregarious locusts to their counterparts of both sexes used as stimulus source and assess the role of olfactory and visual stimuli when provided singly or combined.

II. To monitor and study in detail in the laboratory the behaviour of solitarious desert locusts caught from the field. It will also be investigated whether the observed activity patterns persist in isolated locusts previously reared in the laboratory for many generations. This involves monitoring various activities including walking/running, distance moved, take-off attempts and scanning frequency during daytime and at night.

III. To investigating the oviposition preferences of gravid females among desert plants including specifically preferred plants that may also be associated with mate location by solitarious locusts.

IV. To investigate the reproductive status of solitarious females in selected habitats at the onset and end of a breeding season. Fecundity will also be assessed by monitoring oviposition rate and time delay of gravid female as part of a strategy by solitarious locusts for maximizing their reproductive success.

CHAPTER 2

LITERATURE REVIEW

2.1. Locust biology

2.1.1. Life cycle

The life cycle of the desert locust comprises three stages: egg, hopper and adult. Eggs hatch in about two weeks (the range is 10-65 days). Despite that, no distinct diapause has been observed in the egg development. Meinzingen (1993) and Akowor and Vajime (1995) showed that in the field, some slowing or temporary arrestment of the egg development is possible in conditions of low soil moisture and temperatures. Hoppers develop through five to six stages depending on phase (*solitaria* or *gregaria),* temperature and humidity. This may take 30-40 days, but under optimum conditions gregarious locusts develop faster than the solitarious ones (Duranton and Lecoq, 1990). After fledging, adults mature in about three weeks. However, under harsh conditions, it may take up to nine months, though frequently, it takes two to four months depending on the weather conditions (Steedman, 1988). The longevity of the adult desert locust is about three to five months although this is extremely variable and depends mostly on weather and ecological conditions. With regard to solitarious locusts, hoppers usually develop through six instars before fledging, each moult is indicated by a stripe on the compound eye while their gregarious counterparts fledge after five instars and have a total of six eye stripes (Steedman, 1988).

2.1.2. Solitarious phase

The adult solitarious desert locusts are usually pale grey-brownish in both sexes when mature; males change to pale yellow on sexual maturation and females may show no colour change during maturation when at very low densities. A solitary female usually lays 3-4 pods, each pod containing 100-160 eggs, with egg pods laid at an interval of 7-10 days. Solitarious hoppers have a uniform green colour in early instars (Plate 1), which may become brown in the last two of the six instars (Anonymous, 1982; Steedman, 1988).

2.1.3. Gregarious phase

After fledging, gregarious immature adults are pink and their colour changes gradually to yellow when they become sexually mature, males being brighter than females. A gregarious female locust lays eggs at least three times in its lifetime, usually at intervals of about 6-11 days. At each laying, 2-3 egg pods are deposited with about 60-80 eggs in each (Anon., 1995). The eggs are commonly deposited by groups of females in located areas (egg fields) and up to 1,000 egg pods have been found in one square metre. The eggs are laid in sandy soils at a depth of 10-15 centimetres below the surface. The gregarious locusts have black marks on a yellow background in all instars (Plate 2).

2.2. Locust ecology

During recession periods, the populations of desert locust are low and are restricted to the arid and semi-arid areas of the Sahel, the Middle East and some areas of South-West Asia (Steedman, 1988). However, during outbreak years, large swarms of locusts move out of the recession habitats into a large invasion

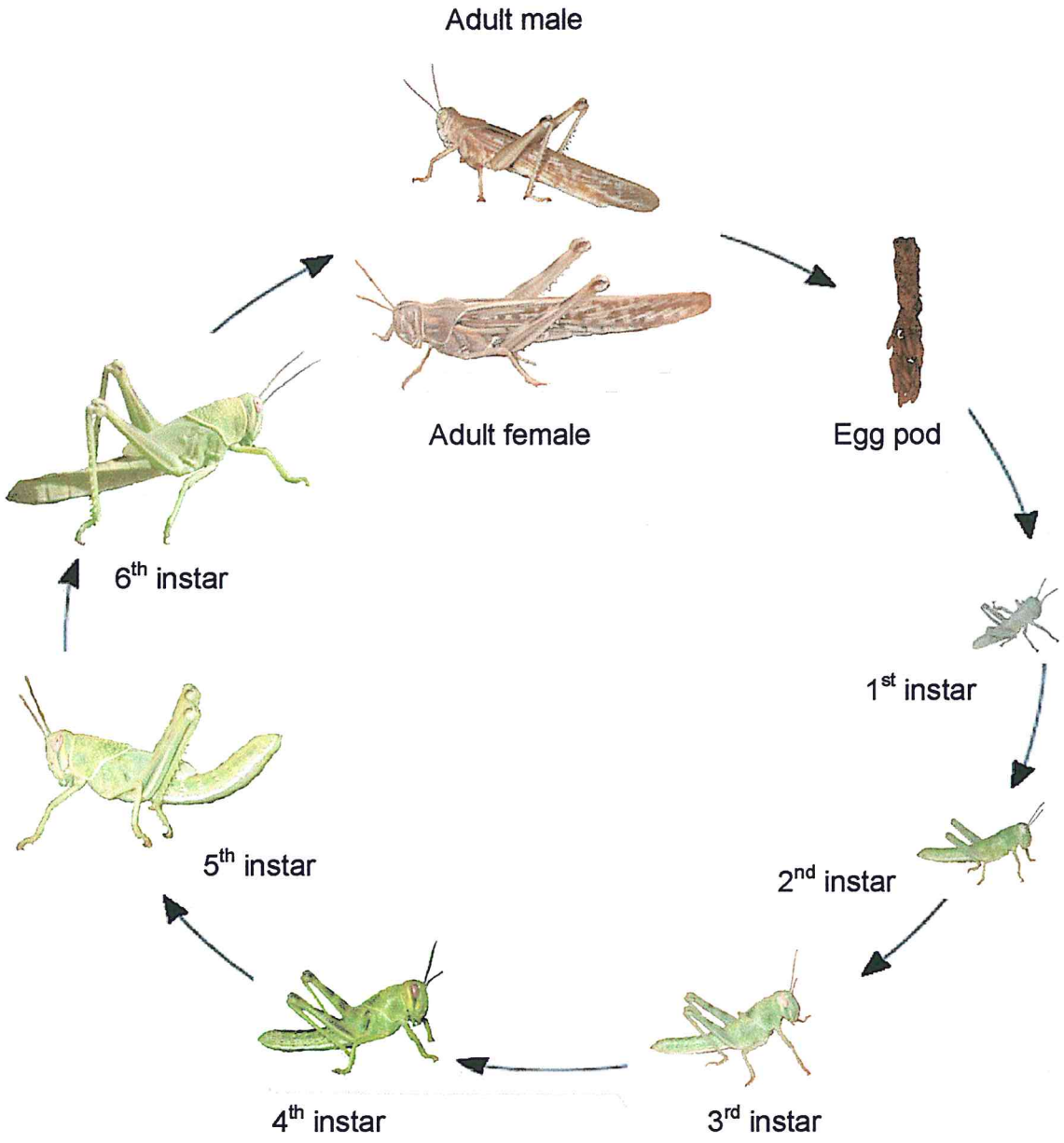


Plate 1. Life Cycle of the solitarious phase of the desert locust, *Schistocerca gregaria*.

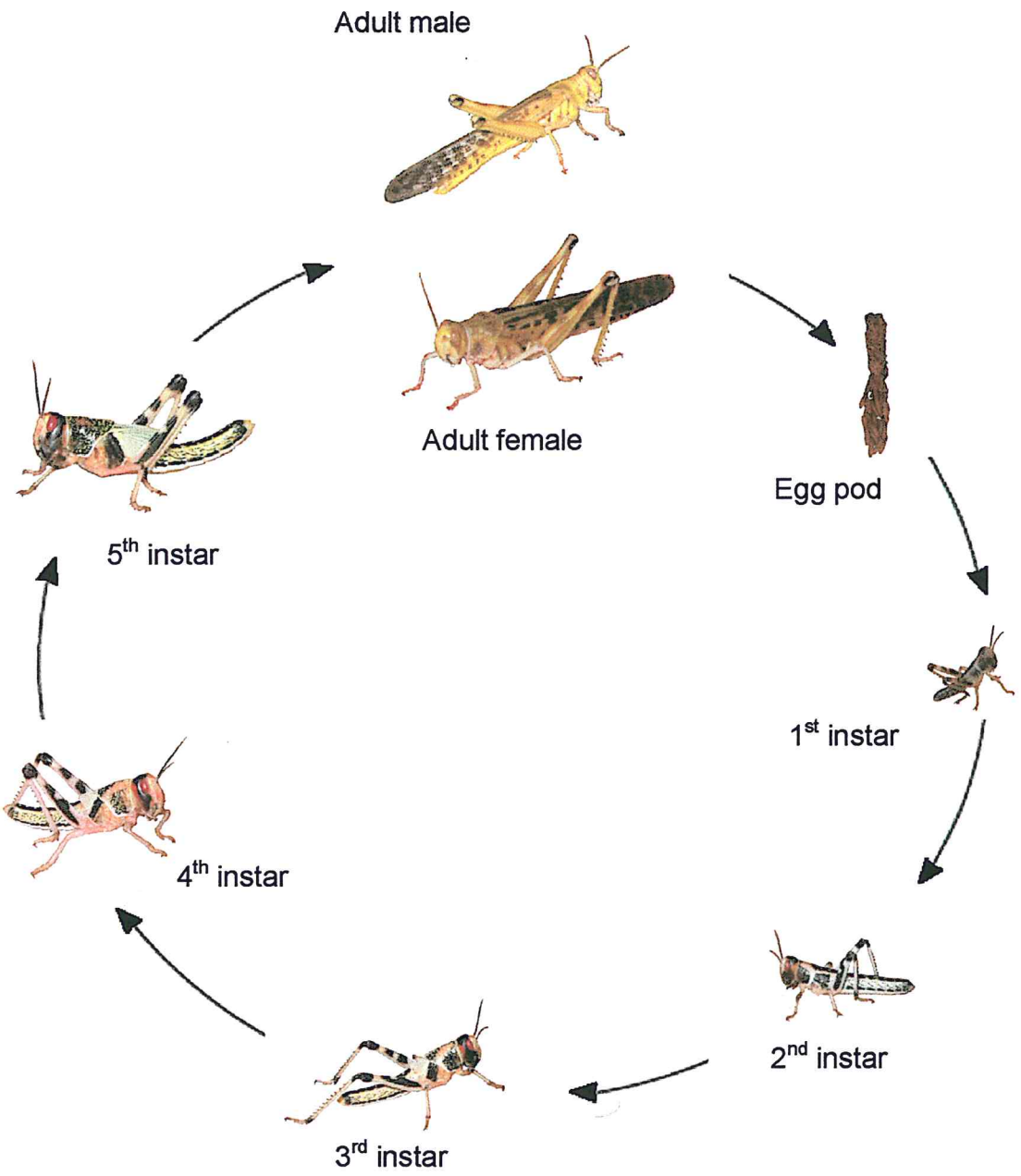


Plate 2. Life Cycle of the gregarious phase of the desert locust, *Schistocerca gregaria*.

area covering portions of 57 countries. Locusts require certain ecological conditions for breeding. Th main variables are rainfall, topography, soil type, vegetation, and temperature.

Rainfall is the most important requirement for producing a favourable breeding environment. Thi because it provides the soil moisture necessary for egg development, and triggers germination and gr of vegetation upon which the hoppers (nymphs) and adults feed. Locusts show a preference for sandy silty soils for egg-laying (Steedman, 1988). The presence of vegetation influences where swarms will settle to lay eggs, the distribution and density of egg pods, and the behaviour of newly hatched hoppe bands. Healthy vegetation, especially annual vegetation that germinates in response to seasonal rains, adequate for the survival of the hoppers by providing both food and shelter. Temperature is the main factor in determining the rate of egg and hopper development (Steedman, 1988).

2.3. Communication in the desert locust

Insects use various modes of communications that involve chemicals, acoustics, and light signalling (Uvarov, 1977). In Acridids, chemical communication is under researched due to the assumption that locusts utilize the non-chemical cues mainly acoustics (Uvarov, 1977, Wittman, 1990). Chemical communication is defined broadly as the release of a chemical substance by one individual, which results in a behavioural and physiological change in another individual. In *Taeniopoda eques* (Romaleidae), blinded males readily mounted and attempted to copulate with dead females, but not dead males (Whitman, 1982a). The active substance was shown to be a contact pheromone (Whitman, 1982b). In contrast in *Hieroglyphus sp.*, males were attracted over a short distance by volatiles emitted by females.

Many other insects use long-range pheromones, (usually attraction of a meter or more) to find mates or mates at food resources (Baker, 1989; Byers, 1989; Ali and Morgan, 1990).

Byers (1991) suggested that it would be interesting to apply a recent mate-finding rate model to locusts to find out whether locusts in the solitarious phase may require to use a long-range pheromone.

A swarm of gregarious phase locusts may contain millions of individuals per km^2 (Singh and Singh, 1977) in which encounters between individuals are frequent within the dense populations. This takes place soon after hatching, when mature adults (about 3 weeks after fledging) start to mate as well as when they encounter gregarious groupings during swarming (Roffey and Popov, 1968). Hence, locusts communicate through chemical cues, in addition to visual and tactile stimuli. At these high densities it would be easy for males to locate females by random wandering (Singh and Singh, 1977). A long-range sex pheromone seems unnecessary, but at densities of a few tens or hundreds per km^2 within recession areas, where desert locusts live as scattered individuals in solitary phase, it seems that the population would become extinct unless a long-range sex pheromone is used (Byers, 1991). A sex recognition pheromone has been shown to exist in *Schistocerca gregaria*, allowing males to recognize females (Amerasinghe, 1978). Inayatullah *et al.* (1994) further demonstrated that females *S. gregaria* released sex pheromone that attracted conspecific males upwind.

Two modes of communication have been documented in the desert locust are intra-specific chemical signals involving use of pheromones produced by nymphal and adult stages of the gregarious phase which mediate cohesiveness, maturation synchrony and oviposition at common sites and, inter-specific signals from other locust species and desert plants (Torto *et al.*, 1994; Niassy *et al.*, 1999; Bashir *et al.*, 2000). Plant signals are either host location and recognition cues (kairomones), defensive chemicals (allomones), or cues that are of adaptive value for both insects and plants (synomones) (Visser, 1986).

2.4. Plant-insect relationships

In the very harsh habitats of the solitarious desert locust, behavioural ecology of these locusts is centred around their host plants. To have a better understanding of the behavioural ecology and biology of solitary populations, it is therefore important to understand the insect -plant interactions in their habitats. Kairomones are interspecific chemical cues that mediate host plant seeking and acceptance by phytophagous insects and other herbivores. In locusts, they may also play a role in the physiology of the locust phase transformation. It has been shown that, two groups of kairomones may influence the physiology and behaviour of locust; volatiles from host plants that are important in the location of food (Haskell *et al.*, 1962, Kendall, 1971, 1972), and non-volatile allelochemicals that are involved in food recognition and acceptance (Woodhead and Bernays, 1978). In the locust habitats, patchiness of habitats is an important factor that influences the phase dynamics of the insects, particularly during the transition period between the dry season with limited vegetation and the onset of the rainy season when green vegetation begins to take root. For any insect in a given habitat, there are resource and non-resource areas. The location, density and quality of resources as well as the structure of the habitat all influence insect activity (Thorsteinson, 1960; Thompson and Price, 1977; Finch, 1980; Kareiva, 1982; Scriber, 1983). A plant may be a suitable feeding site, a rendezvous for mating, a suitable oviposition site and/or shelter (Prokopy *et al.*, 1984). Association of insects with plants is dictated by their need for development and reproduction and for refuge from unfavourable biotic and abiotic factors. One of the more important factors influencing the distribution of solitarious locusts is the distribution of food plants. In different recessions habitats scattered across the Sahelian belt, a broad range of different species of host plants are used for food and shelter. These include *Heliotropium spp.*,

Dipterygium glaucum, Tribulus terrestris, Schouwia purpurea, S. thebaica, Aerva persica, Zygophylum sp., and *Hyoscyamus muticus* (Steedman 1988).

There is a diet relationship between the species of host plant and grasshopper survival, growth, and reproductive performance (Chapman *et al.*, 1979). Detailed studies have demonstrated the importance of particular chemical constituents in the host plants to grasshoppers' survival, including both defensive secondary chemicals (Bernays *et al.*, 1974, Bernays and Lee, 1988) and nutrients (McGinnis and Kasting, 1966).

Steedman (1988) reported that, solitarious desert locusts often associate with *Heliotropium ovalifolium. Dipterygium glaucum, Tribulus terrestris, Schouwia purpurea, S. thebaica, Aerva persica, Zygophylum sp.*, and *Hyoscyamus mutucus* in different recession habitats. Jakson *et al.* (1978) studied the effects of seven of these natural food plants on the phase status of the desert locust, *Schistocerca gregaria,* and monitored changes in colour, morphometrics, number of eye stripes and fecundity. Their results revealed that, millet, *Pennisetum typhoides* and *Sorghum bicolor* enhanced gregarious characteristics while *Dipterygium glaucum* accentuated solitarious traits. In Port Sudan, solitarious desert locusts highly preferred *Heliotropium sp., Pennisetum typhoides, Crotolaria sp.*, and *Dipterigium glaucum* for feeding and oviposition (Bashir *et al.*, 2000). In the harsh habitats, these plants play an important role on the behavioural ecology of these locusts.

2.5. Locust populations movement

The best-documented movements of solitarious locusts are those in the Indo-Pakistani area where Rao (1942, 1960) demonstrated their regular occurrence between the winter and spring breeding areas in Mekran in West Pakistan and in the summer breeding areas in West Pakistan and in Rajasthan in India. These displacements take place in the spring and early summer, and again in autumn before the onset of cold weather (Wallof, 1966). Moreover, green vegetation in the habitats of the desert locust has a survival value as food and shelter and may concentrate and retain populations of solitarious locusts. Egg-laying occurs near vegetation as the requirements of plants and gravid solitarious female locusts are fulfilled by the same humid soil.
Guichard (1955) noted that before the autumn of 1951, after three years of drought in Jebel Soda, Western Libya, the area was uninhabitable and therefore most likely no locusts could have survived in this area since it was devoid of their normal food. In the contrary, during the first week of March, 1952, following the February rains, he found a population of grey adult locusts in the area suggesting that they may have migrated from the south. However, in November, nine months later and following the summer heat, no locusts were found.

2.6. Host plant location and selection

Olfactory cues are mainly utilized by insects to locate a mate, food, and oviposition sites (Baker, 1989; Renwick, 1989). Uvarov (1977) noted that *Schistocerca gregaria* is known to feed on some 400 species of plants. Outside this range some plants are not eaten at all. For example, Husain *et al.* (1946) listed 160 species from 54 families that were readily eaten, 29 eaten with reluctance, and 9 plants from 7 families not eaten at all. Host plants may contribute much to

locust and grasshopper dynamics through their influence on key population parameters. A variety of carefully designed experiments indicated the likelihood of their importance. There is a diet relationship between the species of host plant and grasshopper survival, growth, and reproductive performance (Chapman et. al., 1979). Detailed studies have demonstrated the importance of particular chemical constituents in the host plants to the survival of grasshoppers, including both defensive secondary chemicals (Mulkern, 1972; Bernays *et al.*, 1974, 1980) and nutrients (McGinnis and Kasting, 1966).

2.7. Cues eliciting distant attraction

Plant volatiles play a significant role as cues in host selection by phytophagous insects. One group of host plant volatiles widely studied are the "green leave volatiles" (GLVs) which are primary aliphatic five-or six-carbon alcohols, aldehydes and esters and are released when plant tissues are damaged either mechanically or herbivory (Visser and Avé, 1978; Visser *et al.*, 1979; Dickens *et al.*, 1993; Light *et al.*, 1993).

While plant odours may be taxon-specific, olfactory systems of insects have the capacity to discriminate odours from different plant taxa. However, plant shape and colour are usually less characteristic of taxa because they are variable within given species (Bernays and Chapman, 1994). Moorehouse (1971) showed that, nymphs of *Schistocerca gregaria* were increasingly attracted by the odour of grass in a wind tunnel with increasing starvation period. Lee *et al.* (1987) also showed that nymphs of *Schistocerca americana* responded anemotactically to the odour of mint in a wind tunnel after being conditioned to it. Air passing over an odour source contains pockets of odour-carrying air. These plumes of odours are carried downwind from the

plant such that an insect some distance away from the source detects a series of bursts of odours separated by periods of odourless air (Bernays and Chapman, 1994).

The shape and hue of a plant may compliment other cues (mainly olfactory) in eliciting attraction to the insect. Desert locusts, *S. gregaria,* were attracted to vertical stripes and shapes around an otherwise featureless arena (Wallace, 1959). Previously, Kennedy (1939) had demonstrated that, in the field, locusts on the ground often moved towards clumps of vegetation.

2.8. Effect of food on locust activity

There is evidence that insect activity increases when starved. Ellis (1951) showed a marked increase in the marching activity of *Locusta* hoppers when deprived of food which in return led to decreasing amounts of food in the gut. Aziz (1961) pointed out that, hoppers of *Schistocerca gregaria* starved for 24 to 39 h spent more time in locomotion than did normally fed hoppers. Even six hours of food deprivation can induce continuous marching in locust nymphs in the laboratory (Simpson, and Simpson, 1990). Furthermore, insects with nutrient deficiencies show increased locomotory activity (Barton-Browne, 1975, 1993). Changes in locomotion caused by nutritional state have been interpretated as foraging strategies for heterogeneous environments (Kareiva, 1983; Bell, 1990; Morris and Kareiva, 1990).

2.9. Food consumption and quality

The availability and quality of host plants play an important role in the life cycle of phytophagous insects, and therefore have an ecological bearing on the population abundance of these insects (White, 1969, 1993; Wellington, 1977). Food quality and distribution influence

locust phase status. In particular, host plant quality and locust nutritional state have significant impact on locust ecology and life history (Despland and Simpson, 2000). Different methods have been used to measure the amount of food consumed by locusts during a given period. Odhiambo (1966) estimated food consumption by weighing expelled faeces but this is only roughly correlated to the amount consumed (Norris, 1961). A more accurate method is to compare the weight of food before and after the experiment, a correction of the loss of weight of food through evaporation is determined from a control batch of the same food kept in identical conditions (Davey, 1954; Karandikar, 1933; Nagy, 1952; Rao, 1960). Numerous accounts suggest that poor-quality food plants associated with extreme drought result in poor reproductive performance (Chapman *et al.*, 1979). For example, adults of *Schistocerca gregaria* do not mature sexually during the long, dry periods when they feed on senescent vegetation. However, when new green foliage is available after rains, they mature very quickly due to the high concentrations of the plant growth gibberellin hormone found in the leaves of shrubs (Ellis *et al.*, 1965). Kennedy (1939) suggested that high-quality food might promote population gregarization in the field by accelerating the appearance of more mobile later instar hoppers, decreasing mortality, encouraging immigration from less favourable habitats and allowing the production of two generations within a single season.

McCaffery (1976) showed that both poor quality and low quantities of food reduce or shut off the egg production of female *Locusta migratoria*. For example, poor quality *Agropyron* diets are insufficient to initiate vitollogenesis. It has been shown in the past that green food plants are important for maximum egg production in the locust *Dociostaurus maroccanus* (Merton, 1959) and *Schistocerca gregaria* (Cavanagh, 1963).

Behmer *et al.* (2001) showed that, where locusts had access to two complementary, suboptimal foods, they distributed their feeding between food dishes according to the relative frequency of each food type, thus showing frequency-dependent selection. Since on a per dish basis this involved increased feeding upon the rarer food type, it provides an additional case of antiapostatic selection in herbivores. Chandra and Williams (1983) also found that *Schistocerca gregaria* fed selectively on less-favoured plants when they were relatively less abundant in an experimental arena. They further showed the remarkable capability of locusts to regulate their nutrient intake, in this case in the face of varying relative frequencies of food types of differing nutritional composition in their environment. Moreover, when confined to a single nutritionally imbalanced food, locusts, *Locusta migratoria* and *Schistocerca gregaria*, show clearly defined patterns of trade-off between over-ingesting some nutrients and under-ingesting others. These seemed to differ according to the number of plant species eaten (Raubenheimer and Simpson, 1997, 1999; Simpson and Raubenheimer, 2000).

The amount of food consumed by adult *Schistocerca gregaria* also varies with sexual maturation. The daily consumption by male locusts falls sharply when maturity is attained. Similarly, faeces and body size of females were found to be higher during the period of somatic growth than during the gonoptrophic cycle, respectively (Mordue and Hill, 1970). However, despite that desert locusts are highly polyphagous, they do exhibit food preferences in the field. Some food plants are preferred over others, although the latter may be acceptable foods in laboratory trials while some species are never touched, even by swarms (Kennedy, 1939; Ghaout, 1990; Culmsee, 1997; El Hadj, 1997).

2.10. Effect of plant on locust maturation

Environmental cues and some biotic factors have been shown to influence the rate of development and maturation of solitarious desert locust (Norris, 1964b). Under favourable conditions (30°C and 50% RH average), young adults become sexually mature within three weeks, but maturation may be delayed for several months when unfavourable conditions prevail (Norris, 1957; Stein et. al., 1989). The exact conditions that cause maturation of locusts are not known, but rainfall appears to play an important role (Norris, 1964b). It was found that when solitarious desert locusts are reared in the laboratory, rapid maturation occurs at very low humidity and a minimum of fresh food. However, during summer months in the field, there was a tendency for delayed maturation although there were no changes in the levels of humidity (Norris, 1957).

Carlisle *et al.* (1965) and Marshal and Disney (1957) studied the effect of some aromatic emissions of essential oils derived from *Commiphora* shrubs on the maturation of locusts in the laboratory. Exposure of locusts to these oils triggered sexual maturation. Similar effects have been demonstrated for the essential oils from *Commiphora quadricincta* in Eastern Africa and it has been suggested that other plant species that may have the same ecological niche elsewhere in the locust recession areas may play the same role (Assad *et al.*, 1997; Table 1). Desert locusts use these environmental cues to synchronise their mating to on-coming rains. Sexual maturation in the locust following a period of drought has been observed to occur almost simultaneously at sites hundreds of kilometres apart a few weeks before the arrival of rains (Carlisle *et al.*, 1965). It was found to coincide with the bud burst of certain desert shrubs at the beginning of the rainy season and a few weeks before the appearance of the annual vegetation. These shrubs include species of *Boswellia neglecta* S. Moore and *Commiphora myrrha* (Nees) Engler (Gaffal) which have

Table 1: Principal inter-specific semiochemical signals associated with *S. gregaria* and their effects (Hassanali and Bashir, 1999)

Locust process	Nature of signal	Origin/source	Effect(s) on recipients
Maturation (solitarious)	volatile primer kairomone	Desert plants just before the onset of seasonal rains	Simultaneous maturation of widely scattered solitarious adults before the appearance of seasonal vegetation (Carlisle *et al.*, 1965; Assad *et al.*, 1997).
Mating (solitarious)	volatile releaser pheromone	reproductively active solitarious females	attracts males of both phases (Inayatullah *et al.*, 1994; Mahamat *et al.*, unpublished).
Oviposition (solitarious)	releaser kairomones(?)	specific desert plants preferred for egg-laying	clustered egg-laying by solitarious females promote forced togetherness of hoppers (Bashir *et al.*, 2000).

resinous buds that are the source of the biblical frankincense and myrrh. Marshal and Disney (1957) postulated that desert locusts in the field apparently responded to the scent of the shrubs that first break bud. The effect of the plant-derived oils on the locusts is olfactory and they were found to be ineffective when incorporated into the diet used for rearing locusts (Jackson *et al.*, 1978; Assad *et al.*, 1997).

In conclusion, Assad *et al.* (1997) concurred with suggestions by Carlisle *et al.* (1965) that volatiles from desert shrubs provide the necessary semiochemical signals that trigger sexual maturation in the desert locust prior to the onset of rains. Their results suggest that additional signals may also be involved in modifying the reproductive potential of the insect. An in-depth study of the chemistry of different species of desert plants in different seasons and their relation to locust physiology, behaviour and reproduction in the field is clearly warranted. This will help to elucidate the mechanisms that underlie the population and phase dynamics of the locust.

2.11. Effect of plant on ovipostion

Bashir *et al.* (2000) observed that during the rainy season, the incoming solitarious female locusts preferred to oviposit predominantly in the vicinity of *Heliotropium* sp. and millet seedlings in the Red sea area. Significantly, solitarious nymphs also preferred to feed on these plants. Experiments in cages under field conditions confirmed that solitarious females preferred to oviposit in close proximity to these plants. On the other hand, results of oviposition assays in the laboratory showed that solitarious females were attracted to the froths of egg pods of both phases when these were presented in two-choice assays with untreated controls (Bashir *et al.*, 2000). However, when offered a choice of egg pods derived from gregarious and solitarious females as well as *Heliotropium* sp. or millet plants, solitarious females preferred sand with gregarious locust

egg pods over sand near the host plants or that containing solitarious egg pods. In contrast with solitarious females and in the absence of gregarious egg pods, gregarious females preferred to oviposit in moist sand away from *solitaria* egg pods and plants. However, presence of gregarious egg pods in the sand elicited the highest oviposition by gregarious female locusts.
In other study, McCaffery *et al.* (1998) showed that exposure of egg pods of solitarious females to froth extracts from gregarious females also predisposed the hatchling to gregarious characters.

2.12. Effect of plant on the locust phase

Microstructure of the environment influences the distribution and therefore the behavioural phase state in the desert locust (Kennedy, 1939; Bouaïchi *et al.*, 1996). While dense vegetation promotes solitarization by allowing locusts to avoid one another (Guichard, 1955; Roffey and Popov, 1968; Kennedy, 1939; Bouaïchi *et al.*, 1996), infrequent patches (sparse vegetation) promote encounters between individuals and consequently gregarization may be initiated (Kennedy, 1939). Bouaïchi *et al.* (1996) showed that, provision of only a single site promoted congregation overcoming the tendency of solitarious locusts to ovoid each other. Bashir *et al.* (2000) speculated that the oviposition behaviour of *solitaria* early in the breeding season might contribute to clustering of hatchlings around certain desert plants, thus, forming the onset of pheromone emitting nuclei of gregarizing hoppers.

Jakson *et al.* (1978) studied the effect of seven of the naturally occurring food plants on the phase status of the desert locust, *Schistocerca gregaria,* and monitored changes in colour, morphometrics, number of eye stripes and fecundity. Their results revealed that, *Pennisetum typhoides* and *Sorghum bicolor* (cultivated species) enhanced gregarious characteristics while *Dipterygium glaucum* accentuated solitarious traits. Plant-derived products have also been shown

to influence the phase status of locusts. For example, topical application of neem (*Azadirachta indica*) extracts on gregarious desert locust led to the appearance of solitarious traits (Mishra and Singh, 1992; Langewald and Schmutterer, 1992, Schmutterer *et al.*, 1993; Doumbia, 1994). Although some host plants have been drawn to influence the phase status of locusts under semi-field conditions (Popov *et al.*, 1978), plant architecture appears to be more important in promoting phase change than food quality as dense leafy plants inhibit and sparse ones promote gregarization (Despland and Simpson, 2000). Elsewhere, Nasseh *et al.* (1993) and Langewald and Schmutterer (1995) showed that, limnoids from *Meliacea*e plants induce solitarization of gregarious hoppers.

Host plant density and distribution (cramped or patchy) also play a role in influencing the phase status of the desert locust. Despland and Simpson (2000) showed that in a small population of locusts under semi-field conditions, phase status could be manipulated by small-scale change in the distribution of vegetation. Small-scale distribution of vegetation influences the positive feedback systems that drive desert locust population dynamics by regulating the phase status of local populations and of their progeny. A patchy distribution induces solitarious locusts to aggregate around these resources, despite their inherent behavioural tendency to avoid one another, thus, leading to physical interaction that stimulates phase change (Ellis, 1959; Heifetz *et al.*, 1996; Roessingh *et al.*, 1998). Field observations have shown that gregarization tends to occur in certain plant communities suggesting that, phase change is influenced by the structure and quality of vegetation (Kennedy 1939; Ellis and Ashall, 1957; Roffey and Popov, 1968; Popov *et al.* 1978, 1991; Popov, 1997).

In the scattered resource treatment by Despland and Simpson (2000), diet mixing was easily achieved without increased contact between individuals. This is because the numerous scattered food patches allowed the nymphs to feed and avoid each other, leading to the observed phase shift. Food plant preference also changes between developmental stages (Ghaout, 1990; Bashir, 1996), and is dependent on the length of the period of the plant-insect interaction in a given habitat (Culmsee, 1997). This differential feeding influences the behaviour, particularly habitat selection and marching speed of locust hoppers in the field (Kennedy, 1939; Ellis and Ashall, 1957; Roffey and Stower, 1983): for example, marching bands move faster through shrubby habitats of moderately palatable perennials than they do in sand dune communities where locusts feed extensively on the highly palatable annuals growing between clumps of unpalatable grass (Culmsee, 1997). Popov *et al.* (1978) also noted that, rearing nymphs on *Heliotropium bacciferum* (Boraginaceae) produced gregarious insects although this is quite a dense plant. They hypothesized that plant chemistry may have been involved.

2.13. Combined effects of kairomones and pheromones

Plant volatiles are involved in the sexual behaviour of phytophagous insects through their combined effects with pheromones. The green leaf volatiles, which are released by mechanically damaged plant tissue (Galliard and Matthew, 1977; Hatanaka *et al.*, 1995), induce pheromone release in the emitter and/or synergistically enhance the responsiveness of the recipient (Landolt and Phillips, 1997). Plant-derived chemicals are involved in the sexual behaviour of numerous insect species. After being eaten by an insect, various components may be sequestered and used directly as pheromones or indirectly as precursors of a pheromone. The presence of plant

chemicals also stimulates the *de novo* biosynthesis or the release of insect pheromones. Finally, they may directly influence the sexual behaviour (Ruther *et al.*, 2002).

Swarming males of *Melolontha hippocastani* are known to locate females that stay feeding within the host trees by orienting towards damage-induced plant volatiles (green leaf volatiles) and a sex pheromone. Thus, volatiles emitted by freshly damaged leaves might indicate to a male the presence of a conspesific female that is feeding (Ruther *et al.*, 2002).

CHAPTER 3

MATERIALS AND METHODS

3.1. INSECTS

Locusts used for mate attraction and attraction to plant volatiles experiments were from the ICIPE colony, which was propagated from a stock that originated from the Desert Locust Control Organization for Eastern Africa (DLCO-EA) in Addis Ababa, Ethiopia in 1989. Solitarious males and females were reared separately from first instar hopper to adult stage in banks of eight aluminium cages (10 x 10 x 24 cm each). The top was made of wire mesh for ventilation and the front was plexiglas for visibility (Fig. 2, Plate 3). Cages with locusts were kept in a separate room (1.5 x 4.5 m) at 30 ± 4°C, 40-50% RH, and a photoperiod of 12L: 12D. Gregarious locusts (300-400 individuals per cage) of both sexes were reared under crowded conditions in aluminium cages (50 x 50 x 50 cm each) (Fig. 3, Plate 4) in a well-aerated room (4.5 x 4.5 m) with a duct system that maintained a negative pressure of about 10-15 air changes per hour. Fresh wheat seedlings and wheat bran were provided as a food daily. In all experiments, 23-26 day-old adults were used.

Solitarious locusts were collected from the field around the Tokar Delta on the Red sea coast of Sudan. Each locust was kept isolated in a one-litre ice cream cup for about one week to adapt to the laboratory conditions prior to carrying out the observations. Each cup was ventilated through a small window in the lid that was covered with a piece of fine gauze. For the comparative study, 24-day-old

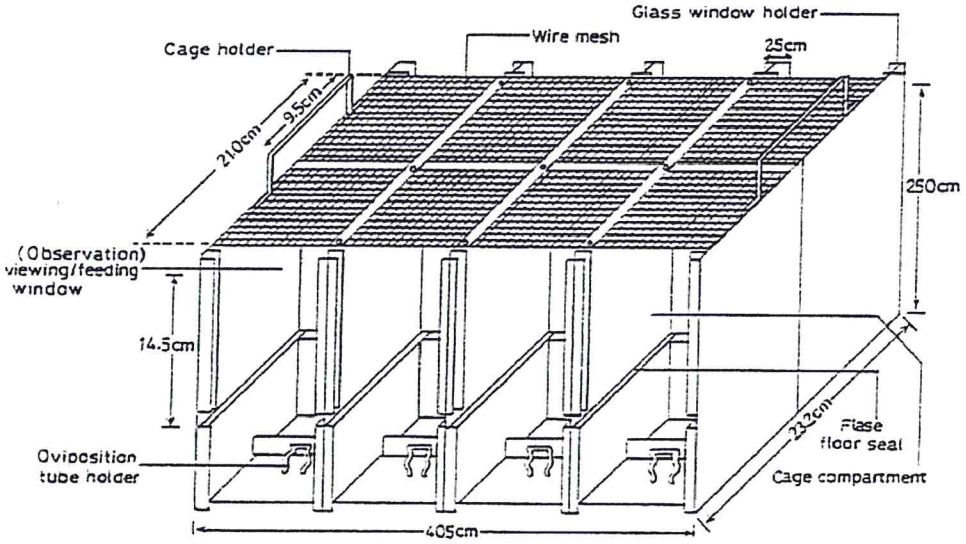


Figure 2. Diagram of eight-banks of a standard cage for rearing solitarious desert locust

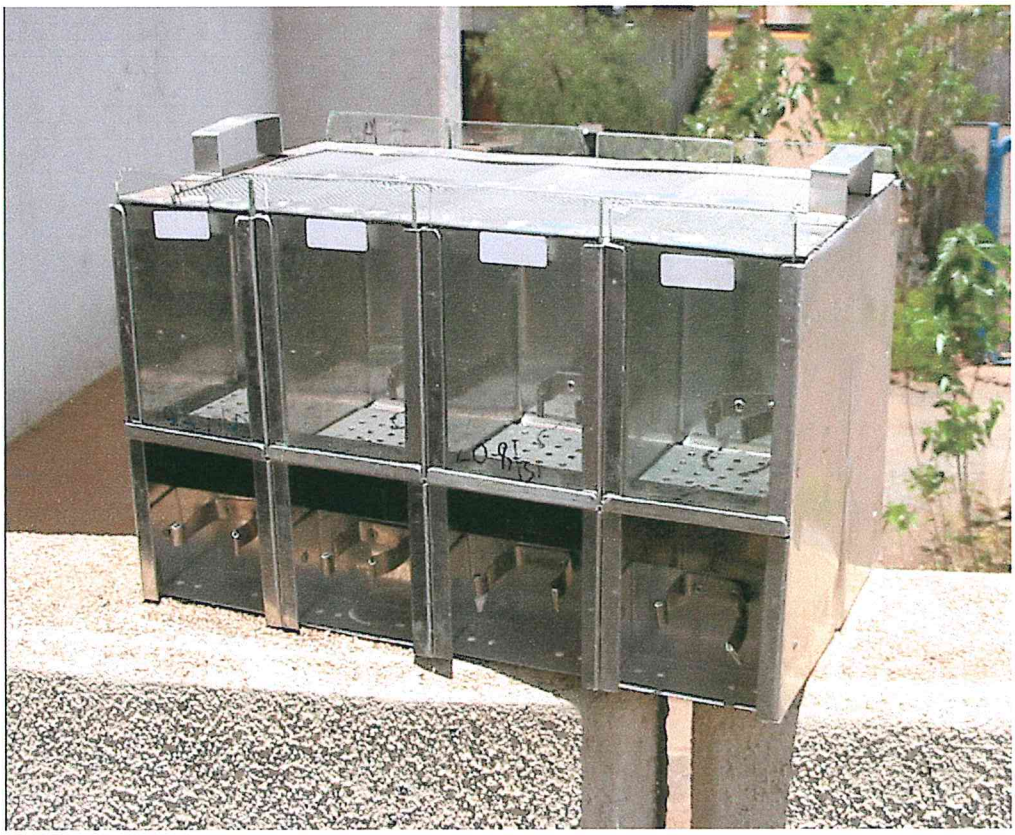


Plate 3. Rearing cage for solitarious desert locust

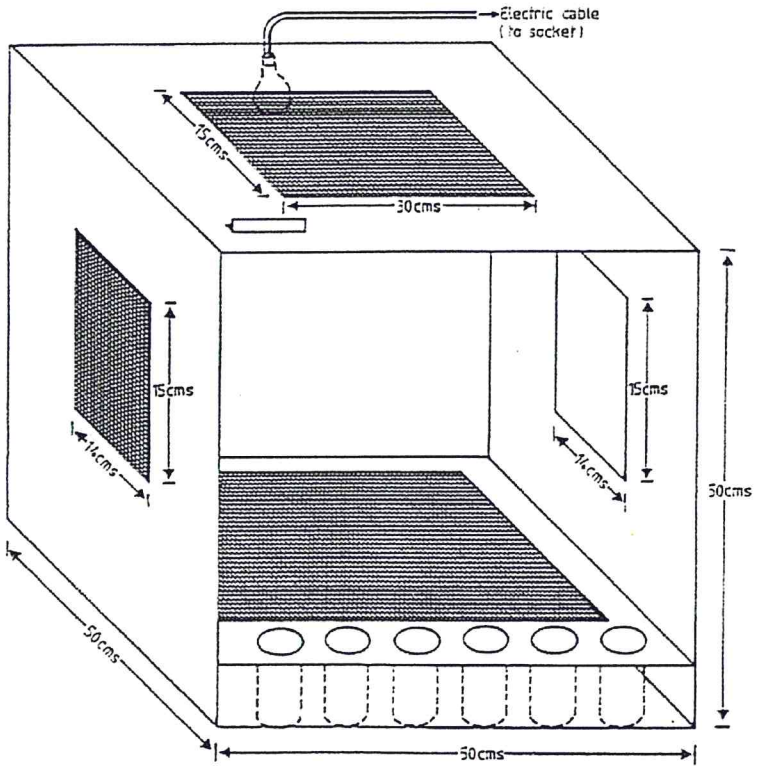


Figure 3. Diagram of standard cage for rearing gregarious desert locust

Plate 4. Rearing cage for gregarious desert locust

solitary-reared locusts that had been kept in the laboratory for 20 generations (equiv. 5 years at 4 generations each) and fed on a mixture of desert plants at the ICIPE field station, Port Sudan were used. Both groups of locusts were kept in a room maintained at the ambient temperature and humidity and a 12L: 12D reversed photoperiod.

For reproductive strategies in solitarious locusts, 24 virgin solitarious females were caught in November 1999, several days after the onset of rains in the Red sea costal plain of Handoub (19° 14'N / 037° 16'E), about 40 km south of Port Sudan. Another collection (24 solitarious females) was also done in the summer breeding area at Tahamyam (18° 22'N / 036° 35'E) about 300 km south west of Port Sudan and separated from the Red sea coastal plain by a belt of hills (Figs. 1 and 8).

3.2. EXPERIMENTAL CAGES

3.2.1. Flat-bed wind tunnel

The assays were performed in a plexiglas rectangular cage (180 cm x 45 cm x 25 cm). At one end of the wind tunnel was a small chamber (10 x 5 x 5 cm), for holding insects prior to release (Fig. 4, Plate 5A). In the upwind end, a small wire mesh box (10 x 10 x 5 cm) covered with black muslin cloth was placed for keeping the target insect. Air passed through an activated granular charcoal filter (4-14 mesh. Sigma Chemical Co. St Louis, USA) at the upwind end of the tunnel into the working area and was sucked out via a PVC duct by an extraction fan. The air speed inside the tunnel was 18-25 cm/s. Smoke was used to visualize the path of the odour plume through the tunnel. The floor of the wind tunnel was covered with hard grey manila paper that had seven equidistant (30 cm spacing) pen stripes marked to enable easy reading on the measurement of the overall movement of the test insect as well as the maximum distance traversed toward the source of stimuli.

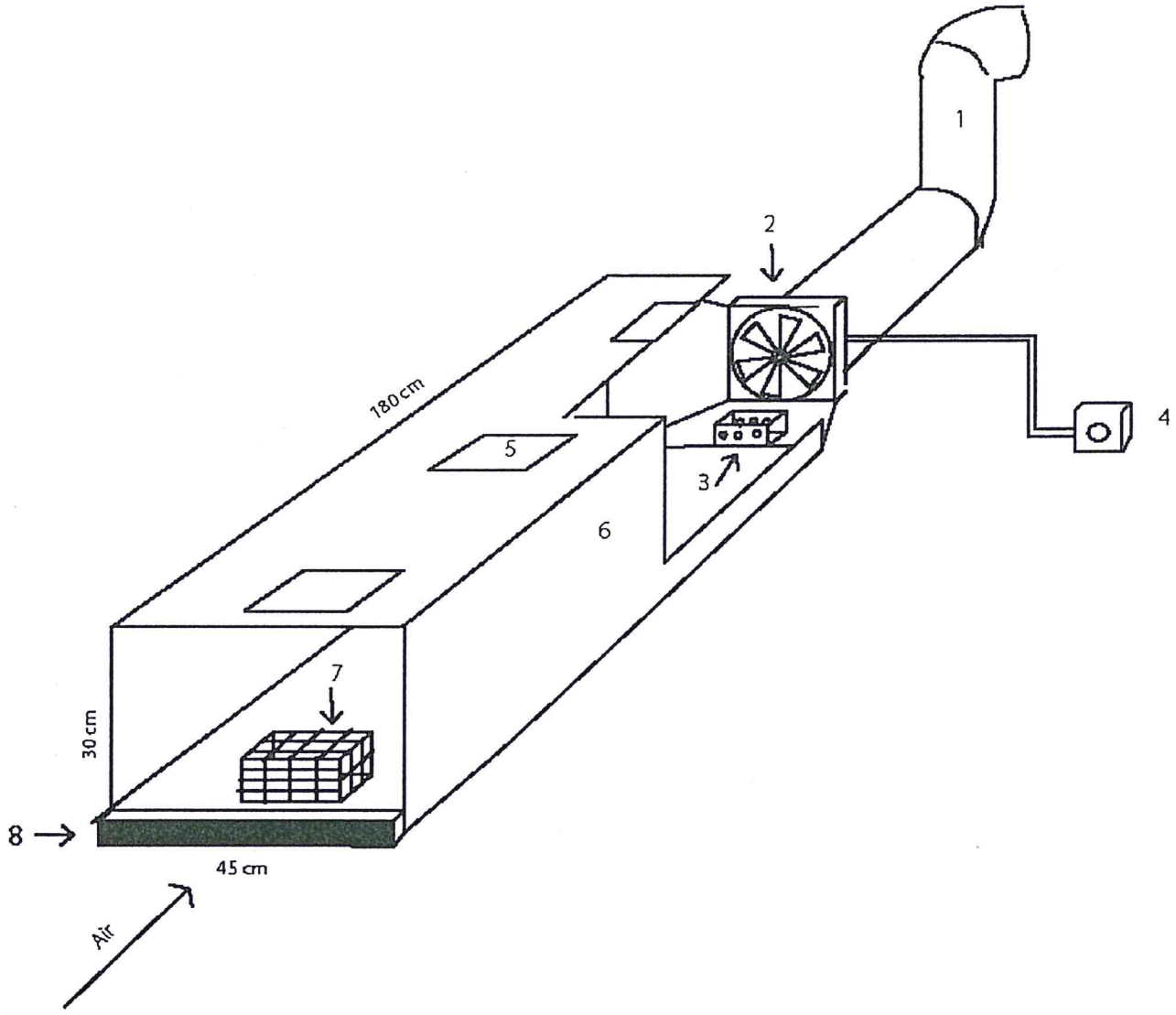


Figure 4. Flat-bed wind tunnel used for observations. 1. PVC air duct; 2. Exhaust fan; 3. Perforated cage for confining test insect; 4. Speed regulator for exhaust fan; 5. Ports for introduction and collection of insects; 6. Working area (plexiglass sides); 7. Wire mesh cage for holding insect used as cue, 8. Activated charcoal and gauze strip for air inlet.

3.2.2. Two-choice wind tunnel

The behaviour of locusts was observed in a rectangular flat-bed wind tunnel (110 × 40 × 40 cm) made of clear perspex (plexiglass) for easy observation and to minimize the tendency of insects to climb up the walls (Fig. 5, Plate 5B). The wind tunnel had two openings (15 cm × 15 cm) with covers on the top side for the placement or removal of locusts. At the bottom of each end, a rectangular opening (25 cm × 2 cm) which was covered with a black muslin cloth formed the air inlet. Air was drawn into the wind tunnel and cleaned using activated charcoal (granular, 4-14 mesh; Sigma Chemical Co.) filters that lined up the air inlets. Subsequent evacuation of the air was through a central port (10 cm × 2 cm) in the floor of the wind tunnel that was connected to an exhaust fan via a duct. The air speed recorded 1-2 cm above the floor of the wind tunnel during observations was 15-20 cm/s.

3.2.3. Oviposition-choice cage

The cages used for oviposition bioassays were made of aluminium (30 x 20 x 20 cm). The sides and roof including the door were made of wire mesh to ovoid accumulation of volatiles within the cage. Light was provided by two 60 W electric bulbs placed about 20 cm over each cage. The false floor in the middle had two egg-laying cups (8.5 cm dia., 9 cm deep) placed at distances of 20 cm from one other (Plate 6).

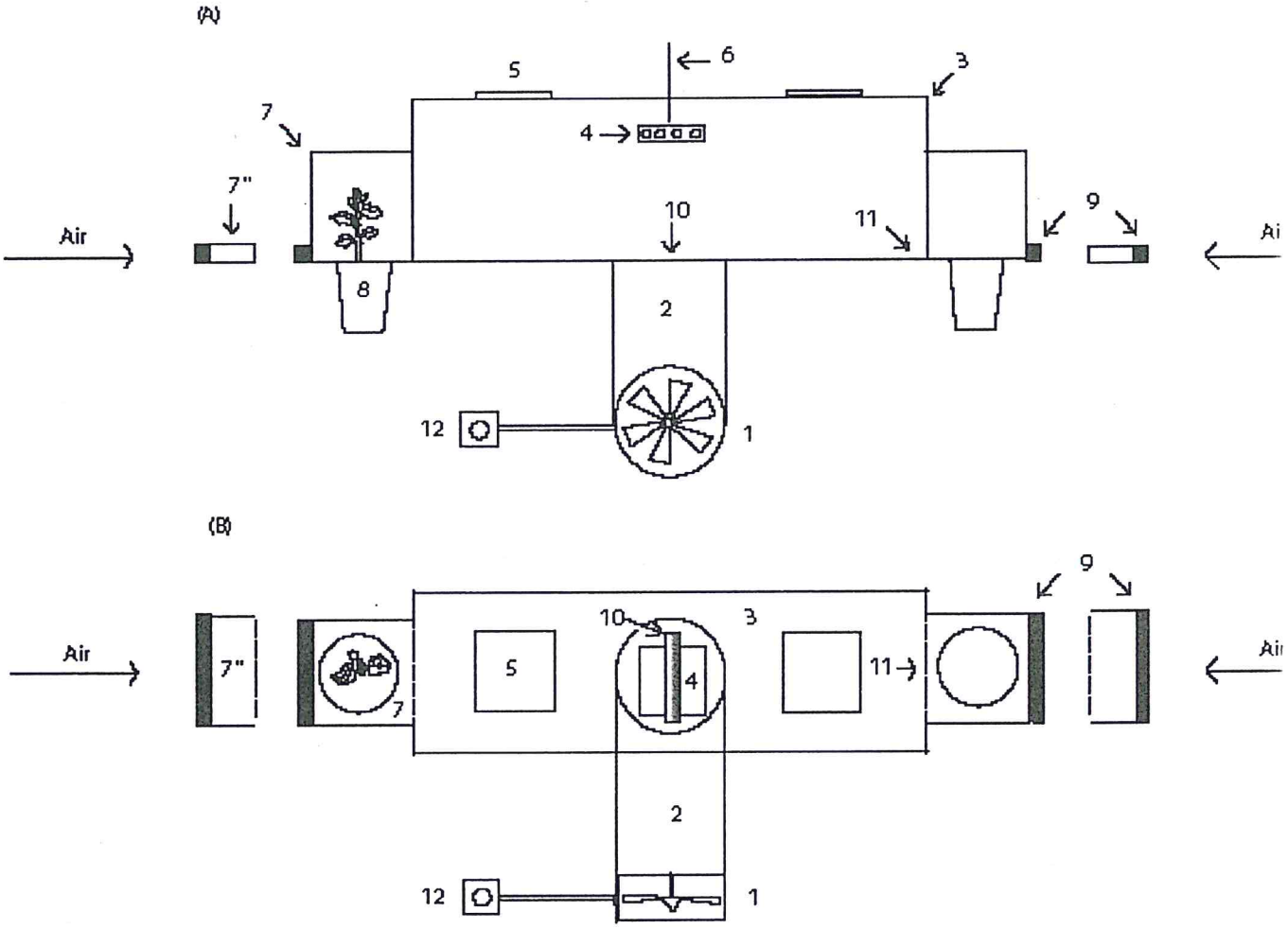


Figure 5. Two-choice wind tunnel used for testing locusts activity and attraction to plant volatiles. (A) side view of the full length and (B) Top view. 1. Exhaust fan; 2. PVC air duct; 3. Working area (transparent perpex); 4. Perforated holding box for test insects; 5. Doors for introduction and collection of insects; 6. Cord for pulling the insect holding box; 7. Chamber for plant material (used for plant odours attraction); 7". Empty chamber (used for locust activity); 8. Potted plant; 9. Net cloth for charcoal filter; 10. Port for air suction; 11. Netting for air inlet; 12. Speed controller for fan.

Plate 5. Flat-bed (A) and two-choice (B) wind tunnels (arrows)

Plate 6. Wire mesh oviposition cage (30 cm x 20 cm x 20 cm)

3.3. COLLECTION OF PLANT VOLATILES

3.3.1. Extraction of essential oils

To isolate sufficient volatile extracts for biological testing, large amounts of plant material (1.5 kg each for each sample of *Triticum aestivum* and *Heliotropium ovalifolium*) were macerated, then chopped, and placed in water (1-2 litres) in a five litre three-necked round-bottomed flask for boiling. Distillates were collected in high grade hexane (99.96%) adopting a simple method described by Likens and Nickerson (1964). This method is based on the principle that odorous compounds, e.g. terpenes and other essential oils are soluble in organic solvents but not in water. Both the steam distillate and the organic solvent condense on the cooling column and drop into the U-shaped Clevenger-type apparatus (Fig. 6, Plate 7). The hexane containing the volatile extracts is immiscible with water and so floats. The water was drained first and the extract collected in a vial.. The extract was then concentrated to 100 µl by using a Rotavapor (Büchi 461, water bath, Switzerland) (Fig. 7, Plate 8), the oil extract was stored at -15°C until use.

3.3.2. Emission of volatiles by plants

Volatiles emission from *H. ovalifolium* was monitored in the field (Salloum, southwest Port Sudan) using C_{18} adsorbent traps. C_{18} was first cleaned in an extraction Soxhlet for 4 days, the adsorbent was then activated in Nitrogen at a temperature of 60-80°C for 5-10 hours. Half gram of the C_{18} adsorbent was then packed in filter paper sachets that were then wrapped in wire gauze. A copper wire was then stapled together with the sachet.

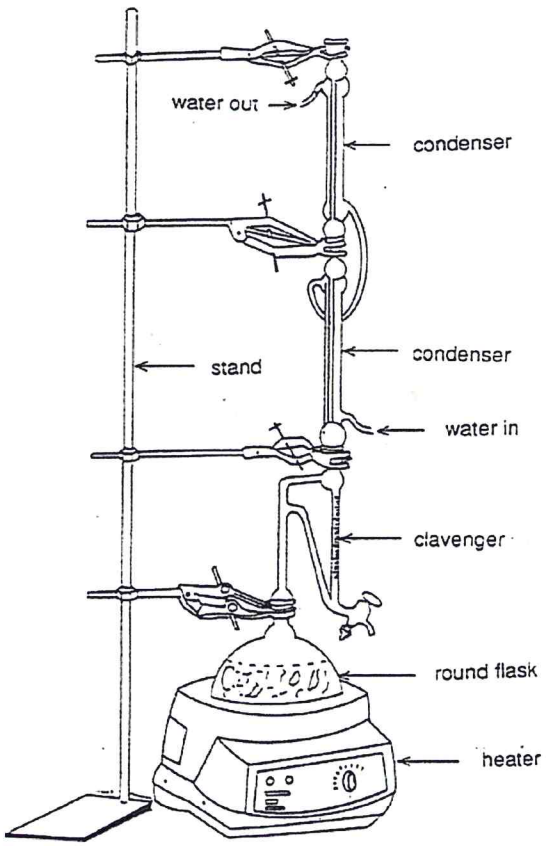


Figure 6. Steam distillation apparatus for collecting plant volatiles

Plate 7. Steam distillation set

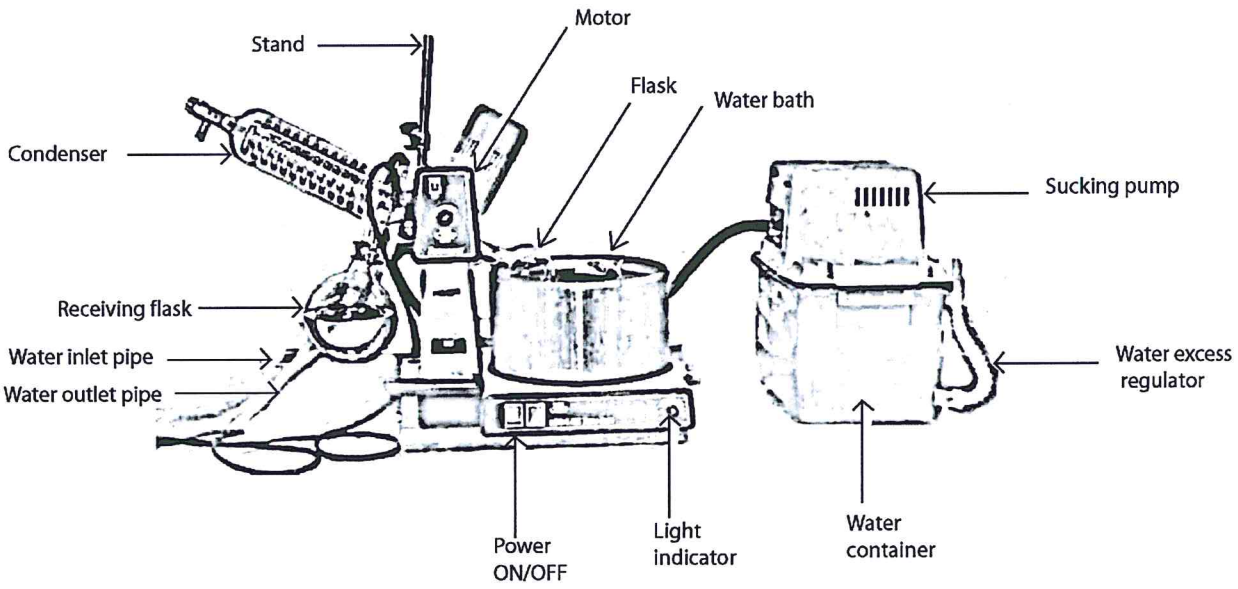


Figure 7. Schematic diagram of Rotavapor (Büchi 461, water bath, Switzerland)

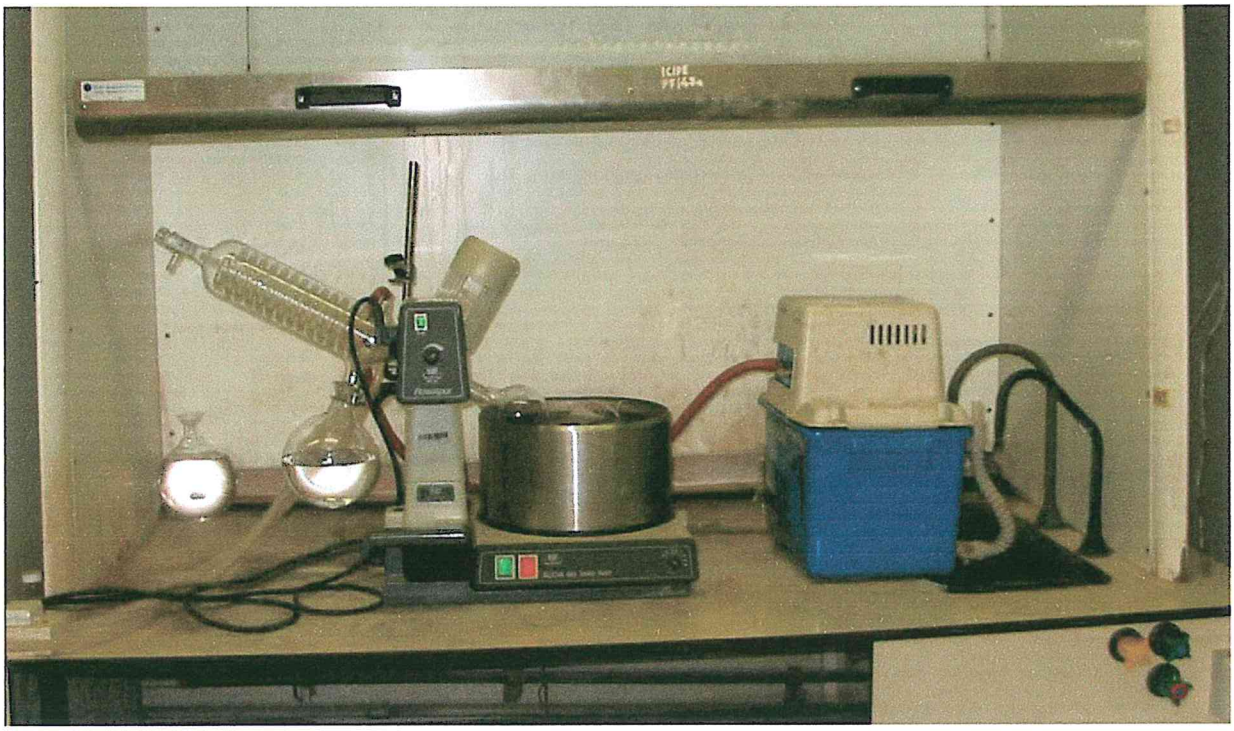


Plate 8. Rotavapor (Büchi 461, water bath, Switzerland)

The adsorbent traps were supported on the stem of the plant. During the day, trapping was done for 8 hours starting at 8:00 am to 4:00 pm while in the night it was from 8:00 pm to 4:00 am. Traps were then sealed separately in vials and stored at 0°C until use. The adsorbents were emptied in a Pasteur pipette and eluted with distilled Dichloromethane (5 ml per sachet). The eluate was concentrated to dryness using liquid nitrogen and then dissolved in 1 ml of dichloromethane to form the stock solution.

Volatiles were analyzed using methods previously described by Torto *et al.* (1994) by capillary gas chromatograph (GC). Aliquots (2 µl) of the extracts, were performed by GC performed on a Hewlett-Packard (HP) 5890 A Series II gas chromatograph (Plate 9) equipped with a flame ionization detector (FID) and a capillary column (Methyl silicone 20 M, 50 m x 0.2 mm ID x 0.2 µm) using nitrogen as the carrier gas at a flow rate of 0.35 ml/min. the oven temperature was initially isothermal at 60°C for 10 min, then temperatures programmed at 5°C/min to 180°C and from 180°C to 220°C at 10°C/min. Chromatographic peaks were integrated using a HP 3396 integrator.

3.4. EXPERIMENTS

3.4.1. Mate attraction in the solitarious and gregarizing desert locust, *Schistocerca gregaria* (Forskål)

3.4.1.1. Behavioural bioassays

The behavioural bioassays were performed in a flat-bed wind tunnel chamber in which insects were observed for their sex-attraction to their counterpart of opposite sex used as a signal source when (i) olfactory, (ii) olfactory and visual, were provided to the test insect. The test insect was

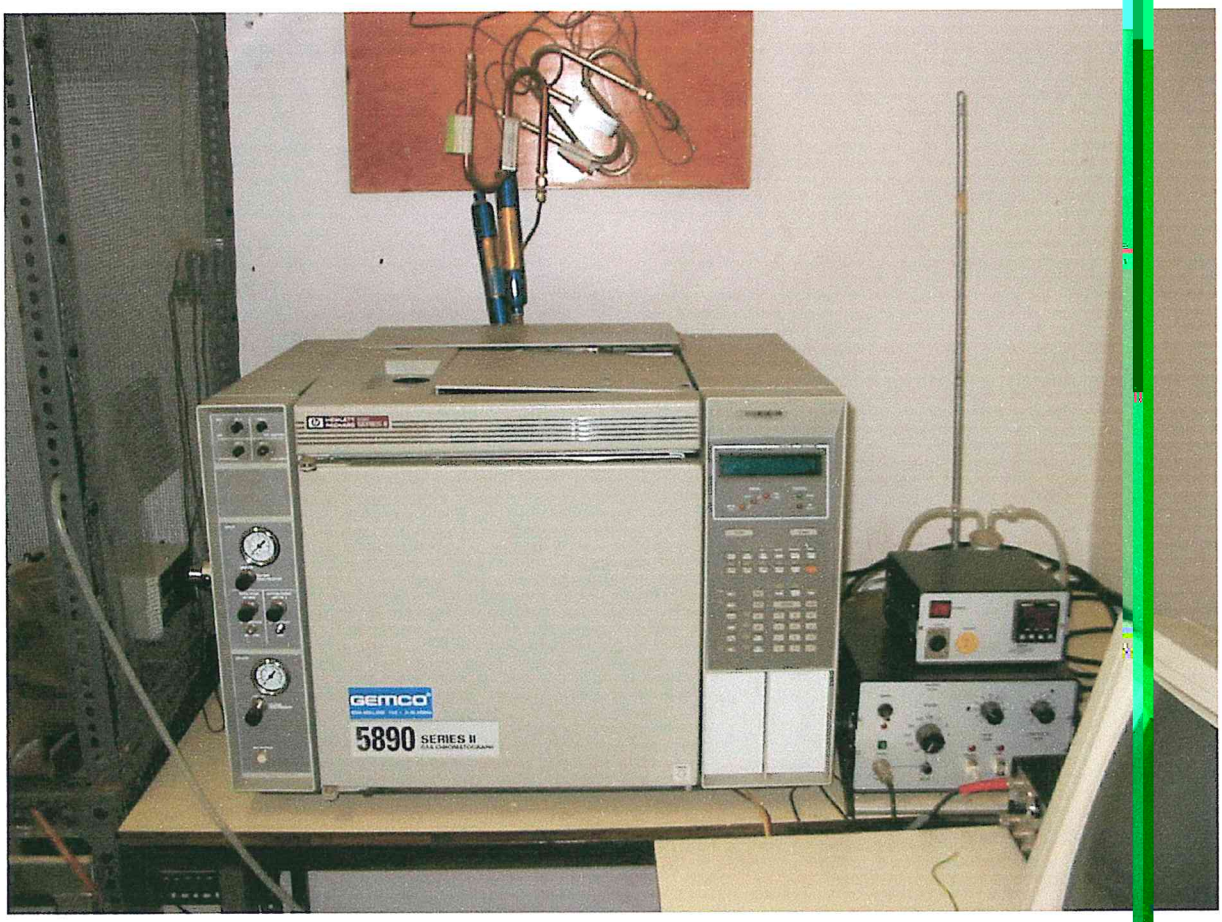


Plate 9. Hewlett-Packard 5890 A Series II gas chromatograph

held for 2-3 min in the holding cage to settle down and then released downwind into the main compartment by pulling up a small door. The target insect (stimulus source) was kept 150 cm away from the test insect in the small wire mesh box (10 x 10 x 5 cm) in the upwind end. For the control observations, no insect was kept in the signal source wire gauze box.

Preliminary observations showed that, most of the insect behaviour occurred within the first 30 min, after the release of the test insect. Various behaviours of each test insect were computed and data was recorded using The Observer Software (version 3.0 for Windows, Noldus Information Technology BV, Wageningen, The Netherlands).

A series of behavioural elements were recorded during the preliminary assays. However, four major behavioural elements were recorded as events and two postures as states that could reliably be observed and recorded in real time. The following behavioural parameters were used in the statistical analyses: nearest distance to the signal source position (distance traversed toward the upwind end), total distance covered by the test insect within 30 min, walking/running frequency, resting frequency (no movement, abdomen touching the floor), jumping or flying frequencies (or abortive flying as it could not be distinguished from one other due to short length of the wind tunnel), scanning (movement of the front part of body to either side in 4-6° according to Wallace (1959)).

3.4.1.2. Pre-rearing of test insects

Solitary-reared insects

During the last 24 days in the rearing of the solitarious insects, test insects were treated as follows:

(i) Insects kept for 24 days in isolation after fledging;

(ii) Insects kept isolated for 16 days after fledging, then grouped for 8 days.

(iii) Insects kept isolated for 8 days after fledging, then grouped for 16 days.

(iv) Insects grouped for 24 days after fledging.

Solitary-reared males were crowded in groups of 4 per cage and supplied with wheat (*Triticum aestivum*) seedling and bran. Solitary-reared females were also crowded in groups of 4 and in treatments (ii) and (iv) above. To gregarize solitarious females, four solitary-reared males were kept in the upper compartment of a bichamber cage (Plate 10) and 4 solitary-reared females in the lower chamber) thus providing olfactory and visual stimuli, but with no tactile contact.

Crowd-reared insects

Gregarious mature males and females that were 24-days-old were taken directly from insectary colony and used in the experiments.

3.4.1.3. Treatments

All insects used as test insects were 24-days-old (23-26 days-old) solitary-reared or gregarious insects. Treatments are summarized in Table 2 in which the sex and the pre-rearing conditions of the test insects were defined as well as the signal type and source provided. All target insects are solitary-reared males or females.

Plate 10. An aluminium bi-chamber bioassay cage for crowding solitary-reared insects. Upper (UC) and lower (LC) compartments, each 20 x 20 x 20 cm.

Table 2: Treatments performed in the flat-bed wind tunnel in studying mate attraction responses of mature solitary-reared, gregarizing and gregarious locusts to stimuli from their opposite sex of solitarious locusts.

Test insect	Pre-treatments condition	Signal source			Signal type	
		Male	female	none	olfactory	olfactory + visual
Solitary-reared male	isolated		x		x	
			x			x
				x		x
Sol. reared female	isolated	x			x	
		x				x
				x		x
Solitary-reared male	crowded 8 days		x		x	
			x			x
		x				x
			x			
				x		x
Solitary-reared male	crowded 16 days		x		x	
	crowded 24 days		x		x	
	crowded 24 days			x	x	
Solitary-reared female	crowded 16 days	x			x	
	crowded 24 days	x			x	
	crowded 24 days			x	x	
Gregarious male	crowded		x		x	
	crowded			x		
Gregarious female	crowded	x			x	
	crowded			x		

3.4.2. Diel behavioural activity patterns in adult solitarious desert locust, *Schistocerca gregaria*

Behavioural assays

Observations were carried out during daytime (10:00 am - 4:00 pm) and after sunset (6:30 - 11:00 pm) local time in Port Sudan. In experiments that were carried out in daytime, five 60 W-bulbs placed one meter directly above the wind tunnel illuminated the working section and there were no other sources of light in the room. An electric fan heater with a thermostat maintained the room temperature at a level similar to that recorded outdoors in sunshine (31.7 ± 3 °C) during the day, and 27.3 ± 1.2 °C at night. At the end of the day, the fan heater was switched off one hour earlier after opening windows of the bioassay room to allow for the equilibration of the indoor temperature with the one outside. Lights were also switched off and observations carried out with the aid of an Infrared viewing device (FJW Optical Systems Inc.; Find-R scope infrared viewing). An additional 5 W red lamp was placed over the wind tunnel to moderate the darkness in the room.

A solitarious male or female locust was held under a small perforated plexiglass cage (10 cm × 4 cm × 4 cm) that had no base placed over the wire mesh covering the central exhaust port on the floor of the tunnel (Fig. 5). The holding cage had a length of nylon string (4 mm thick) attached to the top and running through a small hole (5 mm diam.) in the top of the wind tunnel. The test insect was held under the cage for 2-3 minutes to settle down and the air evacuation system switched on prior to starting the observations. To release the insect, the holding cage was pulled up and secured using the nylon string and the locust was freed in the middle of the wind

tunnel to be observed. The following behaviours of each locust from the two groups were monitored by the same person over the subsequent 30 minutes:

1. Walking and the distance traversed - no attempt was made to evaluate the speed of the movement;
2. Resting - a locust did not change position for 5 seconds or more;
3. Taking off attempts – these were vigorous jumps that were presumed to represent onset of flight that was curtailed by the walls of the chamber; and
4. Scanning – movement of the front part of the body from side to side (≈ 4-6° displacement) with the body anchored by the abdominal tip (Wallace, 1959).

Where applicable, data was recorded as either the proportion of insects performing a given behaviour and/or the frequency of occurrence of the behaviour. Each locust was tested only once and 40 males and 40 females of each group were observed. Occurrence of the behaviours and their frequencies were recorded using "The Event Recorder of The Observer Software" (Noldus Information Technology BV. Version 3.0 for Windows, Wageningen, Netherlands). Temperature and relative humidity in the chamber were recorded before each observation and averaged 31.7 ± 3°C, 55.1 ± 1.5 % (RH) during the day and 27.3 ± 1.2 °C, 65.0 ± 3.9 % after dusk, respectively.

3.4.3 Host plant odour preference by solitarious desert locust, *Schistocerca gregaria* (Forskål)

Behavioural bioassays

EXPERIMENT I: Feeding preferences and consumption rate

In the feeding choice trial, three species of *Heliotropium*, two annuals (H. *ovalifolium, H. arabinensis*) and one perennial *(H. lignosum)* (Plate 11), were presented simultaneously to 20 insects (10 males and 10 females) previously collected from the field (Hoshery, Sudan). The genus *Heliotropium* is relatively common in the Red sea coast with several perennial and annual species (Hassan, 1974). To evaluate the amount plant material consumed, the same amount of each plant was given to insects that were kept individually. The weight of plant material before and after the experiment was compared and a correction of the loss of weight of food by evaporation was determined from a control batch of the same food kept under identical conditions (Davey, 1954; Karandikar, 1933; Nagy, 1952; Rao, 1960). Daily consumption as well as mean quantities eaten from each plant were then calculated after considering corrections for the evaporation loss.

EXPERIMENT II: Attraction to potted plants odours

This experiment was designed to assess how locusts collected from the field respond to volatiles emitted by *Heliotropim ovalifolium* and *Pennisetum typhoides* potted plants transplanted from the field (Plate 12). The protocol was the same as described in experiment I, however, insects were observed for 30 min and attraction to plant volatiles was monitored during the day and night time to determine whether the attraction varied with the time of day.

Heliotropuim arabinensis

H. ovalifolium

H. lignosum

Plate 11. Three main *Heliotropium* species growing in the Red sea coast (Salloum, Sudan)

EXPERIMENT III: Attraction to plant essential oil volatiles

This experiment was designed to assess how locusts respond to *Triticum aestivum*. and *Heliotropium ovalifolium* volatiles after being reared for many generations on *Triticum sp.* Essential oil extracts were obtained from *H. ovalifolium* (Boraginaceae), a dominant desert plant growing in the Red sea coast preferred by the desert locust, *Schistocerca gregaria,* in the field, and *T. aestivum* (Graminaceae), a cultivated plant used as diet for the rearing. Aliquots of 0.01, 0.1, and 1 µl of the essential oils were mixed with paraffin oil to moderate the release. Each was applied on a filter paper strip (1 x 2.5 cm) and used as source of stimuli in the wind tunnel. The test insects were previously deprived from food for 4 hours prior to the test and the behaviour of each was monitored in the wind tunnel for 10 min.

EXPERIMENT IV: Oviposition site

In this experiment oviposition behaviour of solitary-reared female locusts in presence of plant volatiles was investigated. Solitary-reared male and female locusts were paired in a cage for 24 h for mating and then the female was placed in an oviposition cage. The locust was exposed to different concentrations of *H. ovalifolium* volatiles. The volatiles crude extract were diluted with paraffin oil to moderate the release and delivered on strips of filter paper (1 x 2.5 cm) as described by Saini *et al.*, 1995. The treated filter paper strips were then placed into the moistened sand in egg-laying containers about 1 cm below the surface. Filter paper strips treated with similar amounts of paraffin oil were used as control (applied on clean moist sand). The stimulus sources were renewed every two days.

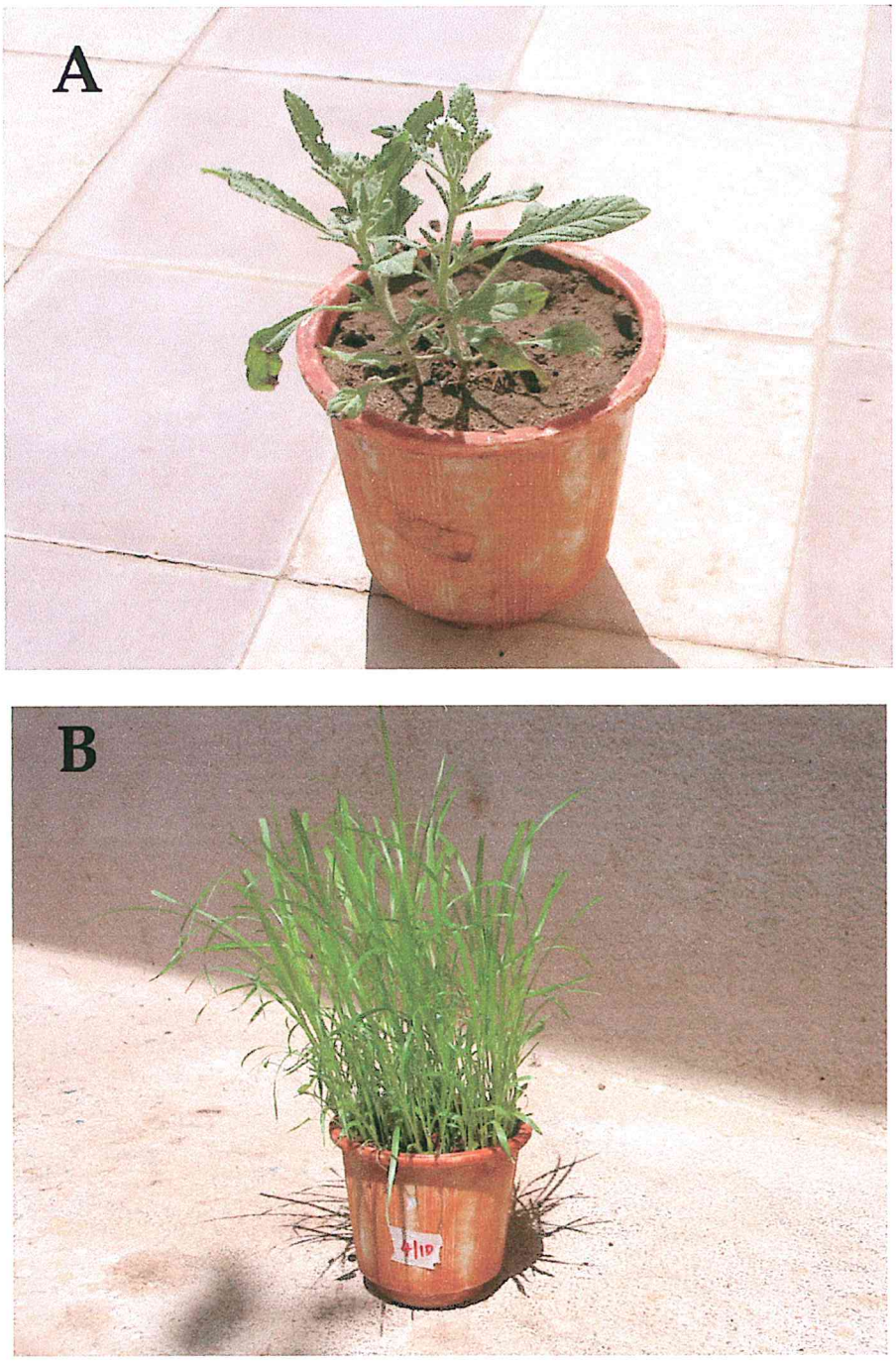


Plate 12. Potted *Heliotropium ovalifolium* (A) and *Pennisetum typhoides* (millet) (B) used in assays for plant volatiles attraction

The treated filter papers had 0.01, 0.1, 0.5, 2.5 and 5 µl of *H. ovalifolium* essential oils. Test and control egg-laying tubes were placed 30 cm apart. Oviposition was recorded by counting the total number of egg pods in both control and test cups containing plant volatiles. Locusts were provided with wheat seedlings and bran for food which were placed in the middle of the cage. This together with alternating the position of test and control egg-laying cups in serial test eliminated positional bias. All the behavioural bioassays were performed in a room at 30±2°C, 40-45% relative humidity and 12L:12D, photoperiod regime.

3.4.4. Some aspects of the reproductive strategy of solitarious female desert locust

In November 1999, 24 virgin solitarious females were caught 7-14 days after the onset of rains in the Red sea coastal plain of Handoub (19° 14'N / 037° 16'E), about 40 km south of Port Sudan (Fig. 8). This area is a winter breeding habitat where populations of solitarious desert locust are prevalent particularly in *wadis* (khors). In the Red sea coast areas, the important desert locust biotopes can be found principally within the *wadis* and the cropping areas (Voss and Dreiser., 1997). From our observations, it was noticed that locust density averaged 2 to 3 individuals per hectare. At the time, the area had received the first rains and only some perennials such as *Panicum turgidum*, *Capparis decidua* and *Suaeda fructicosa* sp. were the only vegetation visible, except perhaps for a few green *Acacia* and *Leptadenia* closer the hills.

Another collection (24 solitarious females) was also made in the summer breeding area at Tahamyam (18° 22'N / 036° 35'E) about 300 km south west of Port Sudan which is separated

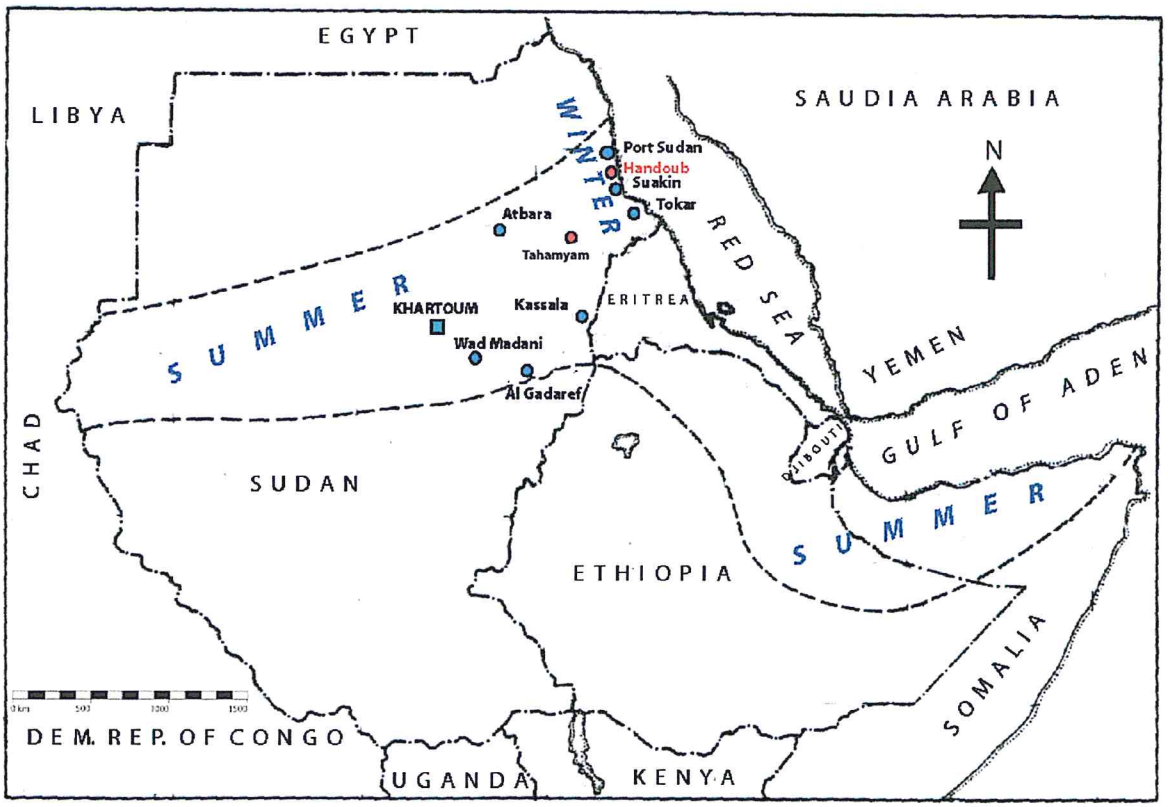


Figure 8. Summer and winter breeding habitats of the desert locust, *Schistocerca gregaria* Forskål

Locusts were collected at Handoub and Tahamyam (marked red) in the hinterland of Port Sudan.

from the Red sea coastal plain by a belt of hills (Fig. 8). In this area, the breeding season was ending and vegetation had started to senesce though there still was some green *Heliotropium sp.* and *Cassia italica* among unweeded millet and sorghum crops. Furthermore, most of the insects caught were mostly associated with *Heliotropium* bushes, but sometimes in open ground. The density was about 1 to 2 insects per hectare.

In the laboratory, females were kept separately in banks of eight aluminium cages (10 x 10 x 24 cm each). The top of each cage was made of wire screen for ventilation and the front was perspex for visibility. They were fed daily with different species of desert plants supplied with wheat bran. For monitoring oviposition, locusts were provided with standard egg-laying cups (9 cm long x 4.5 cm diameter) each filled with sterilized moist sand. The egg-laying was checked daily for each female and the cups were replaced with fresh ones. The egg pods were then incubated for the hatchability records. Oviposition by the two groups of locusts was monitored for about 5 months starting from early November till the end of March. This is usually the length of a period of a season of good rainfall in a full breeding season.

3.5. DATA ANALYSES

Data was analyzed using SAS (SAS Institute Inc., V8, 1987; Cary, North Carolina, USA). Mean distance traversed by test insects as well as behavioural frequencies recorded during observations were subjected to transformation to $\log_{10}(x+10)$ to stabilize the variance, and analyzed using analysis of variance (ANOVA) followed by Student-Newman-Keuls multiple range (SNK test) at $P < 0.05$ (PROC GLM, SAS, The SAS System, version 8.01). Means of percentage of test insects that reached the signal source were compared using Student's t-test.

Separation of means of the frequencies of the behaviours studied between the laboratory-reared and field-collected solitary locusts was carried out using Tukey's Honest Significant Difference (HSD) test for equal replications ($P = 0.05$). The Student's *t*-test was used to evaluate the difference between day and nocturnal activity while the χ^2 test was applied to determine the significance in proportion of insects taking off.

Responses of locusts to plant volatiles were analyzed using Student's t-test. Oviposition choice between treated and untreated sand were analyzed using χ^2 test. Difference between the mean distance traversed by insects towards the source of volatiles and the clean air side were analyzed using Signed Rank Test (Univariate procedure). ANOVA was also used for the separation of means of feeding preferences using LSD test at $p = 0.05$.

The proportions of gravid females at the beginning and at the end of the breeding season were analyzed using χ^2 test, whereas Student's *t*-test was used to evaluate the difference in the number of egg pods laid per female SAS (SAS Institute Inc., V8, 1987; Cary, North Carolina, USA).

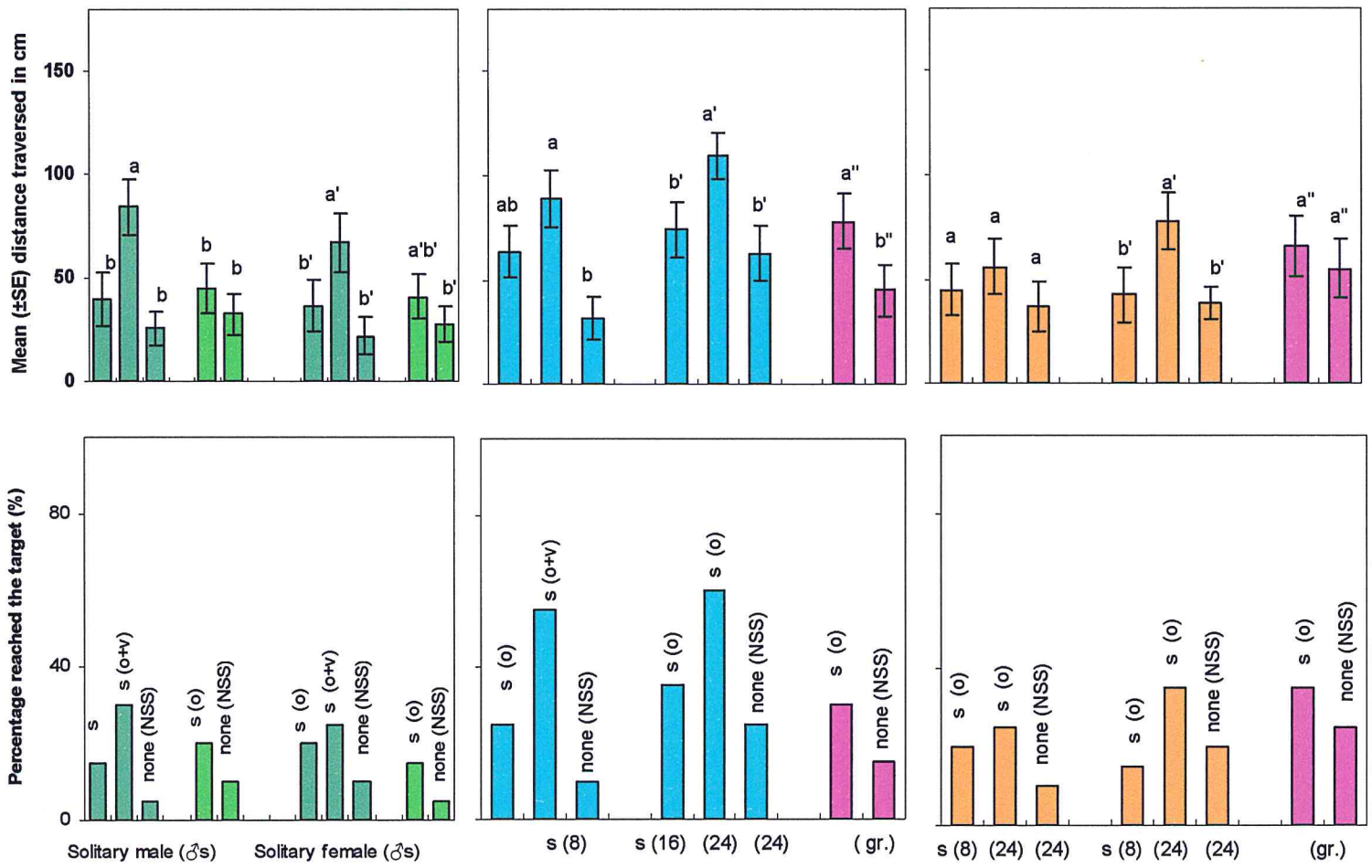
CHAPTER 4

RESULTS

4.1. Mate attraction in the solitarious and gregarizing desert locust, *Schistocerca gregaria* (Forskål)

4.1.1. Behaviour of solitary-reared insects

When only olfactory signal was provided to the test insect, solitary-reared males and females released downwind responded more or less to the signal source (opposite sex kept upwind) but not significant when compared to the control (no target insect kept in the wire mesh box) despite that they traversed more distance (Fig. 9-A1, B1), no significant number of both solitary-reared males ($t = -1.20$, $df = 38$, $p > 0.05$) and females ($t = -0.38$, $df = 38$, $p > 0.05$) reached the signal compared to the control when no opposite sex was kept in the target insect box (Fig. 9-B1). However, when visual cue were provided in addition to the olfactory one, test insects responded more significantly, particularly the males which traversed more distance toward the signal source (Figs. 9-A1). Furthermore, significantly more the solitary-reared males reached the signal source ($t = 2.56$, $df = 38$, $p < 0.05$) compared to the control (Fig. 9-B1; Table 3, see appendices 41-42) whereas the number of solitary-reared females that reached the target was not significant ($t = 1.20$, $df = 38$, $p > 0.05$) (Fig. 9-B1; Table 3, see appendices 41-42). In addition, significantly more behaviour such as walking/running, scanning and jumping were more frequent in test insects of both sexes particularly when olfactory and visual signals were provided (Fig. 10-A).



Test insects

Figure 9. (A): Mean (±SE) distance traversed toward the signal source; (B): Percentage of test insects that reached the signal source after 30 min. ♂s (8): solitary male crowded 8 days; ♂s (16): solitary male crowded 16 days; ♂s (24): solitary male crowded 24 days; ♀s (8), solitary female crowded 8 days; ♀s (24): solitary male crowded 24 days; ♂ (greg.): gregarious male; ♀ (greg.): gregarious female; o: olfactory signal, v: visual signal; NSS: no stimulus; Columns with the same letter are not significantly different at $p < 0.05$ (SNK test).

(see appendices (1-8).

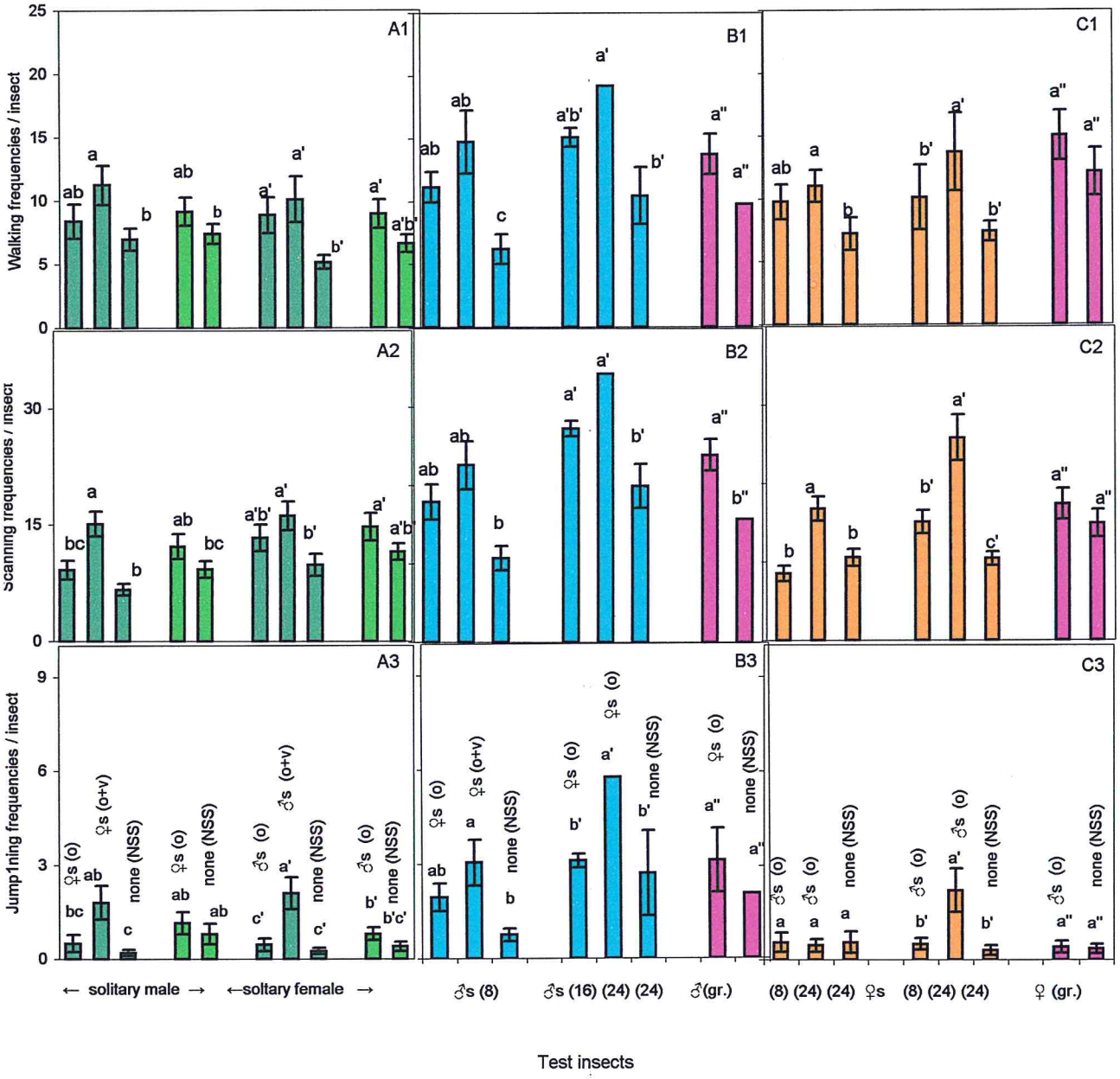


Figure 10. Comparison of behavioural frequencies of test solitarious locusts in presence and absence of their opposite sex: (A), solitary-reared insects. (B), gregarizing and gregarious males. (C), gregarizing and gregarious females. Columns with the same letter are not significantly different at $p<0.05$ (SNK test). (see appendices 9-32).

Table 3: Behaviour of the test insects on approaching the target insect in the wire mesh box. Initial position of the test insect: 150 cm away. Observation time: 30 min. ♂s, solitary-reared male; ♀s, solitary-reared female; ♂s (8), SM crowded for 8 days; O, olfactory signal; V, visual signal.

Test Insect	Signal source	Signal type	% traversed ≥ 100 cm	Numbers that reached the target	Numbers tested
	♀s	O	4	3	20
♂s	♀s	O+V	11	6	20
	None	NSS	3	1	20
	♂s	O	4	4	20
♀s	♂s	O+V	9	5	20
	None	NSS	2	2	20
	♀s	O	7	5	20
♂s (8)	♀s	O+V	19	11	20
	None	NSS	4	2	20

NSS: No stimulus

Furthermore, significant number of solitary-reared males traversed at least 100 cm toward the solitary-reared female when olfactory and visual cues provided ($t = -2.45$, $df = 38$, $p < 0.05$ compared to the treatment when only olfactory cue was provided and $t = -2.45$, $df = 38$, $p < 0.05$ compared to th treatment when no signal was provided) (Table 3, see appendices 41-42). Extra observations showed that from close distance (30 cm instead of 150 cm), a significant proportion of males ($t = 2.75$, $df = 3$ $p < 0.05$) reached the target insect's box when a solitary reared female was kept in and olfactory and visual cue provided for the test insect (Table 4, see appendices 41-42). However, this was not the cas using solitary-reared females as test insects ($t = 1.15$, $df = 38$, $p > 0.05$).

On the other hand, no significant difference related to preference between daytime and night concerning the attraction of solitary-reared insects to the signal source (Fig. 9-A1, B1).

Furthermore, the proportion of the test insects that reached the signal source between daytime and night was not significant ($t = -0.21$, $df = 38$, $p > 0.05$ for males and $t = -0.15$, $df = 38$, $p > 0.05$ for females)

4.1.2. Behaviour of gregarizing insects

Gregarizing males, particularly the ones crowded for 24 days showed significant attraction to solitary-reared females when only olfactory cue provided (Fig 9-A2,B2). They traversed a mean distance of 110 cm towards the signal source at 150 cm upwind. Furthermore, but not significant ($t = 1.96$, $df = 38$, $p > 0.05$) number of them reached the target insect (Fig. 10-B2).

On the other hand, solitary-reared males crowded for 8 days which were subjected to more investigation showed significant attraction to solitary reared females with only olfactory cue provided (Fig. 9-A2) but no significant ($t = 1.20$, $df = 38$, $p > 0.05$) proportion reached the signal source. Meanwhile, when both olfactory and visual signals were provided, they traversed

Table 4: Behaviour of the tests insects on approaching the target insect in the wire mesh box. Initial position of the test insect: 30 cm away. Observation time: 15 min. ♂s, solitary-reared male; ♀s, solitary-reared female; ♂s (8), ♂s crowded for 8 days; O, olfactory signal; V, visual signal.

Test Insect	Signal source	Signal type	Numbers that reached the target	Numbers tested
SM	♀s	O+V	6	10
	None	NSS	1	10
♀s	SM	O+V	3	10
	None	NSS	1	10

NSS; No stimulus

a significant distance towards the signal source at 150 cm (Fig. 9-A2). Furthermore, significant number reached the signal source compared to the control ($t = 2.68$, $df = 38$, $p < 0.05$) and when only olfactory cue was provided ($t = -2.24$, $df = 38$, $p < 0.05$).

On the other hand, females respectively crowded for 8 and 24 days did not gregarize and behaved similarly to solitary-reared ones (Fig. 9-A3, B3) and there was no significant difference ($t = 1.20$, $df = 38$, $p > 0.05$) in individuals that reached the signal source (solitary-reared male). However, when solitary-reared females were crowded together with solitary-reared males with no tactile contact (pre-exposition during rearing, see materials and methods for details), the females that were crowded from fledging for 24 days were significantly more attracted to the signal source and traversed significant distance (Fig. 9-A3, B3). However, no significant difference ($t = 1.01$, $df = 38$, $p > 0.05$) was found when comparing the number of individuals that reached the signal source (Fig. 10-C), but their activity seemed to be affected by their pre-exposition to the gregarizing males as they jumped and scanned the field more compared to the females which were exposed for shorter time (8 days) or the ones that were not pre-exposed to males (Fig. 10-C).

4.1.3. Behaviour of crowd-reared (gregarious) insects

Only gregarious males showed significant attraction to solitary-reared females when olfactory stimulus was provided, traversing longer distance compared to the control when no female was kept upwind (Fig. 9-C,D). However, the number of individuals that reached the signal source was not significant ($t = 0.14$, $df = 38$, $p > 0.05$). On the other hand, gregarious females did not show significant attraction to solitary-reared males kept upwind (Fig. 9-E,F). and the proportion that reached the target was not significant ($t = 0.13$, $df = 38$, $p > 0.05$) compared to the control.

4.2. Diel behavioural activity patterns in adult solitarious desert locust, *Schistocerca gregaria*

4.2.1. Behaviour of solitarious locusts from the field (FCI)

Solitarious locusts that had been caught from the field and kept under laboratory conditions for a week were more active after dusk than during the day or in later hours of the night. There was a considerable increase in the frequency of walking for both male and female locusts within the first two hours after sunset and a subsequent decline in the activity of the insects (Fig. 11-A,B). After dusk, locusts walked significantly more ($t = -5.82$, $df = 78$, $P < 0.0001$ for males; $t = -6.00$, $df = 78$, $P < 0.0001$ for females) than those observed during the day. In daytime, most of the insects remained static or executed very limited movement (Fig. 11-A,B; Table 5). This was also reflected by the distance traversed by the insects which was highly significant (Student-Newman-Keuls multiple range test, $P = 0.05$) after dusk than in daytime (Fig. 14).

Similar day and night patterns were recorded with regard to the frequency of the attempts to take off ($t = -3.60$, $df = 78$, $P < 0.0001$ for males; $t = -1.64$, $df = 78$, $P = 0.104$ for females) (Fig. 12-A,B; Table 5) and scanning ($t = -5.19$, $df = 78$, $P < 0.0001$ for males; $t = -5.22$, $df = 78$, $P < 0.0001$ for females) (Fig.13-A,B; Table 5). However, there was a notable difference between male and female locusts with the males having significantly higher (Tukey's test, $P = 0.05$) take-off frequency than the females at night. Furthermore, *ca.* 74% of the locusts attempted to take off within the first 5 minutes of the 30 min observation period after dusk. This was significantly higher ($\chi^2 = 30.66$, $P < 0.0001$) in the night than in daytime, during which only 30% of the insects made the attempts over a similar period.

On the other hand, some locusts did not attempt to take off at all during the observation period. Only 12.5 % of the insects failed to take off during night observations while a significantly higher ($\chi^2 = 16.82$; $p < 0.0001$) proportion (≈ 41 %) was recorded during daytime (Fig.15).

4.2.2. Comparative behaviour of laboratory-reared insects (LRI)

Solitarious locusts that had been kept in our laboratory's rearing unit for 20 generations had similar behavioural patterns to those of locusts collected from the field but the activity levels were much lower. In addition, the behavioural patterns of male and female laboratory-reared insects in daytime and after dusk were very similar (Figs. 11, 12 and 13).

Frequencies of the behaviours monitored and the distance moved were significantly higher after dusk (especially in the first two hours after sunset) than during daytime: walking ($t = -5.12$, $df = 78$, $P < 0.0001$ for males; $t = -6.51$, $df = 78$, $P < 0.0001$ for females) (Figs. 11-C,D; Table 5), take-off attempts ($t = -2.21$, $df = 78$, $P = 0.03$ for males; $t = -4.05$, $df = 78$, $P < 0.0001$ for females) (Figs. 12-C,D; Table 5), and scanning ($t = -9.56$, $df = 78$, $P < 0.0001$ for males; $t = -11.37$, $df = 78$, $P < 0.0001$ for females) (Figs. 13-C,D; Table 5). The locusts also traversed significantly longer distances after dusk (Student-Neuman Kuels multiple range test, $P = 0.05$) (Fig. 14). Correspondingly, a significantly higher ($\chi^2 = 28.6$; $P < 0.0001$) proportion ($\approx$ 54%) of the locusts attempted to take off in the first five minutes of the observation period compared to 14% in daytime. Also, throughout the observation period 52% of the locusts did not take off during the day while it was only 20% (significant, $\chi^2 = 8.35$; $P \leq 0.01$) after dusk (Fig. 15).

The overall means of frequencies of the various behaviours and the distance moved by solitarious locusts in the two groups are presented in Table 5. Although, the behavioural patterns were similar, male and female locusts caught from the field (FCI) were significantly more active.

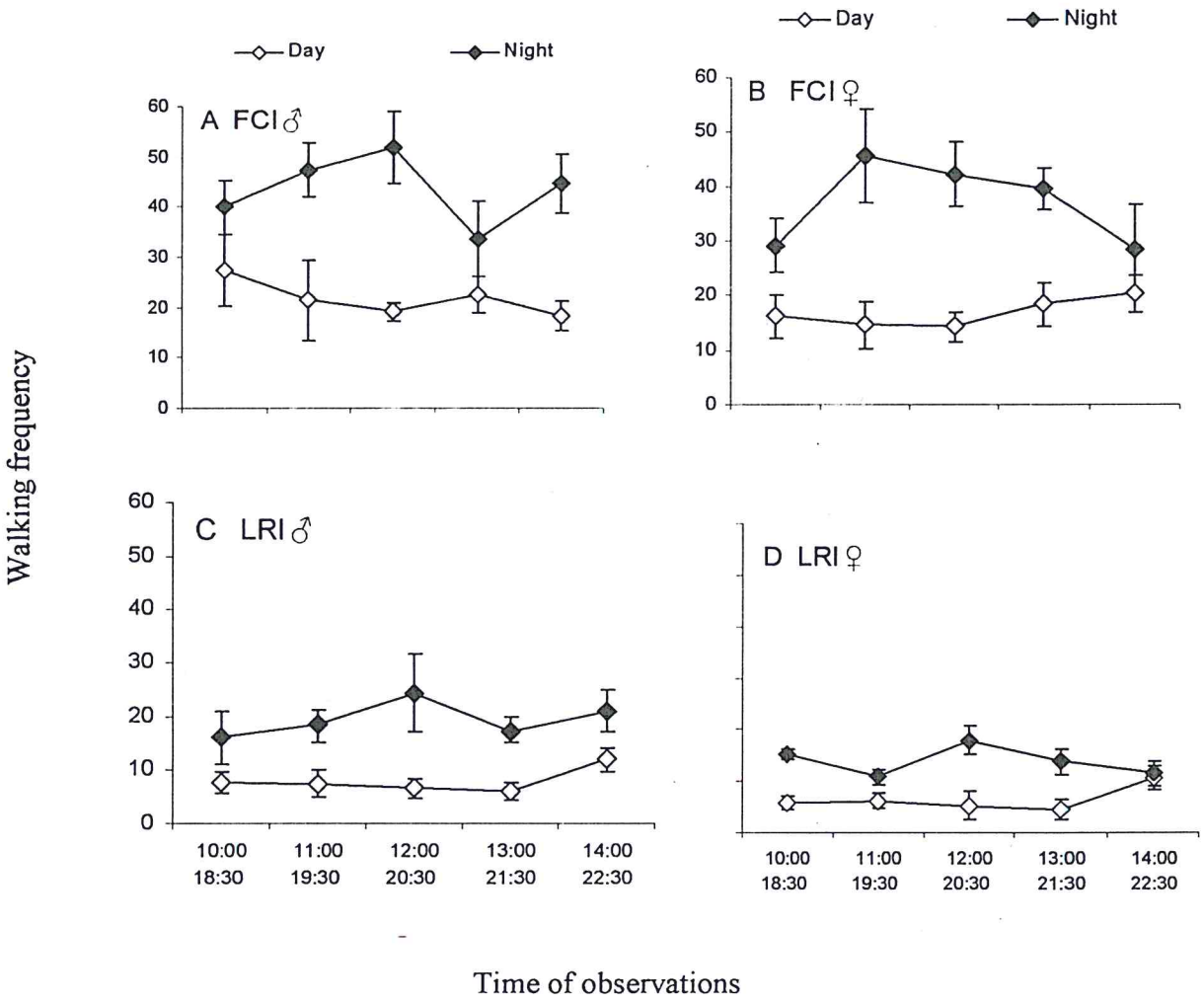


Figure 11. Proportion of locusts walking: Field-collected insects (FCI) males (A) and females (B). laboratory-reared insects (LRI) males (C) and females (D). Bars are standard errors (±SE); N = 40 insects each observed for 30 min for each point.

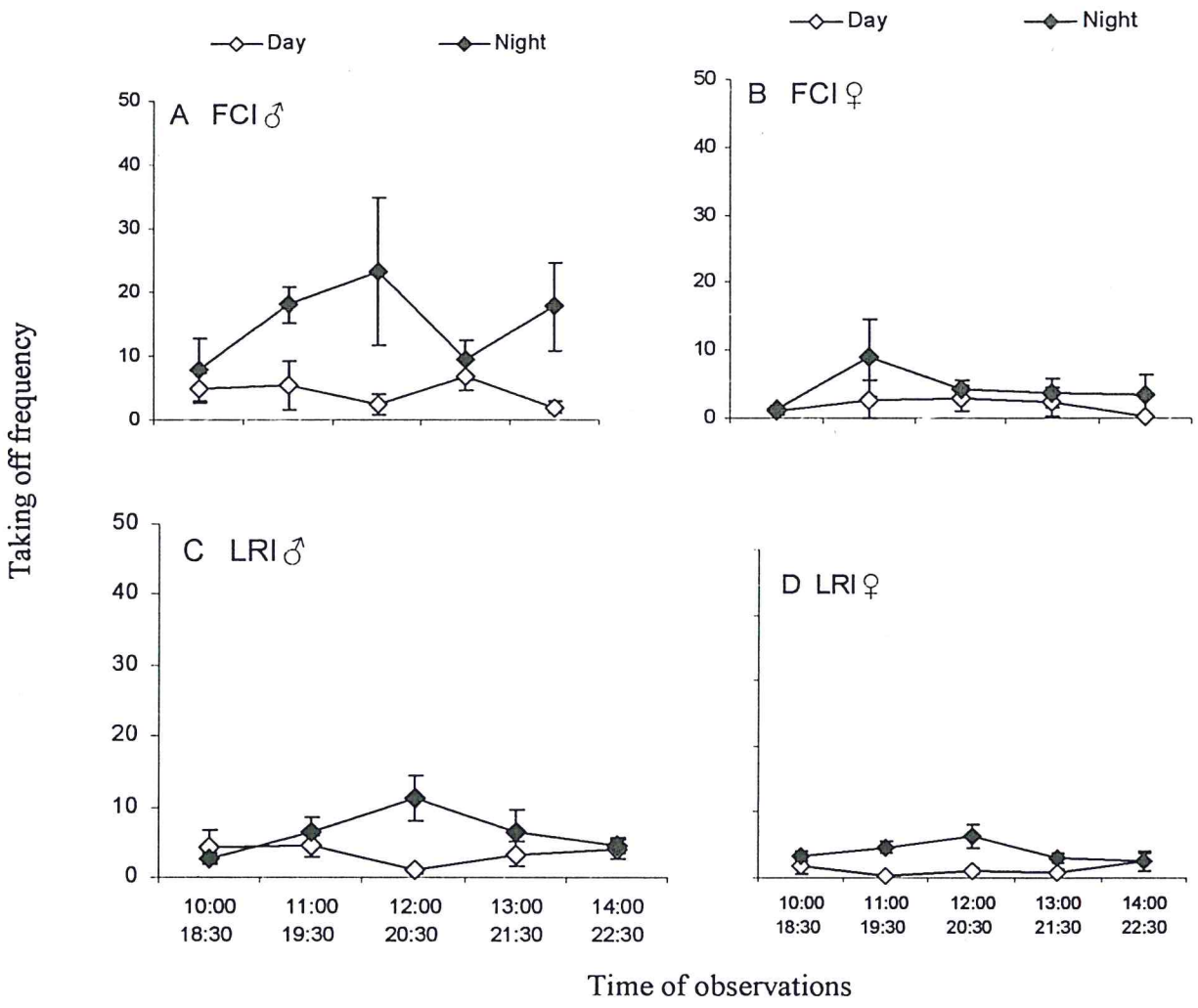


Figure 12. Frequency of take-off by the locusts: Field-collected insects (FCI) males (A) and females (B), laboratory-reared insects (LRI) males (C) and females (D). Bars are standard errors (±SE); N = 40 insects each observed for 30 min for each point.

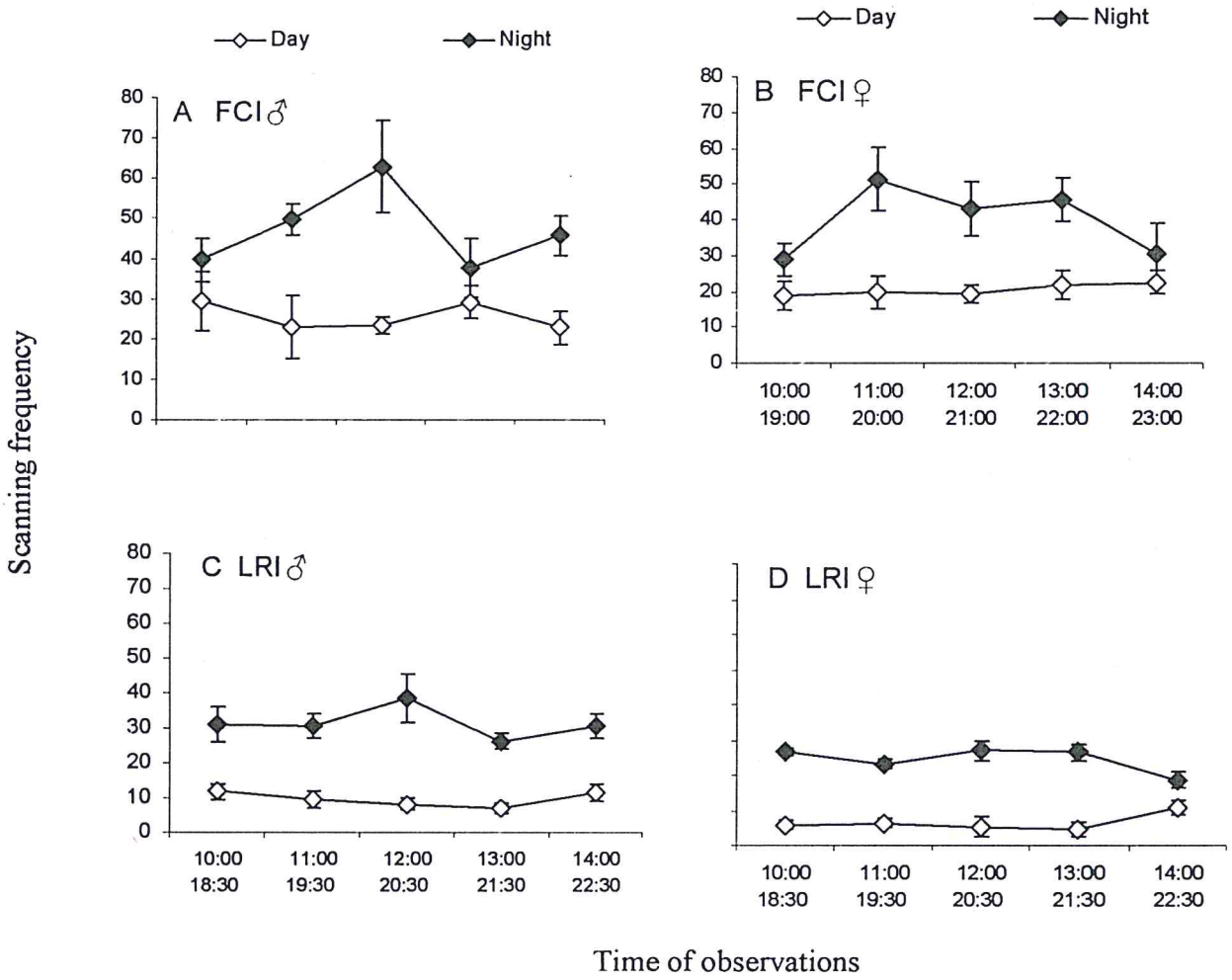


Figure 13. Proportion of locusts scanning: Field-collected insects (FCI) males (A) and females(B), laboratory-reared (LRI) males (C) and females (D). Bars are standard errors (±SE); N = 40 insect each observed for 30 min for each point.

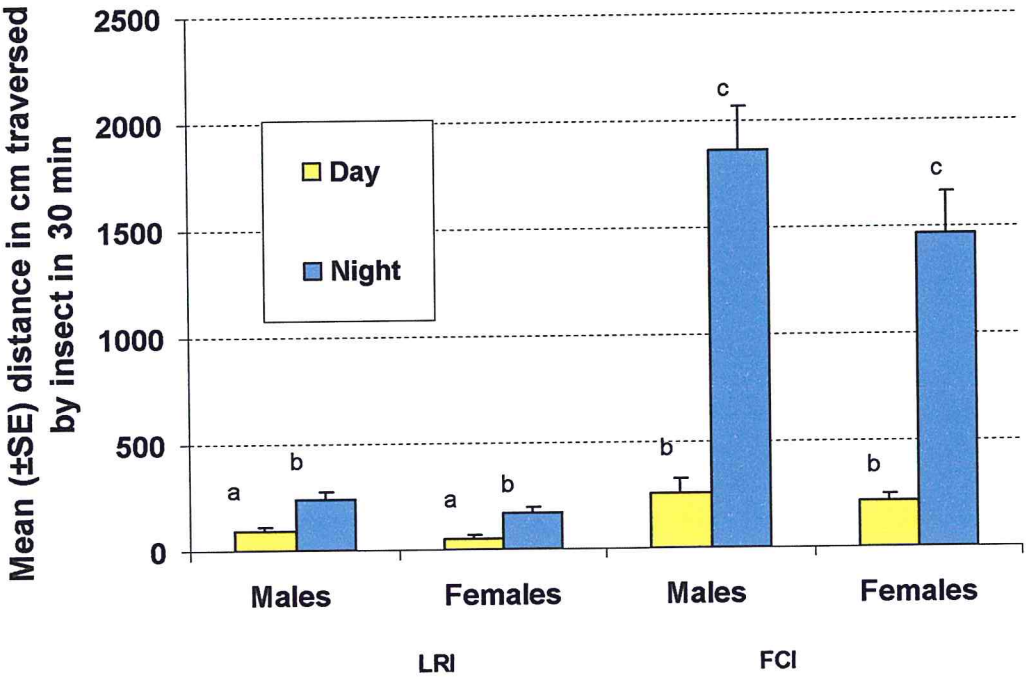


Figure 14. Mean distance traversed by locusts during the 30 min observation period. Means (± SE) marked with different letters are significantly different ($P = 0.05$, SNK test; df = 78, see appendix 39). LRI, laboratory-reared insects; FCI, insects collected from the field.

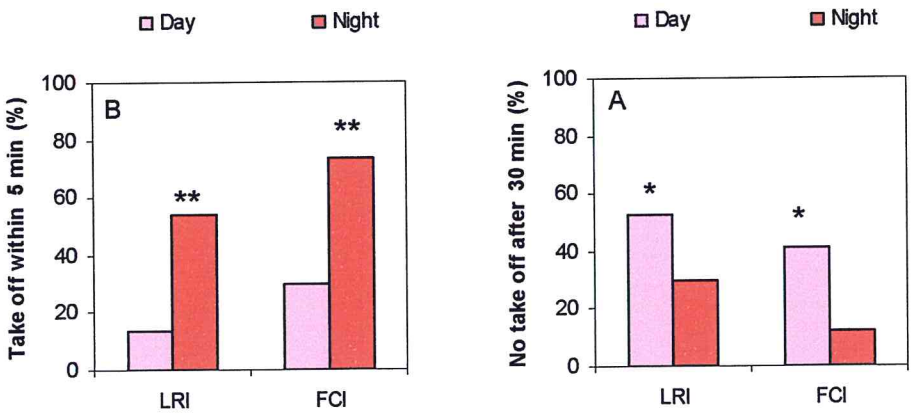


Figure 15. (A) Proportion of insects that did not take off during the observation period and (B) those that took off within the first 5 min of observation. LRI, laboratory-reared insects; FCI, field-collected insects. Differences significant, χ^2 test); *P $\leq$ 0.05, **P $<$ 0.001

Table 5: Comparison of overall mean (±SE) frequencies of walking, scanning, and take-off per insect for locusts caught from field (FCI) and those from the laboratory (LRI) in daytime and after dusk. N = 40 insects for each point.

Locusts	Sex	Behavioural activity (frequency of occurrence/insect)[x]					
		Walking		Take-off		Scanning	
		Day	Night[y]	Day	Night[y]	Day	Night[y]
FCI	Males	21.8±2.3[a]	43.3±2.9[a] *	4.5±1.1[c]	15.3±2.8[c] *	25.7±2.4[e]	47.5±3.4[f] *
	Females	16.9±1.5[a]	37.3±3.0a *	1.8±0.7[d]	4.4±1.4[d] ns	20.5±1.6[e]	39.9±3.4[ef] *
LRI	Males	7.9±1.0[b]	19.6±2.1[b] *	3.5±0.7[cd]	6.4±1.1[d] *	9.7±1.0[g]	31.7±2.1[eg] *
	Females	5.4±0.8[b]	14.1±1.0[b] *	1.3±0.4[d]	4.1±0.6[d] *	6.6±0.8[g]	24.2±1.3[g] *

[x] Means with the same superscript letter in each column for each behaviour are not significantly different (Tukeys' test, p = 0.05, see appendices 33-38).

[y] Difference between daytime and night activity for each sex in a group of locusts: *, significant; ns, not significant (Student's test, $p < 0.0001$)

4.3. Host plant odour preference by solitarious desert locust, *Schistocerca gregaria* (Forskål)

4.3.1. Feeding preferences of field-collected insects among Heliotropium *species (EXPERIMENT I)*

Figure 16 shows that *Heliotropium* annual plants were more preferred than the perennial ones. *H. ovalifolium* and *H. arabinensis* were eaten in approximately the same amount. The feeding behaviour of insects was such that there was a balance between the two plants through feeding alternately between them. This behaviour was observed in both males (Fig. 16A) and females (Fig. 16B).

On the other hand, no significant difference (LSD test at $p = 0.05$) was found between the amounts consumed from the two plants. However, these amounts were significantly more than the amount taken from the perennial *H. lignosum* (Fig. 17) which seemed to be rejected and the mean amount consumed likely occurred after the plant dried up before the food was renewed after every 24 h. However, when leaves of *H. lignosum* were grinded and then applied on filter paper (Watman no. 1) disks and given to the insects with untreated filter papers as control; 2/3 of the disk containing the plant extract were consumed while less than 1/3 of the untreated filter paper disk was consumed (Attiyat, unpublished data).

4.3.2. Response of the field-collected solitarious locusts to Pennisetum typhoides *and* Heliotropium ovalifolium *volatiles (EXPERIMENT II)*

Field-collected insects were significantly ($P < 0.0001$) more attracted to volatiles from the

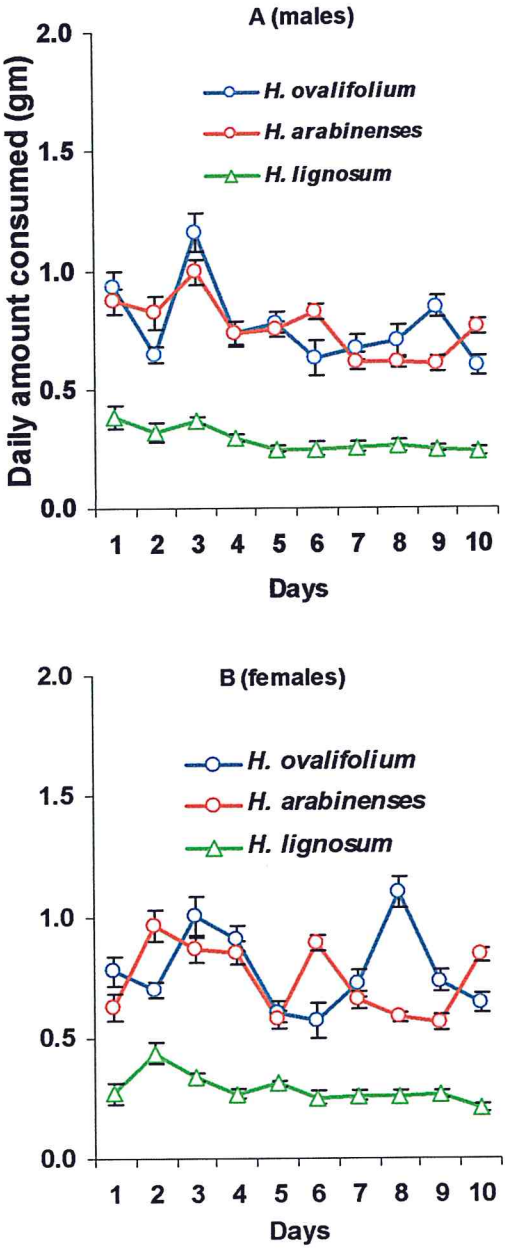


Figure 16. Feeding preferences of field-collected solitarious males (A) and females (B) on three *Heliotropium* species growing in the Red sea coast (two annuals: *H. ovalifolium*, *H. arabinensis*, and one perennial desert plant: *H. lignosum*). Bars are standard errors.

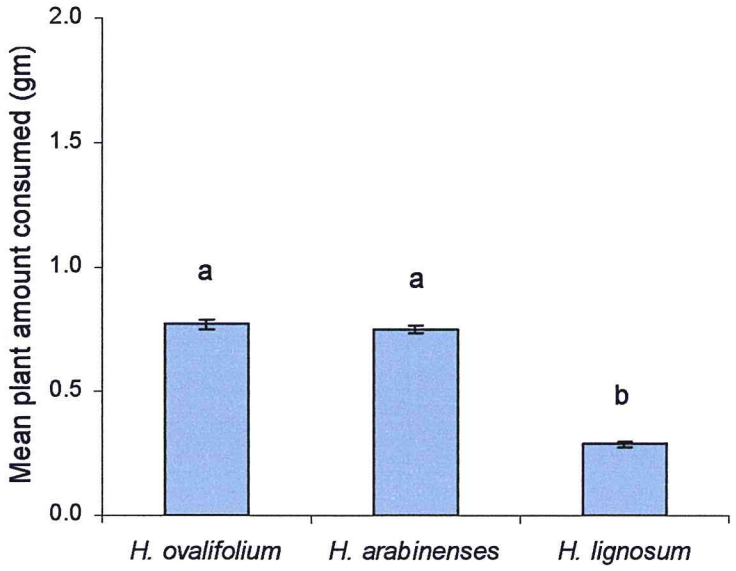


Figure 17. Mean amount (gm) consumed from each plant. Histograms with different letters are significantly different at p = 0.05 (LSD test, see appendix 40). Bars are standard errors.

two plants namely *H. ovalifolium* and *P. typhoides* (bulrush millet) versus clean air in the wind tunnel (Fig. 18). The distance traversed towards the source of plant odour was significantly higher compared to that where only clean air was presented (Fig. 19-B).

When the responses of locusts were observed during day and night, insects behaved almost the same and they were strongly attracted to the volatiles (Fig. 18). GC analyses of the volatiles showed that there were qualitative differences between volatile emission profile of the plant during the day and night time where peaks of the components 3; 9 and 17 released by the plant during daytime were absent at night (Fig. 20). There was also quantitative differences i.e. the amount of the compounds 3, 4, 9 were higher during day, particularly the peak of the component 8 of which the amount released during the day was 18 times higher than the amount released at night. In addition, the compound 17 released during the day was absent at night (Fig. 20).

4.3.3. Response of laboratory-reared solitarious locusts to Triticum aestivum *and* Heliotropium ovalifolium *volatiles (EXPERIMENT III)*

Different amounts of *T. aestivum* and *H. ovalifolium* essential oils were used in the bioassay to investigate the behaviour of solitary-reared locusts previously fed on *T. aestivum* for many generations. At lower doses of *H. ovalifolium* volatiles (Fig. 21), no statistical differences were found ($P>0.05$) between responses to doses 0.01 and 0.1 µl against clean air. However, locusts spent significantly more time ($p < 0.001$) in the side of bioassay chamber with clean air, away from the volatile source when the dosage was increased to 1 µl. Similarly, mean distance traversed was higher in the clean air side of the bioassay chamber (Fig. 21).

With regards to volatile extracts from *Triticum sp.*, insects were moderately more attracted to lower concentration (0.01 µl) compared to the air control (Fig. 21). The attraction to the source of

volatiles was significantly higher ($p < 0.0001$) at a dose of 0.1 µl of essential oil. However, at tenfold higher dose (1 µl of essential oil) of *T. aestivum*, there was no attraction (Fig. 21). Difference between mean distance traversed towards the source of volatile and clean air indicates that insects traversed significantly higher distances towards the source of the volatiles when 0.01 and 0.1 µl were applied. However, they moved away to the opposite side with clean air when higher doses of the volatile were provided (Fig. 19-A), similar to observations on volatiles of *H. ovalifolium*.

4.3.4. *Choice of oviposition in sand impregnated with* Heliotropium *volatile extract by solitarious female locusts previously reared on* Triticum *(EXPERIMENT IV)*

In order to investigate the response of solitary-reared females previously reared on *Triticum aestivum* to volatiles of *Heliotropium ovalifolium*, insects were given a choice between contaminated sand with *H. ovalifolium* volatiles and clean sand (control). At lower doses of the volatiles, no preference ($p>0.05$) was observed and females oviposited randomly in both cups (Fig. 22). Hence, there was no significant difference between the mean number of egg pods laid in clean sand and sand contaminated with 0.001 µl ($t = 0.22$, $df = 8$, $p = 0.83$), 0.01 µl ($t = -0.27$, $df = 8$, $p = 0.79$), 0.1 µl ($t = -0.28$, $df = 8$, $p = 0.78$), and 0.5 µl of essential oil ($t = -0.31$, $df = 8$, $p = 0.76$). However, when sand was contaminated with 2.5 µl, female locusts preferred to oviposit in the clean sand ($t = -2.24$, $df = 8$, $p = 0.05$). Similarly, females lay significantly more egg pods into the clean sand at 5 µl ($t = -3.58$, $df = 8$, $p = 0.0072$).

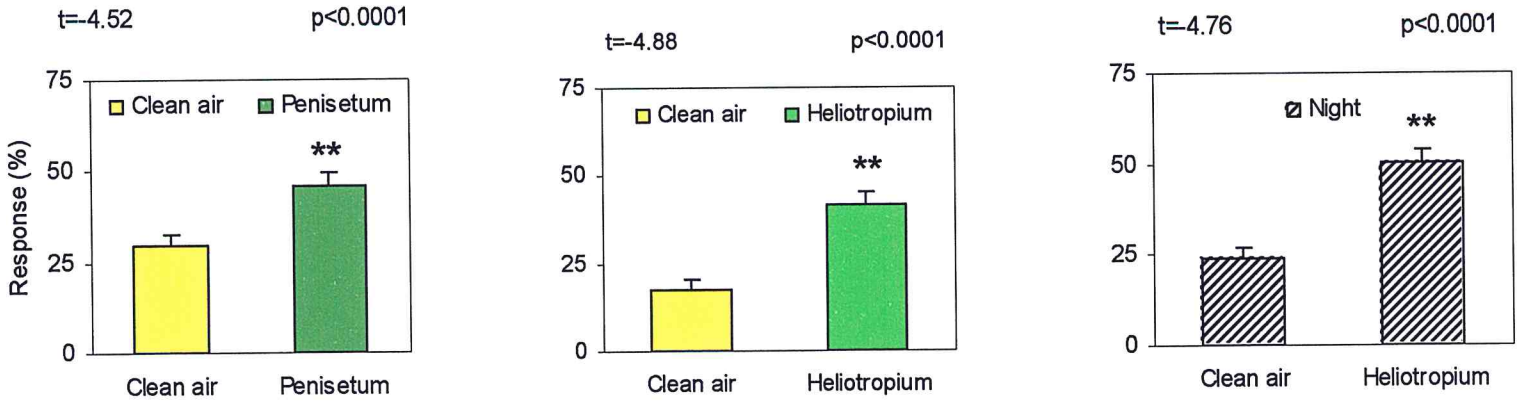


Figure 18. Responses of field-collected insects to odours from potted *Heliotropium ovalifolium* and *Pennisetum typhoides* when presented versus clean air. Columns with asterix are significantly different at $p < 0.05$ (Student t-test), $df = 78$. Bars are standard errors.

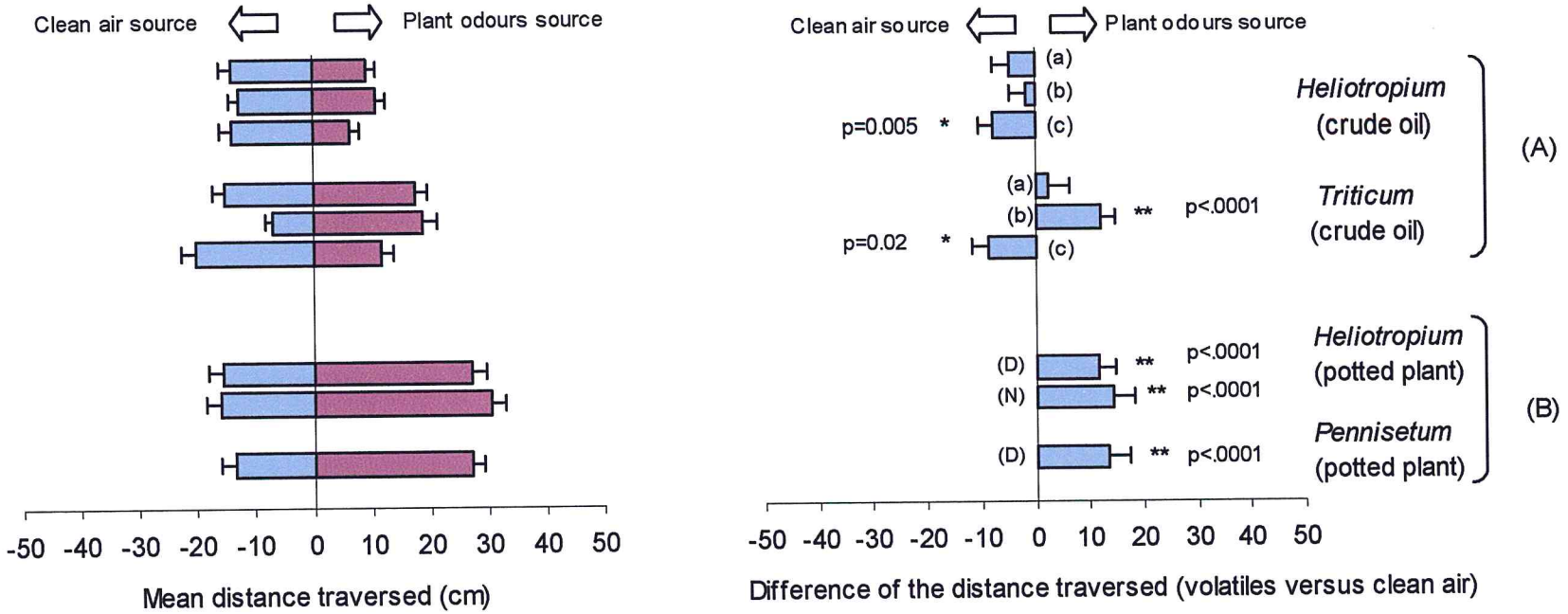


Figure 19. Mean difference in distance traversed (distance traversed towards stimulus minus distance traversed towards clean air) by (A) solitary-reared locusts in response to stimulation with (a) 0.01 (b), 0.1 and (c) 1 µl of essential oil from *T. aestivum* and *H. ovalifolium*; (B) field-collected insects in response to stimulation with odours from potted *H. ovalifolium* and *P. typhoides*. D, daytime responses; N, night time responses.

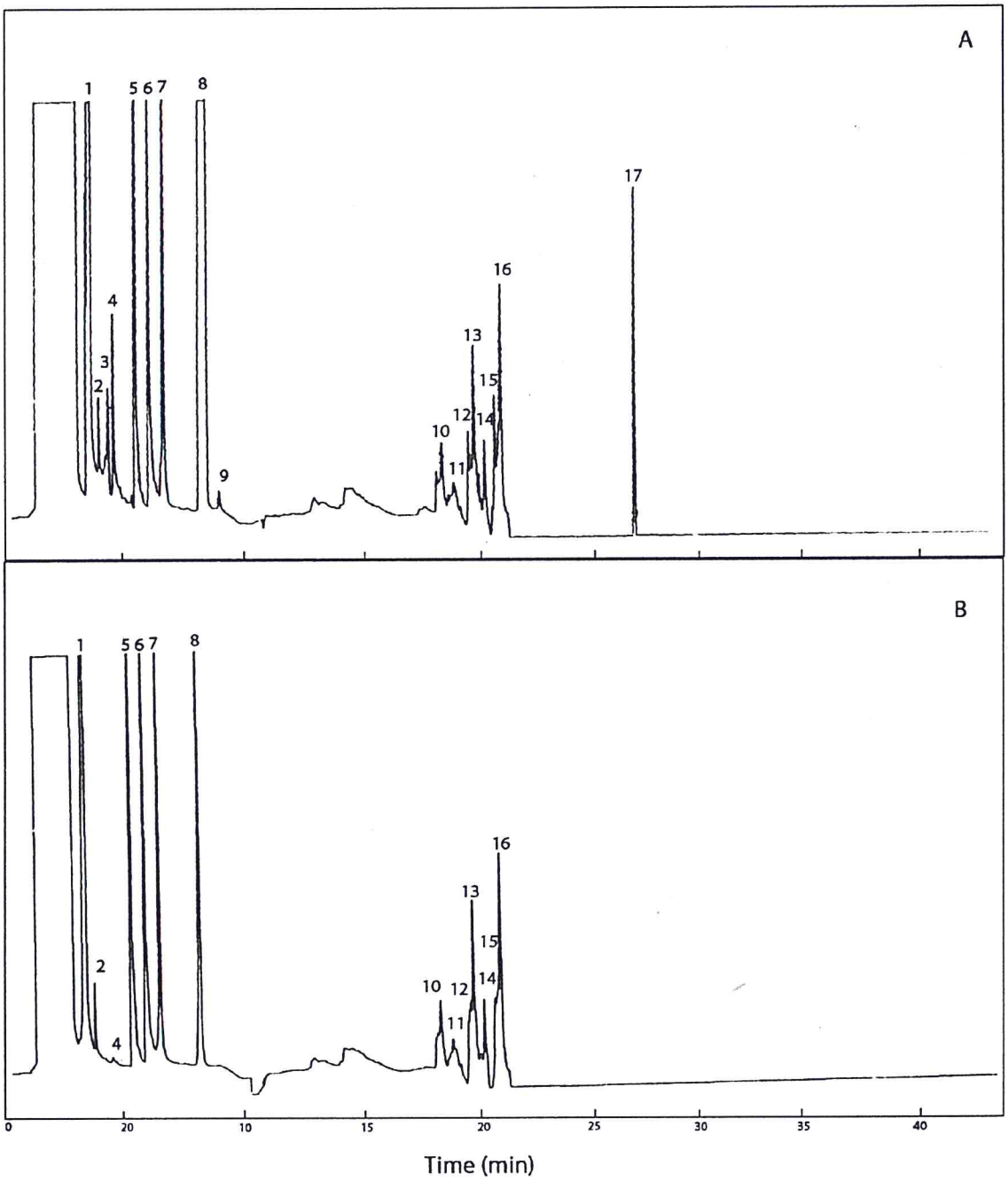
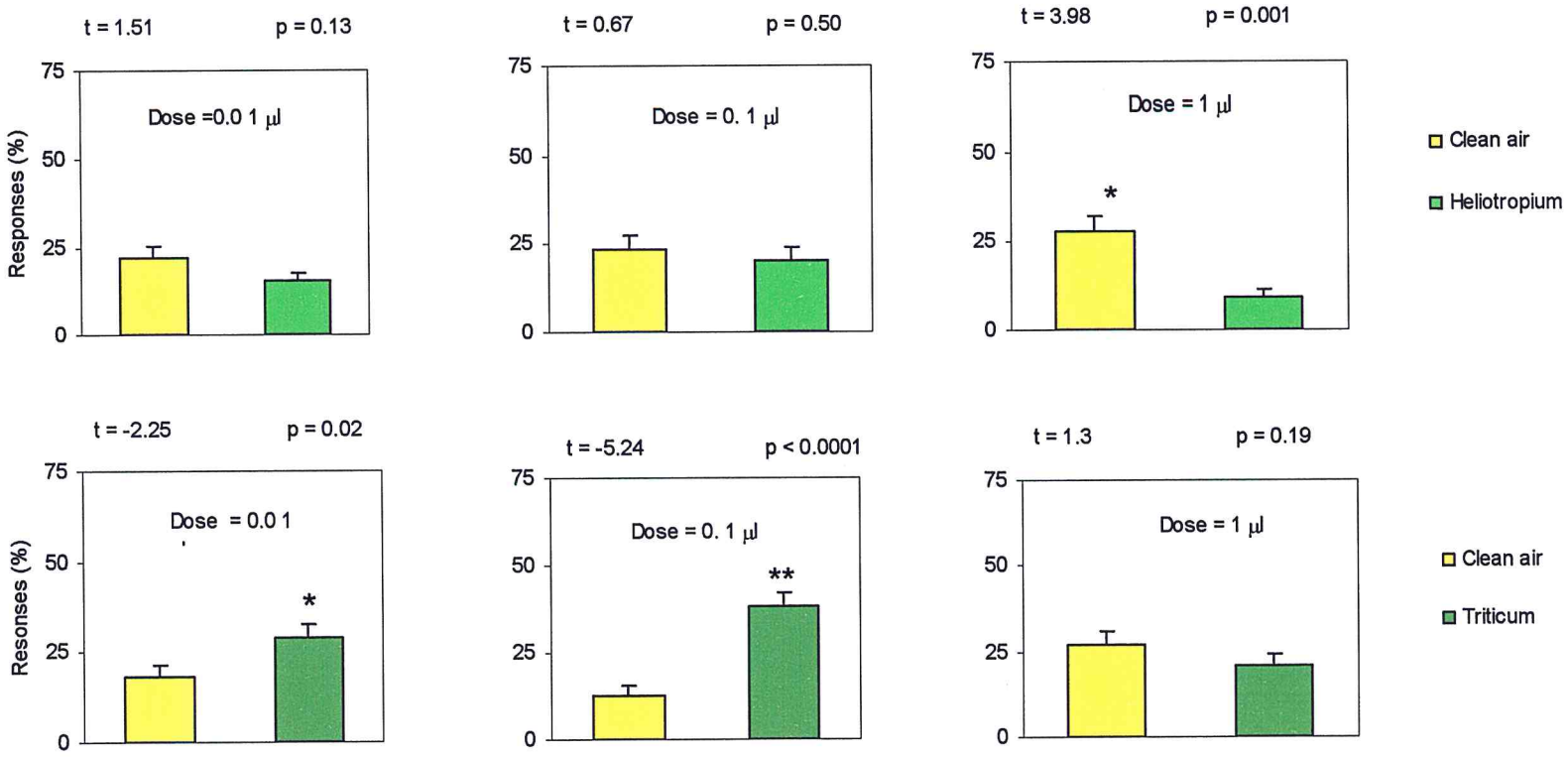


Figure 20. Gas chromatogram of volatile emissions from *Heliotropium ovalifoluim* injected onto a 50-m Methyl silicone 20 M capillary column. (A) volatiles trapped during the day (B) volatiles trapped during night.



.Figure 21. Responses of solitary-reared locusts to volatile extracts of plants used as rearing diet (*Triticum*) and from a preferred desert plant (*H. ovalifolium*) when presented versus clean air. Columns with asterix are significantly different at $p < 0.05$ (Student t-test), df = 78. Bars are standard errors.

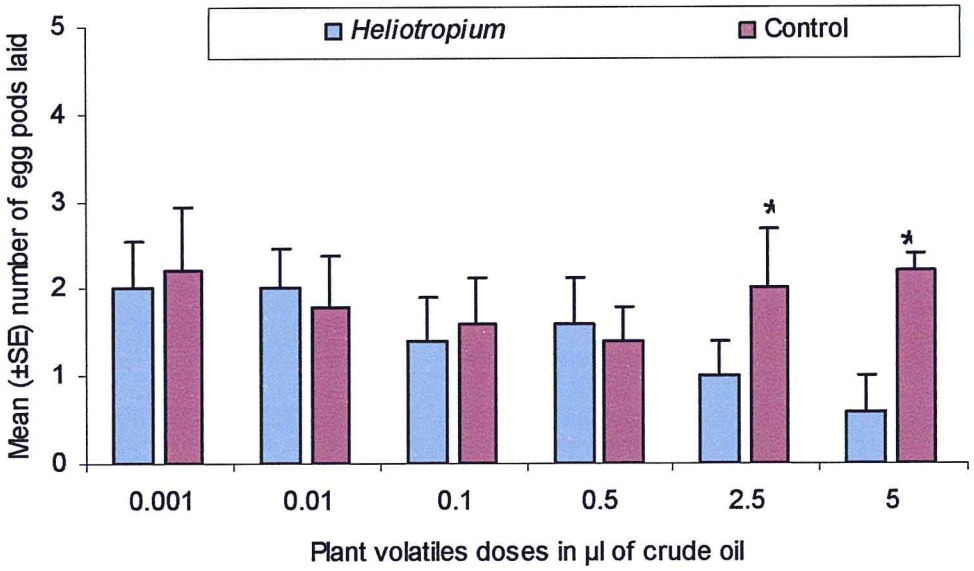


Figure 22. Mean number of egg-pods laid per solitary-reared female in sand contaminated with *H. ovalifolium* sp. essential oils and clean sand. Columns with asterix are significantly different at $p < 0.05$ (Student t-test). Bars are standard errors.

4.4. Some aspects of the reproductive strategy of females solitarious desert locust

All the solitarious female locusts of the group that was collected at the beginning of the breeding season had laid egg-pods compared to the group collected at the end of the breeding season (Fig. 23). All the female locusts caught had laid egg-pods immediately after the first rains and this was significantly higher than the percentage of females that oviposited after they were caught at the end of the breeding season i e 58% (χ^2 = 12.63, P < 0.0004) (Fig. 23). Moreover, solitarious females that were caught at the beginning of the breeding season laid more egg-pods/female than the ones collected when the season was ending (Figs. 23 and 24). The mean number of pods laid by 24 *solitaria* females collected before the rainy season was 4.35 egg-pods (range: 1-12, SE ± 0.73) and was significantly higher (t = -6.09, P < 0.0001, df = 46) than the mean number of egg pods laid by the group of females collected at the end of the breeding season (0.75 pods (range: 0-5, SE ± 0.29)).

According to the number of egg pods all the female locusts collected at the beginning of the rainy season laid eggs regularly (3-12 egg pods per female), despite that no further mating occurred in the laboratory since the presumed one in the field before they were caught. However, only 58% of the females collected at the end of the rainy season from the summer breeding area laid sporadically 1-4 egg pods/female (Fig. 24). Figs. 23 and 24 show that the maximum number of egg pods laid by the group of solitarious females that were caught at the onset of the breeding season was in December, which coincides with the period of the appearance of annual plants in the field.

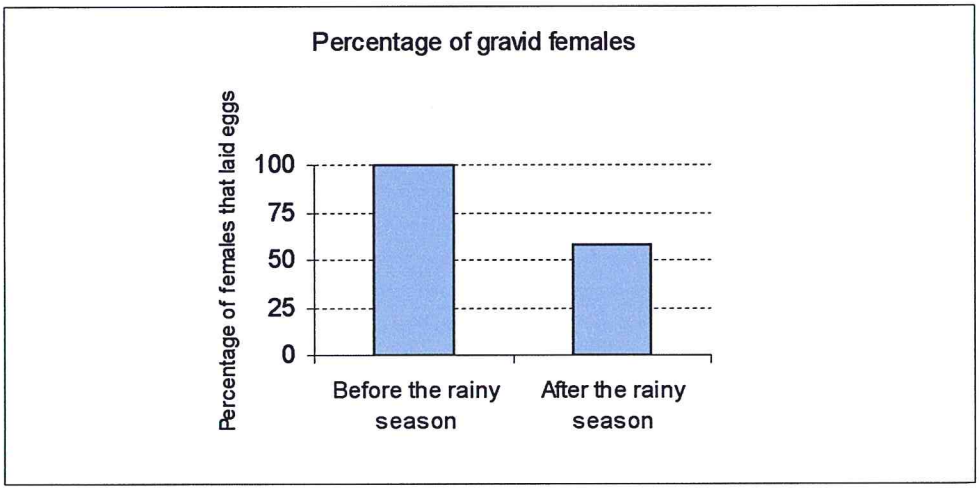


Figure 23. Percentage of gravid females that oviposited at least once after they were caught at the onset (winter breeding) and end (summer breeding) of the breeding season and kept in the laboratory.

Oviposition was monitored throughout the five subsequent months despite that mating took place more than 3 weeks earlier. The low egg-laying observed in females collected at the end of the breeding season can be explained by that these females may have already laid most of their egg pods towards the end of the breeding season. After the incubation of egg pods, hatching occurred within 13-18 days in laboratory conditions and when extrapolated to the field conditions, it was noted that most of the hatching was likely to occur at the end of December and the beginning of January (Fig. 25).

On the other hand, considering that the life cycle of the new progeny would be completed in 35-40 days in the low temperatures of the winter breeding season and that maturation might take place afterwards in 3-4 weeks, the expected adult emergence period and the expected time in which the locusts would have matured was extrapoled as shown in Fig. 25.

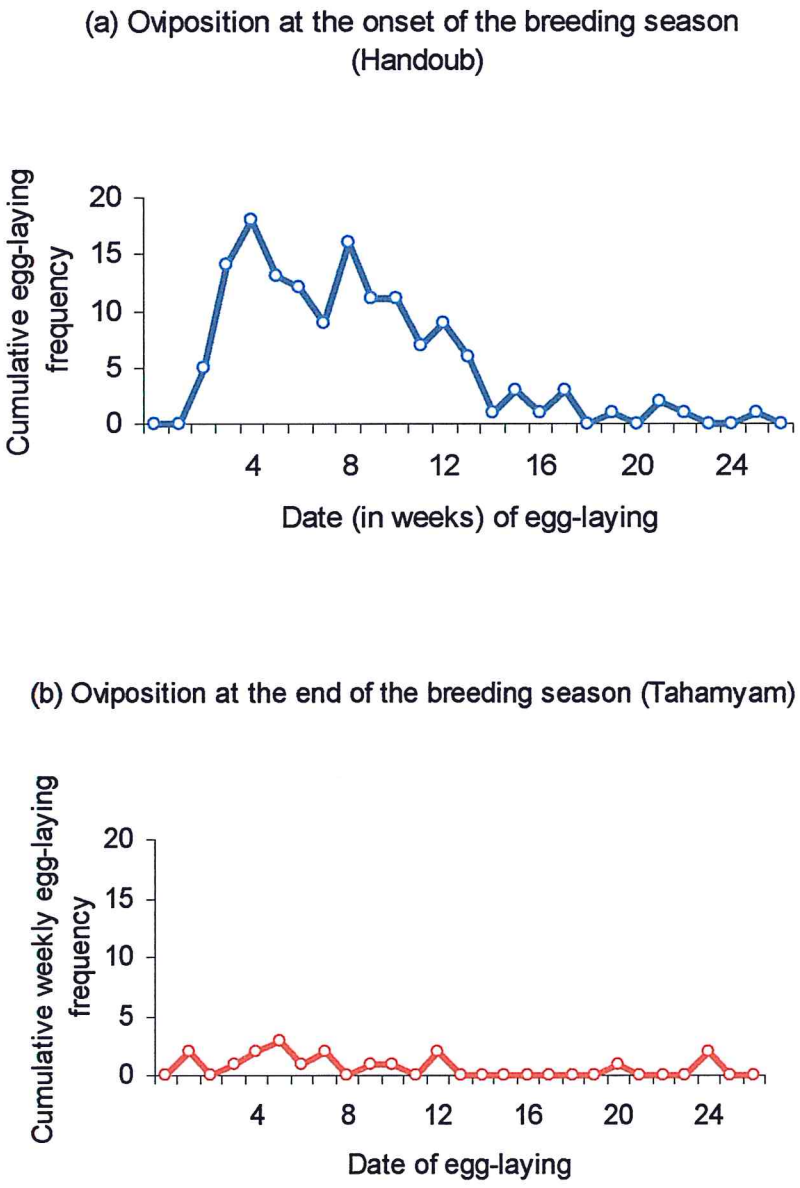


Figure 24. Weekly egg-laying of gravid solitarious females caught (a) at the onset of the breeding season (Handoub) and (b) at the end of the breeding season (Tahamyam).

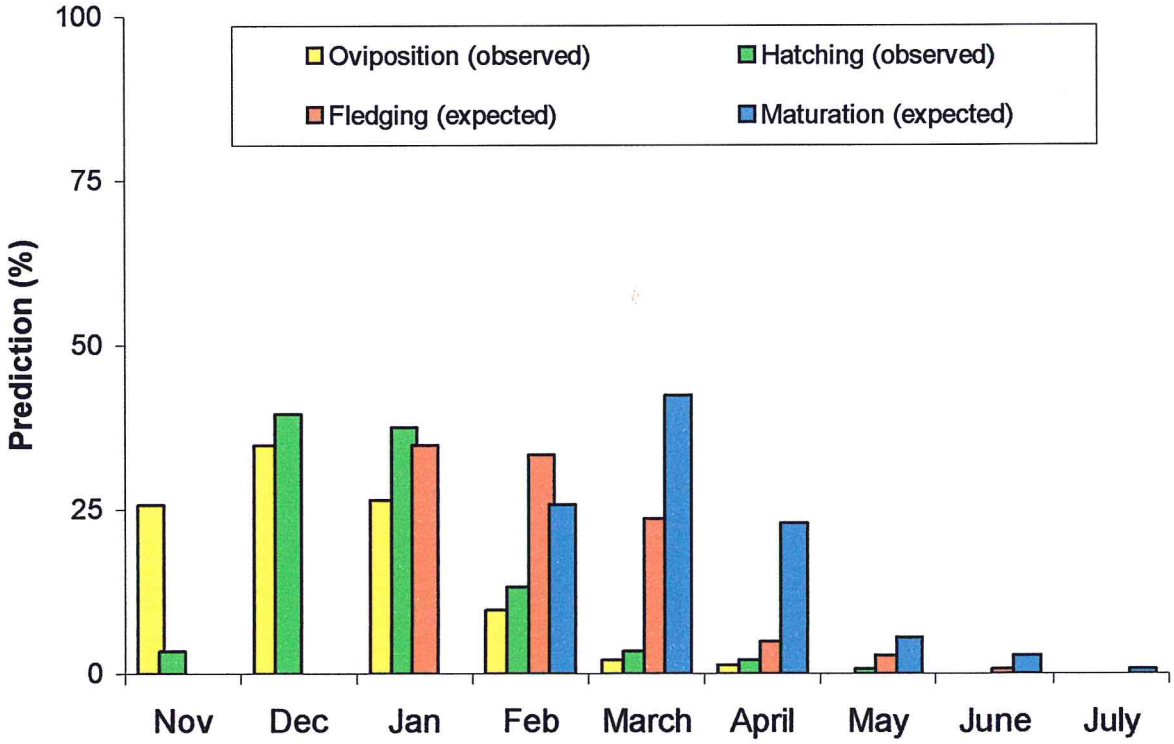


Figure 25. Extrapolation based on the field conditions of the observed oviposition to hatching and predicted adult emergence and maturation during a breeding season (there is overlap of the four processes).

CHAPTER 5

DISCUSSION

5.1 Mate attraction in the solitarious and gregarizing desert locust, *Schistocerca gregaria* (Forskål)

In the field, solitarious locust population densities can be extremely low (Uvarov, 1977) and although patchy distribution of host plants may contribute to bringing the insects together (Plates 13, 14) particularly near preferred plants for feeding, successful mate finding may depend on long-range pheromone signals (Byer, 1991; Hassanali and Mahamat, 1991). In addition, visual cues are important for the insects to locate each other. With regard to distant attractions, olfactory cues play a major role as the sensory system in solitarious locusts has been shown to be more developed and detects a broader range of signals than in the gregarious phase (Ochieng' *et al.*, 1998, 1999, Hansson *et al.*, 1995).

The enhanced attraction of locusts to both olfactory and visual cues when provided simultaneously showed that, visual stimulus is necessary in the overall sexual behaviour of the locusts, in particular when they approach their mate. However, when only the olfactory cue was provided, the test insect gave up searching after sometime. This is mainly because the target insect in this case was excluded from the mate behaviour scene due to its upwind position and also because it was hidden and could not see the test insect, hence, without the necessary visual cues, the hierarchy of behaviours for mate location is disrupted.

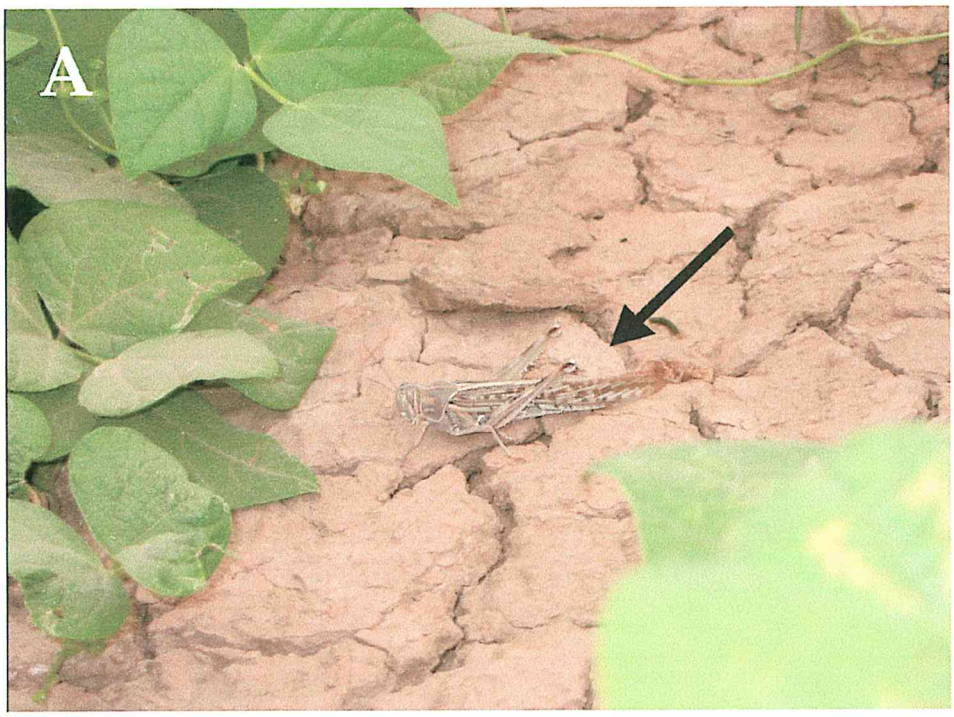


Plate 13. (A) Solitarious female (arrow) near cultivated cow pea - Tokar delta, Sudan; (B) solitarious male (arrow) near *Heliotropim sp.* - Hosheri, Red sea coast

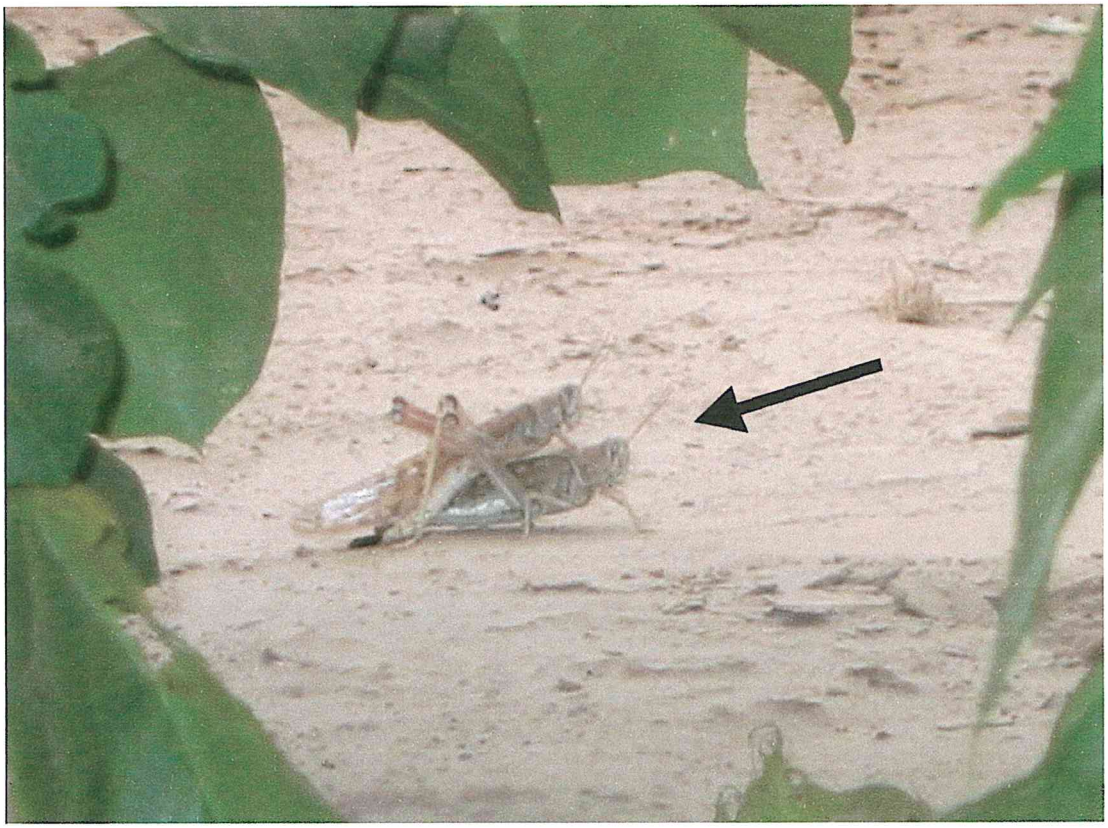


Plate 14. Solitarious male and female mating pair (arrow) near cultivated cow pea - Tokar delta, Sudan.

Caged solitary-reared female (Fig. 26) reacted to the presence of the gregarizing male by moving away while the reaction of a caged male was different (Fig. 27). The female approached the signal source (male locust) and displayed several behaviours. An extraction observations on solitary-reared insects (Table 3) showed that from shorter distance (30 cm), 60% of the solitary-reared males mounted the female's box when both olfactory and visual cues were provided. On the other hand, it was already shown that there is no significant attraction in solitary-reared locusts between daytime and night, despite that solitaious insects, particularly the ones from the field are more active at night than in daytime (Ely *et al.*, in preparation). This suggests that this night activity is probably more related to survival (migration to better habitats, recent rains, ...) rather than to sexual activities.

As reported by Norris (1962) when mature males are crowded together without females they sometimes mount backs of males and attempt copulation. Moreover, the increase in activity of the gregarizing males as we observed is particularly due to the crowding effect (Norris, 1962) giving a newly gregarizing population, particularly the males the capability of mating with females of solitarious populations visited by newly formed swarms.

Females of gregarious (crowd-reared) insects were passive and displayed no calling behaviour (Fig. 9-A3, B3), probably because of that they were grouped together with males and might already been mated similarly to behaviours reported earlier (Norris, 1964; Strong and Amerasinghe, 1977; Amerasinghe, 1978). Strong and Amerasinghe, (1977) further suggested that mate behaviour in gregarious *Schistocerca gregaria* is exhibited only by the male and there being no evidence of female sexual display. In these results, gregarious males showed significant

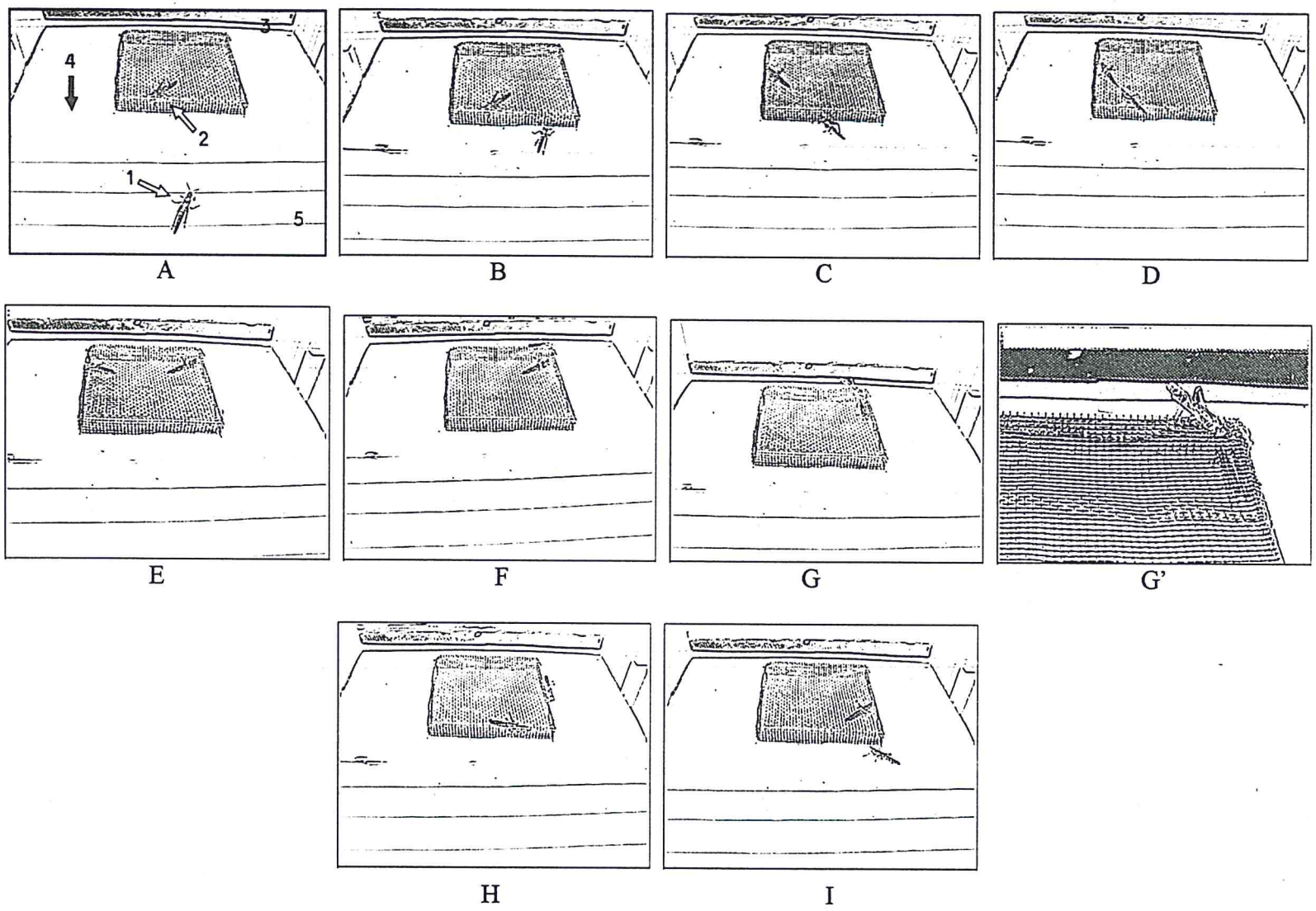


Figure 26. Sequential video frames (A-I) of the behaviour of a previously solitarious male (1) crowded for 8 days around caged solitary-reared female (2). Both olfactory and visual cues present. 3. activated charcoal, 4. air direction, 5. manila paper with stripes on base of chamber

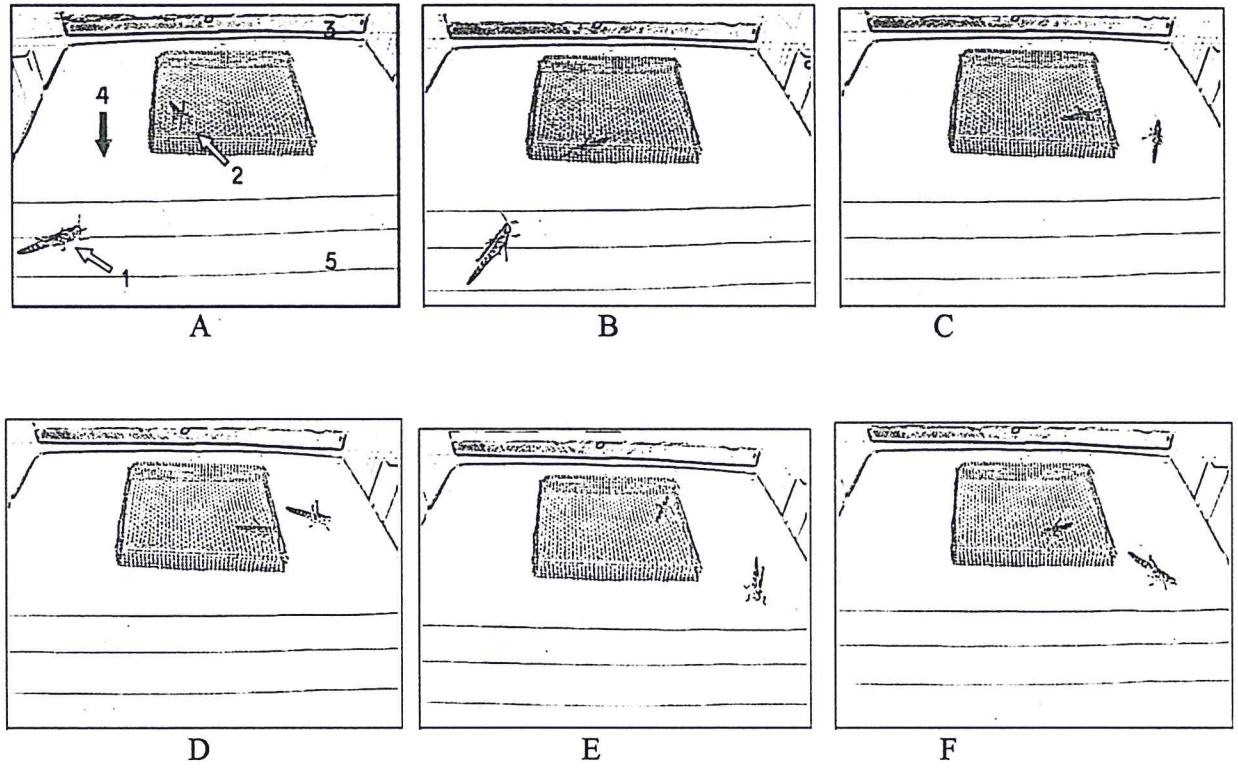


Figure 27. Sequential video frames (A-F) of the behaviour of a previously solitary-reared female (1) around caged solitarious male (2). Both olfactory and visual cues present. 3. activated charcoal, 4. air direction, 5. manila paper with stripes on base of chamber

attraction to solitary-reared females but in a lower degree compared to gregarizing males. The latter shifting from isolation conditions showed more activity than the gregarious males that have been kept continuously in crowding conditions for many generations and therefore, they might have lost some of their gregariousness. Deng *et al.* (1996) showed that solitary males shifted to grouped conditions produced more phenylacetonitrile than gregarious control. This may be an indication that gregarizing populations probably more active in invading areas and recruiting individuals (Njagi and Torto, 1996) as they started producing pheromone and also their strong attraction to their conspecifics of solitarious insects. This may also suggest that solitarization plays an important role in the locust life span in the survival but also giving populations more vigour when conditions are suitable for gregarization processes.

In recent morphological studies, Ochieng' *et al.* (1998) found three types of sensilla housing olfactory receptors on *Schistocerca gregaria* antennae. They had shown that the number of sensilla is higher in solitary-reared locusts than in individuals of gregarious ones. They further pointed out that receptor neurones present in sensilla trichodea are specialized in many insect species to detect pheromone components at low concentrations (Baker, 1989; Masson and Mustaparta, 1990; Hansson, 1995). Meanwhile, the only compound found to be produced by mature solitarious female, (E,Z)-2,6-nonadienal was detected by receptors by neurones present in the male solitary locusts (Ochieng' *et al.* 1999) to a significantly higher degree than in the gregarious males.

The antennae of *Locusta migratoria* have olfactory receptors of two types, A and B (Ameismeier, 1987). Type A has from 20 to 30 neurones, suggesting that this receptor probably functions in cognition of plant odours (Ameismeier, 1987). Type B has only three neurones, more typical of receptors responding to pheromone components. Greenwood and 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 solitarious adult than the gregarious adult. The solitarious 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 and Chapman, 1984; Ameismeier, 1987; Blaney and Simmonds, 1990). Masson and Mustaparta (1990) pointed out that their study support that in *Schistocerca gregaria*, as in other insect species, information about host odour quality, aggregation pheromones, and sex pheromones are conveyed to the brain via a labelled-line mechanism.

On the other hand, high fertility was reported in wild solitarious females at the onset of the breeding season and their ability of laying pods and viable progeny regularly throughout the season (Ely *et al.*, in preparation). This may contribute positively in mate finding suggesting that fertilization of females eggs at the onset of the breeding season might be enough to ensuring without a need for further mating.

5.2. Diel behavioural activity patterns in adult solitarious desert locust, *Schistocerca gregaria*

Diel periodicity in the behaviour of some species of acridids has been observed in the field (Kennedy, 1939; Rao, 1936a, 1960; Volkonsky, 1942; Roffey and Popov, 1968) but no detailed laboratory or field studies on this regard have been carried out. The present results from laboratory observations showed that, solitarious desert locusts, *S. gregaria,* were more active after dusk than

during daytime. The results also conform very well with the documented field observations that solitarious locusts are largely immobile throughout the day and only start flying after sunset (Steedman,1988). The low frequencies of walking (and the distance traversed) and attempts to take off by both male and female locusts at daytime reflect on the inactivity of solitarious locusts during the day. In the field, solitarious locusts start taking off 20-30 minutes after sunset. The flight activity reaches peak after a few minutes later and then declines within the next 3 hours (Kennedy, 1939; Rao, 1936a, 1960; Volkonsky, 1942; Roffey, 1963; Roffey and Popov, 1968). What triggers the onset of the high behavioural activity of the solitarious locusts after sunset? Volkonsky (1939) and Waloff (1963a) suggested that it may be induced by the sudden drop in light intensity. Roffey (1963) observed that, solitarious locusts apparently started taking off without any prior disturbance at evenings when the light intensity decreased from 400 to 3.5 lux. The compound eyes of solitarious locusts are structurally suitable for vision under subdued light and are sensitive to movements rather than sharp images (Roonwal, 1947). Thus, solitarious adult locusts would be expected to be less active in bright sunlight during the daytime as opposed to their gregarious counterparts whose compound eyes are suited for diurnal vision. In daytime, solitarious locusts spend most of the time either resting on the ground or roosting within plant bushes (Steedman, 1988). Another aspect of the very low behavioural activity during daytime is that, it may be a form of crypsis which is adaptively used by solitarious desert locusts to minimize predatory pressure by birds, which are mainly daytime hunters (Steedman, 1988). They are major predators of desert locusts, both the adults in swarms and nymphs in hopper bands.

In the wind tunnel observations carried out after sunset, locusts walked and scanned their field of vision at significantly higher frequencies than during the day. Take-off attempts were also more frequent, in particular, during the first two hours of the night although this activity was

significantly higher throughout the night observation period than in daytime. While the diel behavioural patterns in the two groups of locusts were similar, locusts collected from the field (FCI) were overall more active than those maintained in the rearing facility. These differences may be due to a set of interacting internal factors such as muscle development and the levels of energy reserves in individual insects (Hunter, 1982). These may in turn be dependent on the rearing conditions and other external factors that the locusts are exposed to. For example, in the laboratory, confinement in small cages used for rearing isolated locusts limits their walking movements while they can hardly execute any flight. This might stress the insects and may lead to underdevelopment of flight muscles in the insects as opposed to their field counterparts that undertake short distance and migratory flights. In addition, environmental factors such as temperature and relative humidity under which the locusts are reared and kept may also play a role. In the laboratory, locusts are generally reared under constant controlled temperatures while in the field they are exposed to fluctuating temperatures and humidity. In the field, large scale night flights have been observed to occur when air temperatures are equal to or greater than 24 °C (Rao, 1937; Volkonsky, 1941). Another external factor which may influence the level of behavioural activity of the locusts is food quality which largely determines their energy reserves necessary for flight and other behaviours. The laboratory-reared insects (LRI) are fed mainly on cultivated wheat while solitarious locusts in the field (FCI) have access to a wide variety of desert plants.

The results of this study confirm previous field observations that, solitarious desert locusts are more behaviourally active after onset of dusk than during day. This is manifested as short distance and migratory flights in the field after sunset. While the diel behavioural patterns are preserved in the laboratory-reared solitarious locusts, it was evident that there is a significant

decline in the levels of behavioural activities after several generations. It suggested that, where possible, insects freshly caught from the field are the most suitable for use in bioassays aimed at evaluating and understanding various behaviours of the solitarious desert locust.

5.3. Host plant odour preference by solitarious desert locust, *Schistocerca gregaria* (Forskål)

In order to obtain a better understanding of the behaviour and biology of *solitary* populations, it is crucial to understand their interactions with host plants and their habitat. Kairomones are inter-specific chemical cues, which may mediate host plant seeking and host acceptance behaviour by locusts. They may also play a role in physiological predisposition of solitarious locusts to the gregarious phase. Two groups of kairomones may influence the behaviour of locusts; odours of host plants which play a role in the location of food (Haskell *et al.*, 1962, Kendall, 1971, 1972), and non volatile allelochemics involved in food selection (Woodhead and Bernays, 1978). Despite that, Acridoids are known to be polyphagous feeding on a broad range of host plants, it is possible that they have a hierarchy of host plant preference.

In the wind tunnel experiments, solitarious adult *Schistocerca gregaria* (Forskål) previously reared for many generations on *Triticum aestivum*. (wheat) were strongly attracted to chemical components in the volatiles from *Triticum aestivum* as probably they may have olfactory receptors that are specifically tuned to these compounds. Njagi and Torto (1996) had shown that, gregarious nymphal desert locust that were reared on certain grasses responded strongly to the odours of these plants. They suggested that, locusts reared on a given plant on many generations may learn to associate the odours of the plant with the food resource, and therefore, respond strongly to the former. This may pastly explain the observation that, solitarious locusts reared in

the laboratory that have never encountered *H. ovalifolium* species, were not attracted to the volatiles of these plants and elicited other behaviours in the insects. Concentrations of 2.5 µl or higher of *H. ovalifolium* volatiles were repellent to the locusts. Norris (1968) in an experiment with gregarious phase showed similar results where females preferred to oviposit away from fresh grass, suggesting a repellent effect. This may account for the location of gregarious locust egg pods in the field at some distances from plants.

Field-collected insects responded positively to both volatiles from potted *Heliotropium ovalifolium* and *Pennisetum typhoides*. Acridids are known to have evolved to be polyphagous and the majority of the species today maintain a broad diet (Bernays and Chapman, 1994). Thus, it was critical for them to also develop olfactory systems that are capable of discriminating their host plants from the non-hosts and a digestive enzyme that enables them to effectively utilise a wide range of plant materials. Also, Bashir *et al.*, (2000) showed that solitarious gravid females oviposit near host plants preferred for feeding. This exposes their progeny to these plants *(H. ovalifolium* and *P. typhoides)* among the other host plants and their volatiles may have a conditioning effect on the hatching nymphs, hence, the subsequent preference irrespective of other plants in the habitat. Solitarious locusts for this work had been collected from an area where *P. typhoides, Sorghum bicolour, H. ovalifolium* and *H. arabinensis* were predominant. In the field, females will tend to specialize on the most abundant host plants for feeding and oviposition. This in turn ensures availability of sufficient food for their progeny. Solitarious nymphs also prefer to feed on these plants (Bashir *et al.*, 2000).

Locusts are attracted to certain chemical substances present in a wide variety of plants (Haskell *et al.* 1962). Any locust downwind and within the range of olfactory detection of areas

of lush vegetation releasing an attractive odour, will be able to move towards them provided that the wind speed is below the flying speed.

In other recession habitats of *Schistocerca gregaria*, *H. ovalifolium* may be a minor part of the desert flora or is not there. Thus solitarious locusts may associate with prevalent species of plants such as *Tribulus spp.*, *Schouwia purpurea*, *S. thabaica*, *A. persica* and *Hyoscyamus muticus* in West and Central Africa (Roffey and Popov, 1968; Hemming *et al.*, 1969; Steedman, 1988; Ghaout *et al.*, 1991).

When several plants were offered for food, annuals were mostly preferred for feeding over the perennials (Fig. 16). Changes the behaviour of an insect in response to their nutritional environment can be understood as adaptive mechanisms for achieving adequate and balanced nutrient intake (Simpson *et al.*, 1995). In the field, annual plants that emerge after the rainy season play a crucial role in providing the necessary nutrients. The amount of *H. lignosum* plant material ingested probably occurred after most of the repellent compounds evaporated since the fresh plant material was rejected and in the field, it releases strong volatile odours that are detectable from a distance. Food selection by locusts in the field might also be altered by conditioning, as a result of experience. Bernays and Chapman (1970) found that, a population of *Chorthippus parallelus* from a habitat in which *Dactylus glomerata* was common, readily accepted the plant, whereas insects from a population where that plant was uncommon did not. Polyphagous insects such as *S. gregaria* detect a wide range of odours, be it from host plants and/or non hosts. These volatiles may be associated with the nutritional status of the plant and play important roles not only in host location and oviposition site selection, but also in some physiological processes in the desert locust, e.g. sexual maturation (Carlisle *et al.*, 1965, Ellis *et al.*, 1965, Assad *et al.*, 1997). In the patchy habitats of the solitarious desert locust, host plant

volatiles may play a critical role in mate finding by attracting insects of different sexes to the same patch of plants. The insects may then locate each other by detecting any mate recognition cues that may be produced by the male or female, or both of them.

5.4. Some aspects of the reproductive strategy of females solitarious desert locust

Mate finding among gregarious population largely depends on the frequent encounters between the insects (Ellis, 1959; Kennedy, 1951; Roffey and Popov, 1968). In the contrast, solitarious populations live in very low density with the individuals scattered over widely separated recession areas. In the following discussion, a model (Fig. 28) describing the life-history of desert locust populations, during the recession periods is proposed based on rain patterns and the plant phenology in the locust habitats..

The results showed that, the solitarious females caught migrating into the breeding area just before the onset of rains were already mated (Fig. 24). This predisposes them to finding good egg-laying conditions (e.g. moistened sand) and later, ample plant material for food. Mating had taken place before the appearance of any annual vegetation as collection of the females was done a few days after the first rains in the area. Two possibilities giving rise to this suggestion are summarized in Fig. 28. Firstly, the incoming solitarious females were either already mated in some other areas that dried out where forced encounters between opposite sexes were facilitated by the shrinking food reserves prior to arriving at a new area of recent rains. Secondly, they may have matured and mated after their arriving in the new habitat, depending on regeneration of perennial plants (Carlisle *et al.*, 1965; Ellis *et al.*, 1965; Assad *et al.* 1997).

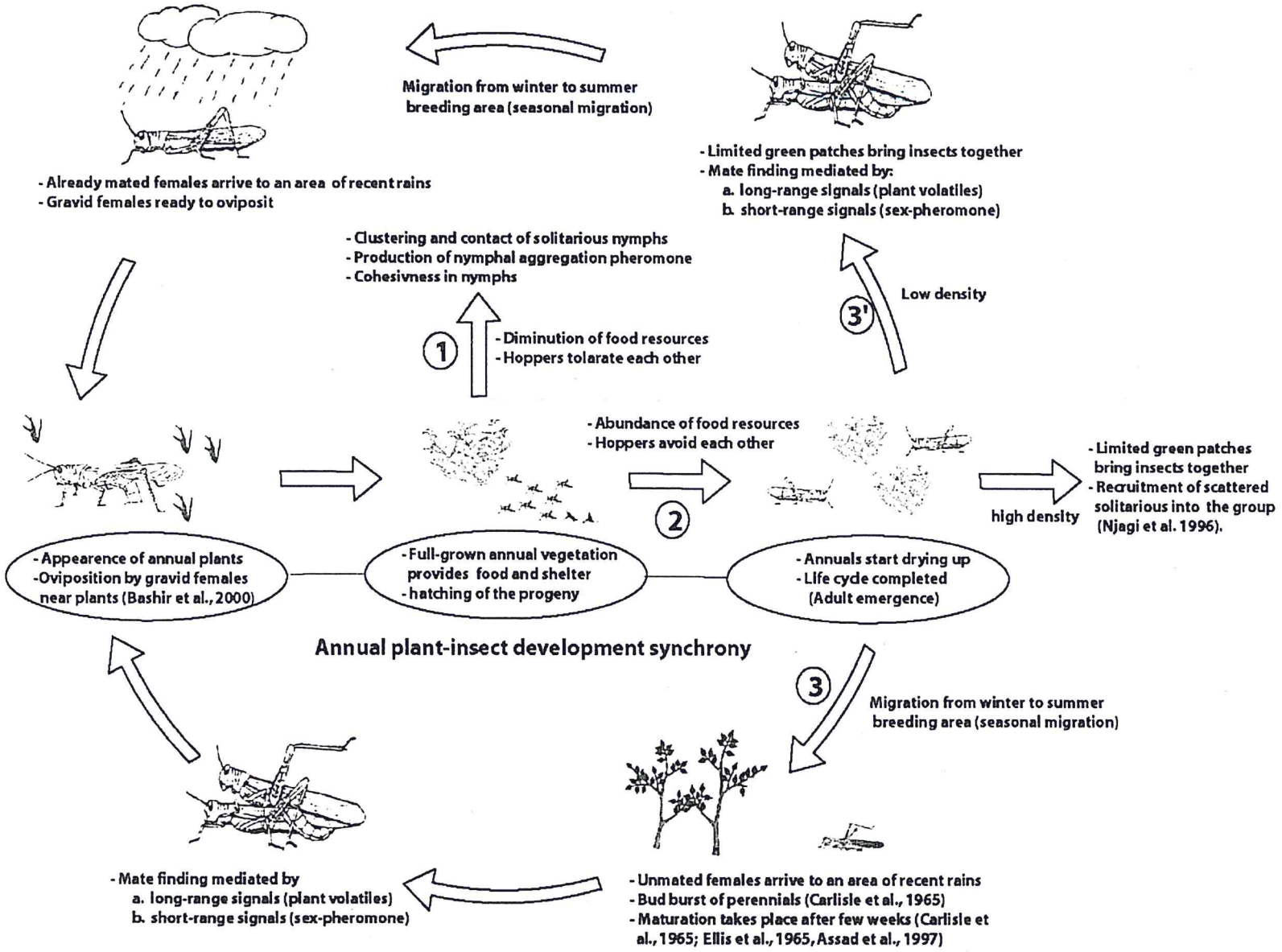


Figure 28. A model of life-history strategies of solitarious female locusts during a breeding season

The results also provide evidence on the high fecundity of the solitarious females in the field. Female locusts kept isolated from males, oviposited regularly for about 5 months, most of the oviposition taking place within the first two months (December-January). This suggests that, since mate finding may be difficult when individuals of opposite sex are widely scattered, solitarious females may compensate for this by their high fecundity during the breeding season. This ensures that oviposition is spread out over the rainy season and during their reproductive period.

Under field conditions, females of swarming populations may lay two or three times in a season (Popov, 1958) and that the mean number of eggs per pod ranges from 53 to 81 (Ashall and Ellis, 1962). Under laboratory conditions, solitary females have been found to lay more egg pods, and with a larger number of eggs per pod than gregarious ones (Pavillon, 1960). There are no field data on number of egg-layings in wild solitarious female, but repeated egg-laying is likely to occur (Wallof, 1966; Steedman, 1988). Present results show that, solitarious females caught at the onset of the breeding season laid up to 12 egg pods per female with a mean number of eggs per pod ranging from 85 to 160. Similarly, in the field, Ashall and Ellis (1962) found the mean number of eggs in pods laid by wild solitary females to be as high as 95 and 128. In other field observation, solitarious females in a low-density scattered population in Tamesna in Niger, laid between 90 and 146 eggs (mean of 123 egg/pod) (Popov, 1958).

At the end of the breeding season, the low number of egg pods per female and eggs per pod recorded for the solitarious females is probably due to the observation that they had laid earlier in the season. It was evident that peak egg-laying coincided with the period of appearance of the annual vegetation in December/January the field (Fig. 28). This concurs with previous observation that solitarious females prefer to oviposit in the proximity of some species of desert plants which

also biases the preference for feeding on certain hosts by emerging nymphs (Bashir *et al.* 2000). The observations suggest that, female solitarious locusts may have a strategy for synchronizing their oviposition with the appearance of annual plants. Also, there may be synchronization between hatching and the phenology of the vegetation which is usually sufficiently full-grown at the time when most of the hatching occurred, that ensures a sustainable food supply and shelter for hoppers. Such plant-insect development synchrony has been observed for the maturation of the gregarious desert locust (Popov, 1958; Norris, 1962, 1964, Uvarov, 1966; Richards and El Mangoury, 1968; Mahamat *et al.*, 1993; Torto *et al*, 1994) and the communal oviposition by gregarious females (Rai *et al.*, 1997; Saini *et al.*, 1995; Torto *et al.*, 1999).

After the winter rains in the Red sea coastal plain, a variety of annuals sprout, mainly grasses. However, *Heliotropium* sp., a very common annual that grows on the soft sand along the dune margins, may provide a sustained food supply as well as shelter for the newly emerging generation to complete their developmental cycle, since the vegetation remain green up to April. Volkonsky *et al.* (1939) describing the breeding of locusts in Algerian Sahara in spring, observed various stages of development include 4^{th} and 5^{th} instars and adults. Amongst the annuals present at the time, same plants such as *Schouwia purpurea* seemed to be important in the development of locusts. However, during a winter breeding season in Port Sudan hinterland, only one generation may breed as conditions are not suitable for a second generation. In the field, *S. gregaria* not only has located scarce and seasonal suitable habitats, but also has to exploit them optimally. It is well known that in general, the presence of favourable environmental conditions and an increasing number of locusts can lead to local outbreaks, regional upsurges and, in more favourable conditions to plagues (Wilps, 1997). However, contrary to this, in the Red sea coast, during the

two breeding seasons, there were no local outbreaks despite the presence of favourable conditions.

In gregarious phase, egg-laying occurs only a day or two after the onset of rains (Roffey, 1963). In the present study, the mean egg-laying time was two to three weeks from the time the females were caught and further time had elapsed since the preceding mating. The time period between mating and first oviposition seems to be longer in solitarious females compared to their gregarious counterparts. This may depend on the quality of the available food in the field prior to germination of annuals after the onset of rains. In the Red sea coastal plain, the extreme heat (more than 48°C) and humidity (around 80%) may not be sustainable for locust survival. In addition, the vegetation during this period is dry and the only available green plants are *Suaeda fruticosa* sp. bushes. This is a salty perennial plant colonizing vast areas which is not eaten by locusts. Thus, the appearance of solitarious individuals following the onset of rains is an immigration from other habitats such as the summer breeding areas in which the breeding season was ending. Hence, in Sudan, solitarious populations were found throughout the year in two main distinct recessions regions, winter breeding habitats in the north-east particularly along the Red sea coastal plain where solitarious locusts are present from November to April, and summer breeding habitats in central and western parts of the country that are suitable for breeding between June and October. Similar observations on regular seasonal displacements of scattered populations between the late summer-early winter breeding areas in north-western Niger and the winter and spring breeding areas in central and northern Sahara had been recorded earlier (Volkonsky and Volkonsky, 1939, 1940, 1940a, 1942) and Volkonsky (1941). It is highly probable that more or less regular movements of non-swarming populations, similar to

movements of gregarious swarms may occur between other seasonal breeding areas limited by appropriate wind systems (Waloff, 1966).

5.5. CONCLUSIONS

- Gregarizing males are more strongly attracted to solitarious females than their solitarious counterparts. This may constitute a basis of a recruitment mechanism into a gregarizing population.
- The significantly stronger attraction of test insect to the signal source when both olfactory and visual cues were provided, showed that, both cues are necessary in mate location.
- Gregarizing males are more active than gregarious ones showing the importance of solitarization in the overall vigour of the insects.
- These results conform with documented field observations that solitarious locusts are largely immobile throughout the day and only start flying after sunset.
- Locusts freshly caught from the field are the most suitable for use in bioassays aimed at evaluating and understanding various behaviours of the solitarious desert locust.
- While the diel behavioural patterns are preserved in the laboratory-reared solitarious locusts, it was evident that there is a significant decline in the levels of behavioural activities after several generations.
- Feeding choice among 2 annuals and a perennial *Heliotropium* species growing in the same area (Red sea coast) showed that the annuals were more preferred than perennials; balanced regularly their food intake between the 2 annual plants
- Solitarious females caught migrating in the area at the onset of rains were already mated compared to the ones caught at the end of the breeding season

5.6. Suggestions for future studies

Based on results of the present study, the following areas can be studied in detail in the future:

- Monitoring of sex pheromone production in solitarious locusts populations in the field by trapping volatiles from both males and females under different conditions. For example in presence and absence of preferred desert plants because plant volatiles may enhance the release of sex pheromones shown for other insects (Ochieng and Baker, 2001).

- Monitoring displacements of solitarious desert locust population and migration in the field between two continuous areas (summer and winter breeding habitats for example) particularly at the beginning and the end of the rainy season. This requires catching as many individuals as possible, in particular the new generation at the end of the summer breeding season. These would then be marked and released and then, recapture studies in other areas e.g. the winter breeding habitats may reveal their migratory movements.

- Investigating in the desert plants chemistry by identifying and when possible isolating their compounds in order to be tested in behavioural bioassays. The identification of the compounds released by the desert plants during day and night will be interesting.

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APPENDICES

Appendix 1. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (solitary-reared male) in presence and absence of target insect (solitary-reared female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	1.90	0.38	2.37	0.0436
Error	114	18.32	0.16		
Corrected total	119	20.23			

R. Square	CV	Root MSE	Transformed mean
0.09	26.04	0.40	1.54

Appendix 2. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (solitary-reared female) in presence and absence of target insect (solitary-reared male) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	1.18	0.23	1.60	0.1644
Error	114	16.76	0.14		
Corrected total	119	17.94			

R. Square	CV	Root MSE	Transformed mean
0.06	26.23	0.38	1.46

Appendix 3. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (gregarizing males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	1.38	0.69	4.77	0.0122
Error	57	8.24	0.14		
Corrected total	59	9.62			

R. Square	CV	Root MSE	Transformed mean
0.14	20.85	0.38	1.82

Appendix 4. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (gregarious males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	1.65	0.65	4.20	0.0474
Error	38	5.93	0.15		
Corrected total	39	6.58			

R. Square	CV	Root MSE	Transformed mean
0.10	23.35	0.39	1.69

Appendix 5. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (gregarizing males previously crowded 8 days) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	4	2.22	0.55	3.27	0.0146
Error	95	16.15	0.17		
Corrected total	99	18.37			

R. Square	CV	Root MSE	Transformed mean
0.12	25.22	0.41	1.63

Appendix 6. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (grouped solitary-reared females not exposed to males pheromones) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.48	0.24	1.34	0.2712
Error	57	10.27	0.18		
Corrected total	59	10.75			

R. Square	CV	Root MSE	Transformed mean
0.04	27.64	0.42	1.53

Appendix 7. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (grouped solitary-reared females exposed to males pheromones) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	2.06	1.03	6.52	0.0028
Error	57	9.03	0.15		
Corrected total	59	11.10			

R. Square	CV	Root MSE	Transformed mean
0.18	25.19	0.39	1.58

Appendix 8. Analysis of variance (SNK test) of the mean distance traversed (representing the nearest position to the signal source) by the test insect (gregarious females) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.06	0.05	0.27	0.6067
Error	38	8.09	0.21		
Corrected total	39	8.15			

R. Square	CV	Root MSE	Transformed mean
0.007	28.16	0.46	1.63

Appendix 9. Analysis of variance of the behaviour (walking frequency) of the test insect (solitary-reared male) in presence and absence of target insect (solitary-reared female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	1.14	0.03	2.30	0.0497
Error	114	1.41	0.01		
Corrected total	119	1.55			

R. Square	CV	Root MSE	Transformed mean
0.09	8.92	0.11	1.24

Appendix 10. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (solitary-reared female) in presence and absence of target insect (solitary-reared male) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	0.17	0.03	2.90	0.0167
Error	114	1.38	0.01		
Corrected total	119	1.56			

R. Square	CV	Root MSE	Transformed mean
0.11	8.98	0.11	1.22

Appendix 11. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (solitary-reared male) in presence and absence of target insect (solitary-reared female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	0.36	0.07	5.67	0.0001
Error	114	1.47	0.01		
Corrected total	119	1.84			

R. Square	CV	Root MSE	Transformed mean
0.19	8.75	0.11	1.30

Appendix 12. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (solitary-reared female) in presence and absence of target insect (solitary-reared male) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	0.22	0.04	2.59	0.0294
Error	114	1.94	0.01		
Corrected total	119	2.16			

R. Square	CV	Root MSE	Transformed mean
0.10	9.78	0.13	1.33

Appendix 13. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (solitary-reared male) in presence and absence of target insect (solitary-reared female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	0.04	0.007	2.87	0.0176
Error	114	0.31	0.002		
Corrected total	119	0.35			

R. Square	CV	Root MSE	Transformed mean
0.11	5.03	0.05	1.03

Appendix 14. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (solitary-reared female) in presence and absence of target insect (solitary-reared male) using different signal stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	5	0.06	0.011	5.11	0.0003
Error	114	0.26	0.002		
Corrected total	119	0.32			

R. Square	CV	Root MSE	Transformed mean
0.18	4.66	0.05	1.03

Appendix 15. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (gregarizing males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.22	0.11	5.70	0.0055
Error	57	1.09	0.02		
Corrected total	59	1.31			

R. Square	CV	Root MSE	Transformed mean
0.16	10.12	0.13	1.37

Appendix 16. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (gregarious males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.05	0.05	2.13	0.1526
Error	38	0.92	0.02		
Corrected total	39	0.97			

R. Square	CV	Root MSE	Transformed mean
0.05	11.88	0.15	1.30

Appendix 17. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (gregarizing males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.28	0.14	7.66	0.0011
Error	57	1.07	0.02		
Corrected total	59	1.35			

R. Square	CV	Root MSE	Transformed mean
0.21	8.87	0.13	1.54

Appendix 18. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (gregarious males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.13	0.13	5.91	0.0199
Error	38	0.85	0.02		
Corrected total	39	0.98			

R. Square	CV	Root MSE	Transformed mean
0.13	10.34	0.15	1.44

Appendix 19. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (gregarizing males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.07	0.03	1.78	0.1774
Error	57	1.22	0.02		
Corrected total	59	1.30			

R. Square	CV	Root MSE	Transformed mean
0.06	13.20	0.14	1.11

Appendix 20. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (gregarious males) in presence and absence of target insect (solitary-reared female) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.006	0.006	0.68	0.4144
Error	38	0.32	0.009		
Corrected total	39	0.32			

R. Square	CV	Root MSE	Transformed mean
0.02	8.72	0.09	1.08

Appendix 21. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (gregarizing males previously crowded 8 days) in presence and absence of target insect (solitary-reared male or female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	4	0.29	0.07	4.85	0.0013
Error	95	1.45	0.01		
Corrected total	99	1.74			

R. Square	CV	Root MSE	Transformed mean
0.17	9.71	0.12	1.27

Appendix 22. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (gregarizing males previously crowded 8 days) in presence and absence of target insect (solitary-reared male or female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	4	0.34	0.08	4.90	0.0012
Error	95	1.67	0.01		
Corrected total	99	2.02			

R. Square	CV	Root MSE	Transformed mean
0.17	9.57	0.13	1.38

Appendix 23. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (gregarizing males previously crowded 8 days) in presence and absence of target insect (solitary-reared male or female) using different stimuli.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	4	0.07	0.019	4.64	0.0019
Error	95	1.39	0.004		
Corrected total	99	0.47			

R. Square	CV	Root MSE	Transformed mean
0.16	6.16	0.06	1.05

Appendix 24. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (grouped solitary-reared females not exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.07	0.03	2.60	0.0828
Error	57	0.76	0.01		
Corrected total	59	0.83			

R. Square	CV	Root MSE	Transformed mean
0.08	9.12	0.11	1.27

Appendix 25. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (grouped solitary-reared females exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.19	0.09	6.95	0.0020
Error	57	0.79	0.01		
Corrected total	59	0.98			

R. Square	CV	Root MSE	Transformed mean
0.19	9.15	0.11	1.28

Appendix 26. Analysis of variance (SNK test) of the behaviour (walking frequency) of the test insect (gregarious females) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.08	0.08	3.83	0.0578
Error	38	0.85	0.02		
Corrected total	39	0.93			

R. Square	CV	Root MSE	Transformed mean
0.09	11.15	0.15	1.34

Appendix 27. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (grouped solitary-reared females not exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.24	0.12	10.34	0.0001
Error	57	0.67	0.01		
Corrected total	59	0.92			

R. Square	CV	Root MSE	Transformed mean
0.26	8.20	0.10	1.32

Appendix 28. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (grouped solitary-reared females exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.52	0.26	18.86	< 0.0001
Error	57	0.79	0.01		
Corrected total	59	1.32			

R. Square	CV	Root MSE	Transformed mean
0.39	8.41	0.12	1.40

Appendix 29. Analysis of variance (SNK test) of the behaviour (scanning frequency) of the test insect (gregarious females) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.02	0.02	1.08	0.3048
Error	38	0.63	0.01		
Corrected total	39	0.65			

R. Square	CV	Root MSE	Transformed mean
0.03	9.26	0.13	1.39

Appendix 30. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (grouped solitary-reared females not exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.00	0.00	0.02	0.9835
Error	57	0.12	0.002		
Corrected total	59	0.12			

R. Square	CV	Root MSE	Transformed mean
0.00	4.56	0.04	1.02

Appendix 31. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (grouped solitary-reared females exposed to males' pheromone) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	0.05	0.02	6.85	0.0022
Error	57	0.20	0.003		
Corrected total	59	0.25			

R. Square	CV	Root MSE	Transformed mean
0.19	5.73	0.06	1.03

Appendix 32. Analysis of variance (SNK test) of the behaviour (jumping frequency) of the test insect (gregarious females) in presence and absence of target insect (solitary-reared male) using olfactory stimulus.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	1	0.00	0.00	0.03	0.8737
Error	38	0.03	0.00		
Corrected total	39	0.03			

R. Square	CV	Root MSE	Transformed mean
0.00	3.03	0.03	1.01

Appendix 33. Analysis of variance (Tukey's test) of the behaviour (walking frequency) of laboratory-reared and field-collected insects during daytime.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	2.41	0.80	32.67	< 0.0001
Error	156	3.84	0.02		
Corrected total	159	6.25			

R. Square	CV	Root MSE	Transformed mean
0.38	11.92	0.15	1.31

Appendix 34. Analysis of variance (Tukey's test) of the behaviour (walking frequency) of laboratory-reared and field-collected insects at night.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	2.94	0.98	38.89	< 0.0001
Error	156	4.66	0.03		
Corrected total	159	7.60			

R. Square	CV	Root MSE	Transformed mean
0.38	11.28	0.17	1.53

Appendix 35. Analysis of variance (Tukey's test) of the behaviour (scanning frequency) of laboratory-reared and field-collected insects during daytime.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	2.65	0.88	40.42	< 0.0001
Error	156	3.41	0.02		
Corrected total	159	6.07			

R. Square	CV	Root MSE	Transformed mean
0.43	10.85	0.14	1.36

Appendix 36. Analysis of variance (Tukey's test) of the behaviour (scanning frequency) of laboratory-reared and field-collected insects at night.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	1.02	0.34	10.82	< 0.0001
Error	156	4.91	0.03		
Corrected total	159	5.93			

R. Square	CV	Root MSE	Transformed mean
0.17	14.91	0.17	1.19

Appendix 37. Analysis of variance (Tukey's test) of the behaviour (jumping frequency) of laboratory-reared and field-collected insects during daytime.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	0.21	0.07	4.66	0.0038
Error	156	2.36	0.01		
Corrected total	159	2.57			

R. Square	CV	Root MSE	Transformed mean
0.08	11.35	0.12	1.08

Appendix 38. Analysis of variance (Tukey's test) of the behaviour (jumping frequency) of laboratory-reared and field-collected insects at night.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	3	0.21	0.07	4.66	0.0038
Error	156	2.36	0.01		
Corrected total	159	2.57			

R. Square	CV	Root MSE	Transformed mean
0.08	11.35	0.12	1.08

Appendix 39. Analysis of variance (SNK test) of the mean distance traversed by laboratory-reared and field-collected insects during daytime and at night.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	7	82.36	11.76	58.67	< 0.0001
Error	312	62.57	0.20		
Corrected total	319	144.93			

R. Square	CV	Root MSE	Transformed mean
0.56	19.73	0.44	2.27

Appendix 40. Analysis of variance (LSD test) of Mean amount (in grams) consumed by filed-collected locusts from three *Heliotropium* species.

Source	df	Sum of Squares	Mean square	F value	Pr > F
Treatment	2	2.47	1.23	353.82	< 0.0001
Error	597	2.08	0.003		
Corrected total	599	4.55			

R. Square	CV	Root MSE	Transformed mean
0.54	30.03	0.06	0.19

Appendix 41. Proportion of test insects that % traversed ≥ 100 cm

Code	Test insect	Signal source	Replicate	M	S	P	Comparison	s	$\bar{t}$	$\bar{t} \geq t_{tabl}$ $t_{tab} = 2.02$
S1	♂s	♀s	O	4	20	0.20	S1 vs S2	0.14	-2.45	*
S2	♂s	♀s	O+V	11	20	0.55	S1 vs S3	0.12	0.42	ns
S3	♂s		NSS	3	20	0.15	S2 vs S3	0.14	2.92	*
S4	♀s	♂s	O	4	20	0.20	S4 vs S5	0.14	-1.75	*
S5	♀s	♂s	O+V	9	20	0.45	S4 vs S6	0.11	0.89	ns
S6	♀s		NSS	2	20	0.10	S5 vs S6	0.13	2.69	*
S7	♂s (8)	♀s	O	7	20	0.35	S7 vs S8	0.12	-5.12	*
S8	♂s (8)	♀s	O+V	19	20	0.95	S7 vs S9	0.14	1.08	ns
S9	♂s (8)		NSS	4	20	0.20	S8 vs S9	0.10	7.36	*