

**Diel behavioral activity patterns in adult solitary
desert locust, *Schistocerca gregaria* Forskål.**

**Sidi Ould Ely^{1,2}, Peter G. N. Njagi¹, Magzoub Omer Bashir^{3,4}, Salah El-Tom El-Amin⁴ and
Ahmed Hassanali^{1,5}**

¹International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30772, Nairobi, Kenya

²Centre National de Lutte Antiacridienne, B.P. 665, Nouakchott, Mauritanie

³ICIPE Field Station, P.O. Box 1213, Port Sudan, Sudan

⁴Faculty of Agriculture, Crop Protection, P.O. Box 32, Khartoum North, Shambat, Sudan

⁵Chemistry Department, Kenyatta University, Nairobi, Kenya

Abstract: The responses of adult solitary desert locust to odors from a host plant were evaluated in a two-choice wind tunnel. Solitary desert locusts collected from the field (Red Sea Coast) were more attracted to volatiles from potted *Heliotropium ovalifolium* in scotophase than in photophase. The attraction towards the host plant odors rather than to clean air, in both photophase and scotophase, concurs with previous observations on oviposition preferences near these plants. Diel behavioral activity patterns of adult solitary desert locust *Schistocerca gregaria* (Forskål) that were collected from the field in Port Sudan were investigated by monitoring scanning, resting, taking off, and walking/running in a wind tunnel. Solitary 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, solitary locusts collected from the field were significantly more active. In the scotophase, the former traversed distances that were about seven times those covered by laboratory-reared locusts. Overall, the results show that the repertoire of behavioral activities of solitary locusts is maintained in laboratory-reared insects, albeit at a lower level. The implications of these observations in the behavioral ecology of the desert locust are discussed.

Key words: Solitarious desert locust, activity patterns, *Heliotropium ovalifolium*, photophase, scotophase, wind tunnel.

INTRODUCTION

Among the two phases (solitarious and gregarious) of the desert locust, *Schistocerca gregaria* (Forskål), the active solitarious locusts are primarily present during long drought periods and are mainly confined to some patchy habitats of the arid areas in the Sahel (Uvarov, 1921; Roffey, 1982). A number of field observations on solitarious locusts suggest nocturnal behavior of this phase of the insect. They have been reported to be cryptic during the day, spending more time either resting on the ground or roosting within bushes, and only fly when they are disturbed or flushed (Steedman, 1988). On the other hand, in warm weather, they have been reported to start flying after dusk and continue being active during the early part of the night (Roffey and Popov, 1968). These night flights sometimes culminate into migrations of the solitarious locusts into distant habitats in swarms, like their gregarious counterparts, leading to unexpected locust infestations, and, it has been suggested that they can fly distances of up to 1000 km (Rao, 1936b; 1942; 1960; Waloff, 1963; Roffey, 1963). 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). More recently, Riley *et al.* (1995) made an attempt to monitor migrating solitarious individuals flying at high altitudes at night using vertical-looking radar (VLR).

Host plants contribute significantly to locust and grasshopper dynamics because of dietary relationship between preferred host plants and grasshopper survival, growth, and reproductive performance (Chapman *et al.*, 1979). Moreover, preference for specific desert plants for oviposition is envisaged to play a significant role in initiating congregation of scattered solitarious locusts in the field (Roffey and Popov, 1968; Hassanali and Bashir, 1999; Bashir *et al.*, 2000; Woldewahid G. 2003 Hassanali *et al.*, 2005).

However, no definitive studies associated with the diel behavioral patterns of solitarious desert locusts have been reported, unlike gregarious locusts on which extensive information is available. Methodical attempts to address this gap is an important prerequisite for understanding the behavioral and population dynamics of the solitarious phase and, therefore, the subtleties that underlie the phase dynamics of the insect.

In the present study, we examined the behavioral responses (scanning, resting / walking / running, flying attempts, and distance moved) of field caught solitary desert locusts that were exposed to odor plumes originating from potted *Heliotropium ovalifolium* during photophase and scotophase (artificially induced). The activity patterns of these insects were also monitored in detail in the laboratory. For comparison, we also studied the behavioral patterns of isolated locusts that had been reared in our laboratory for many generations.

MATERIALS AND METHODS

Insects

Solitary desert locusts aged between 3 and 4 weeks old, were collected from the field around the Tokkar Delta on the Red Sea Coast of Sudan. Each locust was kept isolated in a 1L 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 comparison, 24-day-old solitary-reared locusts that had been kept in the laboratory for 20 generations (corresponding to five years) 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 photoperiod which is roughly the same as in natural conditions at Port Sudan.

Wind tunnel

The behavior of locusts was observed in a rectangular flat-bed wind tunnel (110 × 40 × 40 cm) made of clear Plexiglas for easy observation and to minimize the tendency of insects to climb up the walls (Fig. 1). 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 extraction 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. When using potted plants (*Heliotropium ovalifolium*), small chambers (25 cm W x 2 cm H x 5 cm L) were replaced by bigger chambers (25x25x25 cm) that

could fit the potted plant (Fig.1). Plants were hidden from insects tested by black sugar paper.

Behavioral assays

Observations were carried out during photophase (10:00 h - 16:00 h) and after sunset during scotophase (19:00 h- 23:00 h) in Port Sudan. In experiments that were carried out in photophase, five 60 watt bulbs placed one meter directly above the wind tunnel illuminated the experimental 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 ($31.7\pm 3^{\circ}\text{C}$) during the day and $27.3\pm 1.2^{\circ}\text{C}$ at night. The relative humidity was $55.1\pm 1.5\%$ and $65.0\pm 3.9\%$ respectively. 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 Find-R scope viewing device (FJW Optical Systems Inc., USA). An additional 5-watt red lamp was placed over the wind tunnel to moderate the darkness in the room.

A solitary male or female locust was held in a small perforated Plexiglas cage (10 cm x 4 cm x 4 cm) that had no base placed over the wire mesh covering the central exhaust port on the floor of the tunnel (Fig. 1). The holding cage had a length of nylon string (4 mm thick) attached to the top and running through a small hole (5 mm diameter) in the top of the wind tunnel. The test insect was held under the cage for 2-3 minutes to allow it to acclimatize and the air evacuation system was 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 then free to move toward the middle of the wind tunnel. The following behaviors of each locust from the two groups were monitored by the same person over the subsequent 30 minutes: (i) scanning – movement of the front part of the body from side to side ($\approx 4\text{-}6^{\circ}$ displacement) with the body anchored by the abdominal tip (these movements have been suggested to be important in estimating the distance to the nearest visible object in the insect's field of vision; Wallace, 1959; Uvarov, 1966, 1977); (ii) flight attempts – these were vigorous jumps that were presumed to represent onset of flight that was however curtailed by the walls of the wind tunnel; (iii) walking and the distance traversed - no attempt was made to evaluate the speed of the movement; (iv) resting – characterized by a locust that did not change position for 5 seconds or more; (v) mean distance traversed towards the plant source when potted *H. ovalifolium* was included. The data were recorded as either the proportion of insects performing a given

behavior and/or the frequency of occurrence of the behavior. Each locust was tested only once and 40 males and 40 females of each group were observed (laboratory reared and field-collected locusts). Occurrence of the behaviors and their frequencies were recorded using The Observer 3.0 (Noldus Information Technology BV. Wageningen, Netherlands).

Statistical analysis

Data were analyzed using SAS (SAS Institute Inc., V 8.02, Cary, North Carolina, USA). For the wind tunnel experiments, separation of means of the frequencies of the behaviors studied between the laboratory-reared and field-collected solitary locusts was carried out using Least Significance Difference (LSD) test for equal replications ($P < 0.05$). Student-Newman-Keuls multiple range test at $P < 0.05$ was used to analyze behavioral activity of solitary locusts from the field. Tukey's studentized range test, at $P < 0.05$, was used to compare distance traversed by locusts during photo- and scotophases. The comparative behavior of lab and field locusts was analyzed using Student-Newman-Keuls multiple range test, $P < 0.05$. The Student's t -test was used to evaluate differences between photophase and scotophase while the χ^2 test was applied to determine the significance in the proportion of insects attempting to take off.

RESULTS

Behavior of solitary locusts from the field in presence of potted host plant

Males showed significantly more activity in the presence of host plant odors during scotophase relative to photophase compared to females, which showed less activity (Table 1, Fig. 5). The mean distance traversed and the proportion of males and females that reached the target were recorded (Table 2); both sexes traversed significantly greater distance toward the source of stimulus compared to the clean air side and a significant proportion of these reached the source (Table 2).

General behavioral activity of solitary locusts from the field

Solitary locusts that had been caught from the field and kept under laboratory conditions for a week were mainly more active after dusk than during the day or later hours in the night.

After dusk, there was a considerable increase in the frequency of scanning, jumping, and walking for both male and female locusts within the first two hours after sunset and a subsequent decline in the activity of the insects (Figs. 2A-C, 3A-C). In photophase, most of the insects remained static or executed very limited movement (Figs. 2A-C, 3A-C). This is also reflected by the distance traversed by the insects which was highly significant (Tukey's studentized range test, $P < 0.05$) after dusk than in photophase (Fig. 4A).

However, there was a notable difference between male and female locusts with the males having significantly higher (Tukey's test, $P < 0.05$) activity 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 ($\chi^2 = 30.66$, $P < 0.0001$) than in photophase, during which only 30% of the insects made the attempts over a similar period (Fig. 4B). Furthermore, 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 photophase (Fig. 4C).

Comparative behavior of laboratory-reared locusts

Solitarious locusts that had been kept in our laboratory's rearing unit for 20 generations had similar behavioral patterns to those of locusts collected from the field but the activity levels were much lower. In addition, the behavioral patterns of male and female laboratory locusts in photophase and after dusk were very similar (Figs. 2D-F, 3D-F). Frequencies of the behaviors monitored (scanning, jumping and walking) and the distance moved were significantly higher at the onset of dusk (especially the first two hours after sunset) than during daytime. The locusts also traversed significantly longer (Tukey's studentized range test, $P < 0.05$) distance after dusk (Fig. 4A). In addition, a significantly higher ($\chi^2 = 28.6$; $P < 0.001$) proportion ($\approx 54\%$) of the locusts attempted to take off in the first five minutes of the observation period compared to 14% in photophase (Fig. 4B). Furthermore, throughout the observation period, 52% of the locusts did not take off during the day while only 20% ($\chi^2 = 8.35$; $P \leq 0.01$) failed to take off after dusk (Fig. 4C). Thus, behavioral patterns of the two groups of solitarious insects were similar, although both male and female locusts caught from the field were significantly more active (Tukey's studentized range test, $P < 0.05$) and traversed about seven times the distance covered by the laboratory-reared insects after dusk (Fig. 4A).

DISCUSSION

In order to obtain a better understanding of the behavior and biology of *Schistocerca gregaria* populations, it is important to understand their interactions with host plants and their habitats. Kairomones are inter-specific chemical cues, which may mediate host plant seeking and host acceptance behavior by locusts; they may also play a role in physiological predisposition of solitary locusts to the gregarious phase (Haskell et al., 1962). Two groups of kairomones may influence the behavior of locusts; odors of host plants which play a role in the location of food (Haskell et al., 1962, Kendall, 1971), and non-volatile allelochemicals involved in food selection (Woodhead and Bernays, 1978). Observations on field collected solitary locusts in the present study confirm that both sexes of this phase are attracted to volatiles emanating from *H. ovalifolium*, previously shown to be a preferred plant for oviposition and feeding by solitary phase desert locusts in the field (Bashir *et al.*, 2000; Woldewahid, 2003). However, the response of the insect was much more pronounced in the scotophase.

Diel periodicity in the behavior 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 have been carried out. The present results from our laboratory observations show that solitary desert locusts, *S. gregaria*, are more active after dusk than during daytime. The results also conform to the documented field observations that solitary 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 the inactivity of solitary locusts during the day. In the field, solitary locusts start taking off 20-30 minutes after sunset. The flight activity reaches peak and then declines within the next 3 hrs (Kennedy, 1939; Rao, 1936a, 1960; Volkonsky, 1942; Roffey, 1963; Roffey and Popov, 1968). What triggers the onset of the high behavioral activity of the solitary locusts after sunset? Volkonsky (1939) and Waloff (1963) suggested that it may be induced by the sudden drop in light intensity. Roffey (1963) observed that solitary 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 solitary locusts are structurally suitable for vision under subdued light and are sensitive to movements rather than sharp images (Roonwal, 1947). Thus, solitary 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). Low behavioral activity during daytime may also aid crypsis which is adaptively used by solitarious desert locusts to minimize predatory pressure by birds, which are mainly daytime hunters (Steedman, 1988). Birds are the 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 scanned their field of vision and walked 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 behavioral patterns in the two groups of locusts were similar, locusts collected from the field 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 and are unable to execute any flights. 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 (Rao, 1936b; 1942; 1960; Waloff, 1963a; Roffey, 1963). 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 (Waloff, 1953). 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 behavioral activity of the locusts is food quality which largely determines their energy reserves necessary for flight and other behaviors (Hunter, 1982).

In conclusion, the results of this study confirm previous field observations that solitarious desert locusts are more behaviorally 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 behavioral patterns are preserved in the laboratory-reared solitarious locusts, it was evident that there is a significant decline in the levels of behavioral activities after several generations. We suggest that, where possible, insects freshly caught from the field are most suitable for use in

bioassays aimed at evaluating and understanding various behaviors of the solitary desert locust.

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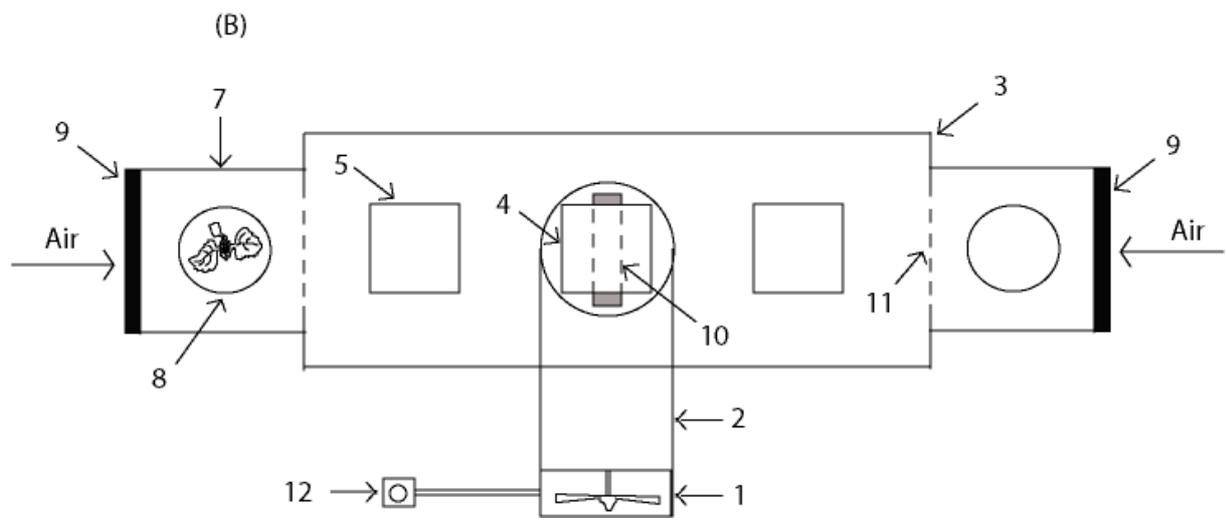
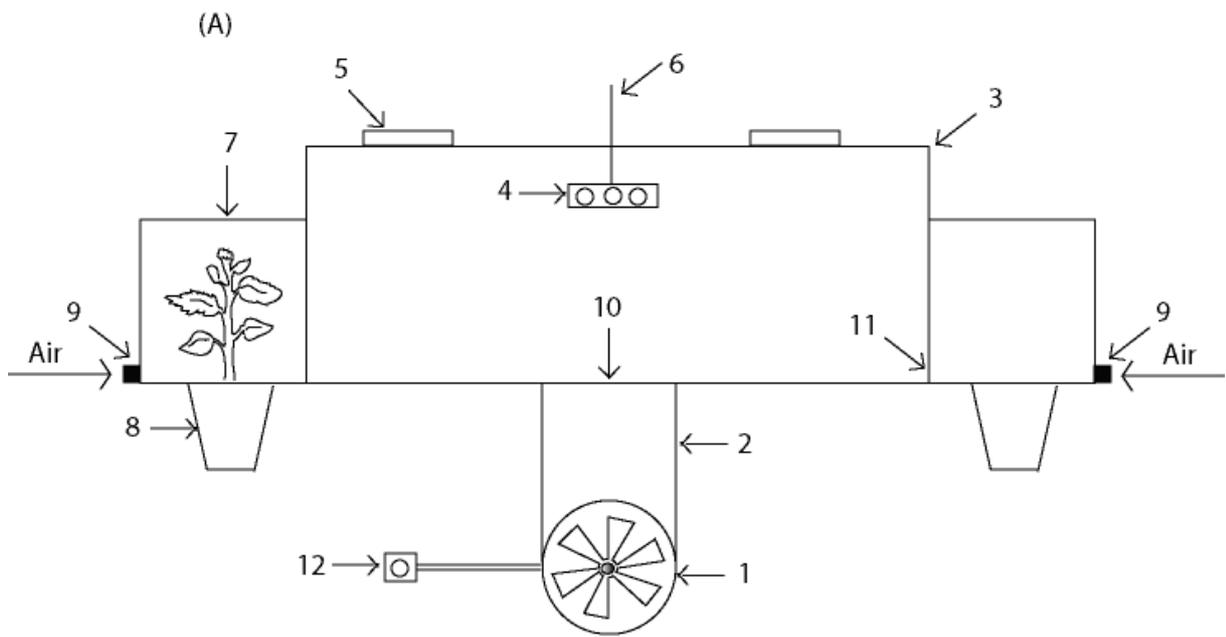
Fig. 1. Diagram of the flat-bed wind tunnel used for testing plant volatiles. (A) Side view of the full length. (B) Top view. 1, Exhaust fan; 2, Cylindrical duct; 3, Wind tunnel chamber (transparent perspex); 4, Test insect holding box; 5, Doors for introduction and collection of insects; 6, Cord for pulling the insect box up; 7, Section for holding plant; 8, Potted desert plant; 9, activated charcoal filter; 10, wire mesh strip for air outlet; 11, wire mesh strip for air inlets; 12, Fan speed controller

Fig. 2. Activity of mature field-collected (A-C) and laboratory-reared (D-F) solitary males. Bars represent standard errors (\pm SE); N = 80 insects used for each of the three behaviors.

Fig. 3. Activity of mature field-collected (A-C) and laboratory-reared (D-F) solitary females. Bars represent standard errors (\pm SE); N = 80 insects used for each of the three behaviors.

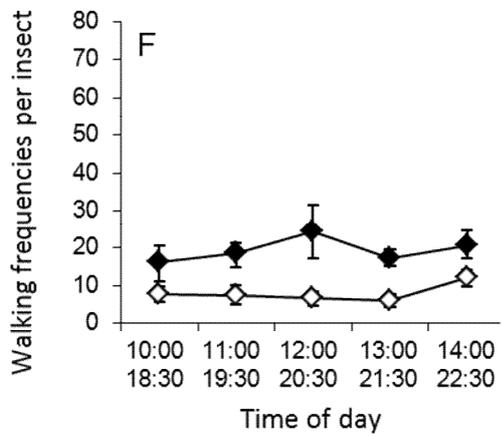
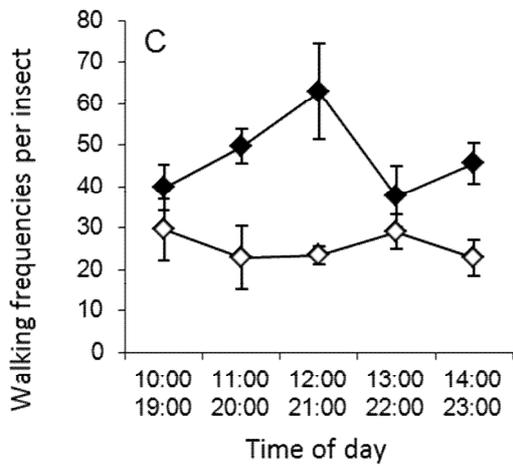
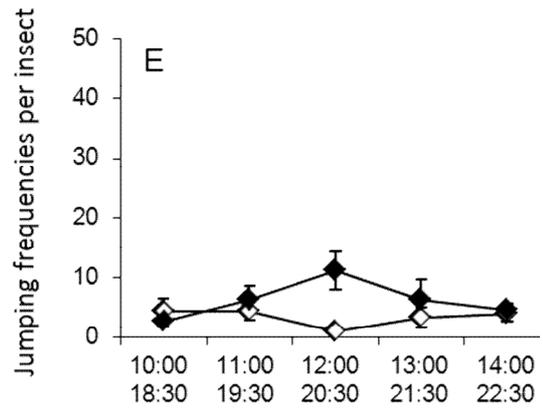
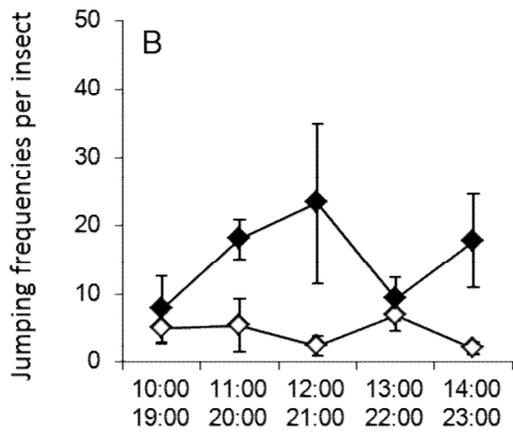
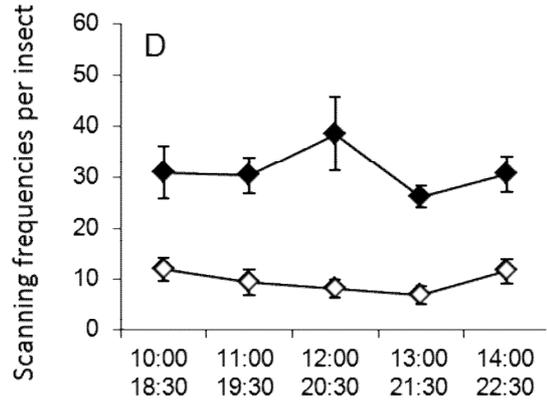
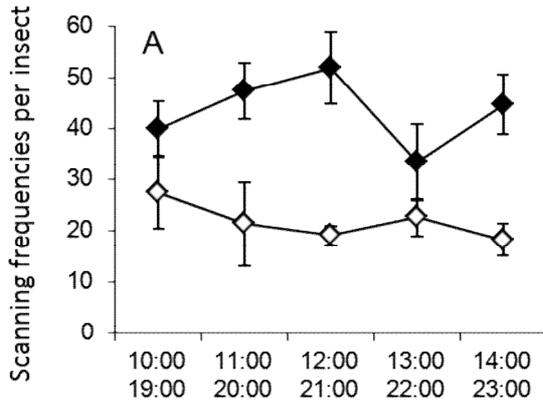
Fig. 4. (A), Mean distance traversed by locusts during the 30 min observation period. Columns marked with different letters are significantly different ($P < 0.05$, Tukey's studentized range test). (B), proportion of insects that took off within the first 5 min of observation and (C), those that did not take off during the observation period.

Fig. 5. Difference between photophase and scotophase activities of mature field-collected solitary locusts. Bars represent standard errors (\pm SE); N = 80 insects used for each of the three behaviors. Student's t test (***) = significant at $P < .001$; ** = significant at $P < .01$; * = significant at $P < .05$; ns = not significant $P > .05$)



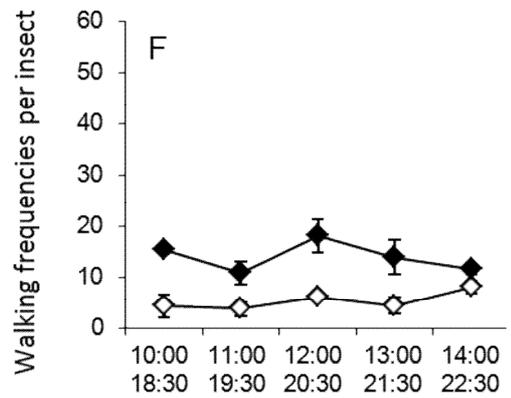
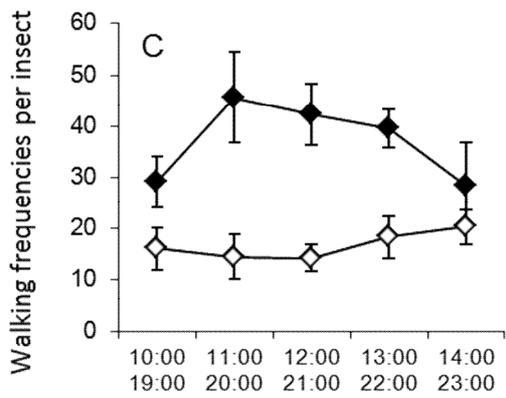
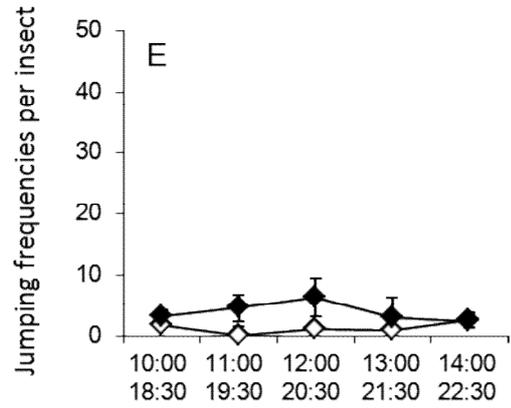
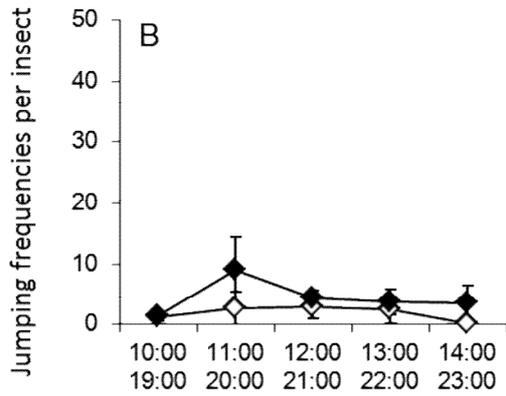
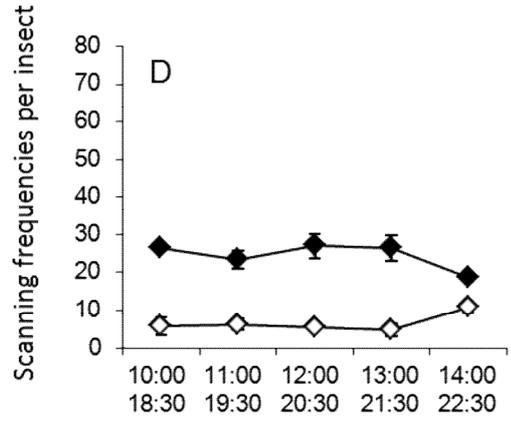
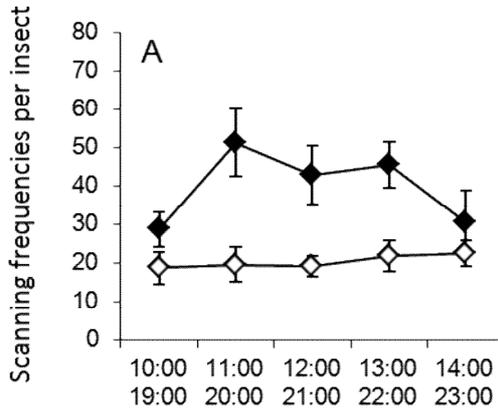
◇ Photophase

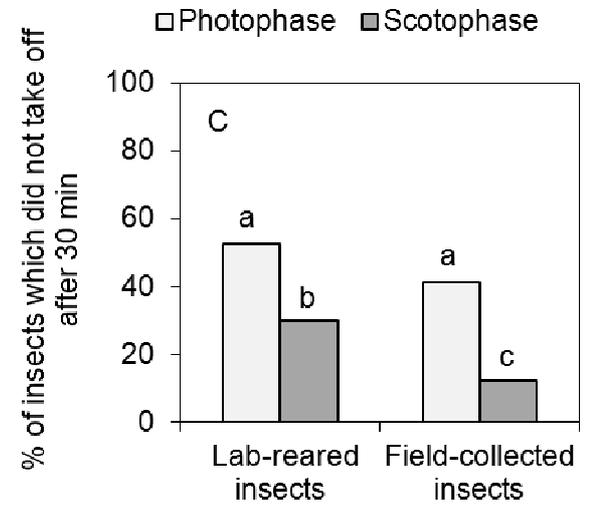
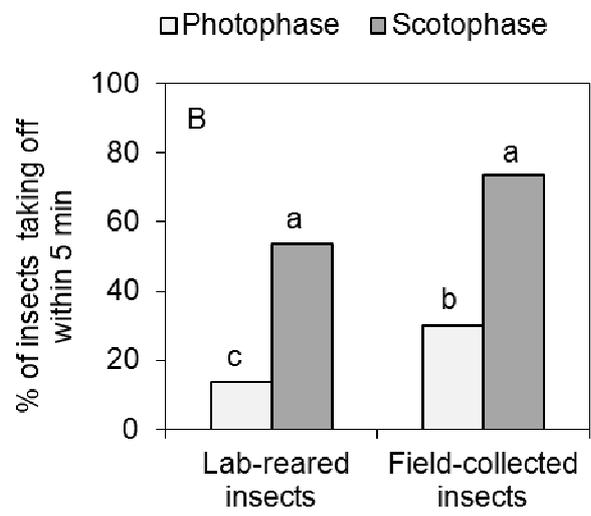
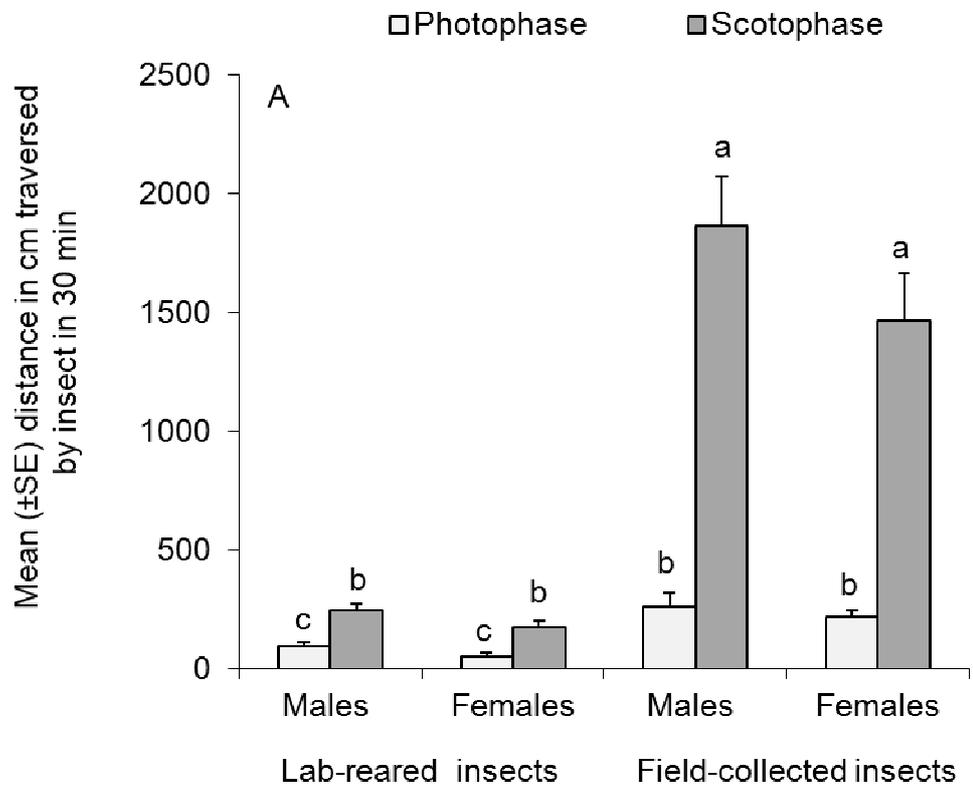
◆ Scotophase



◇ Photophase

◆ Scotophase





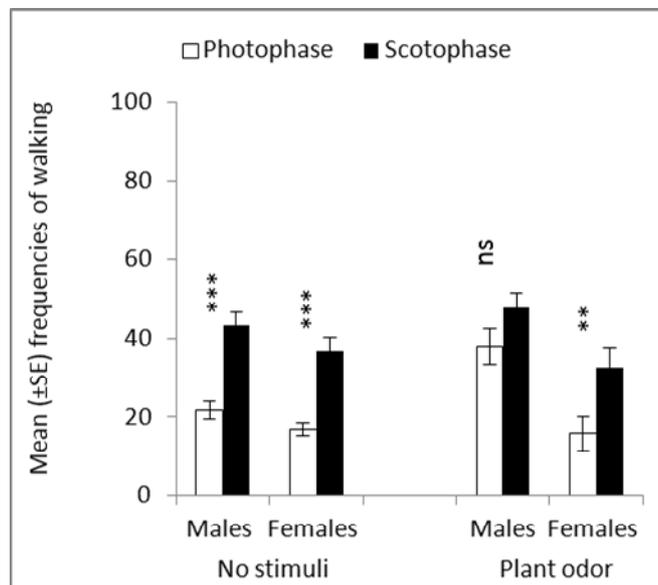
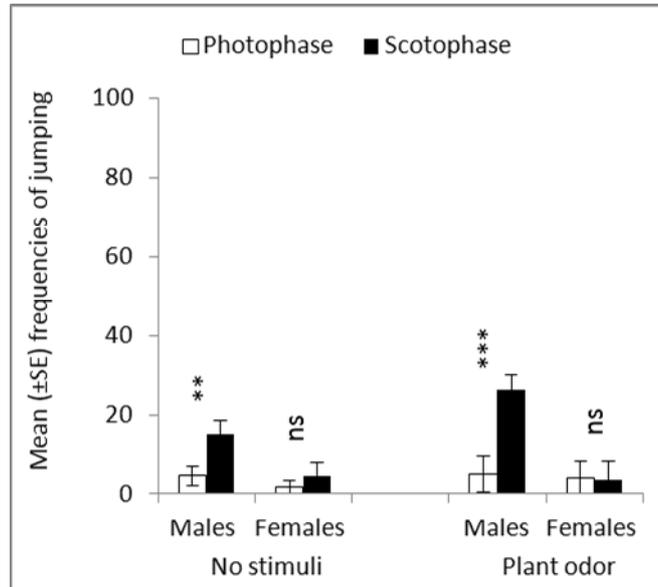
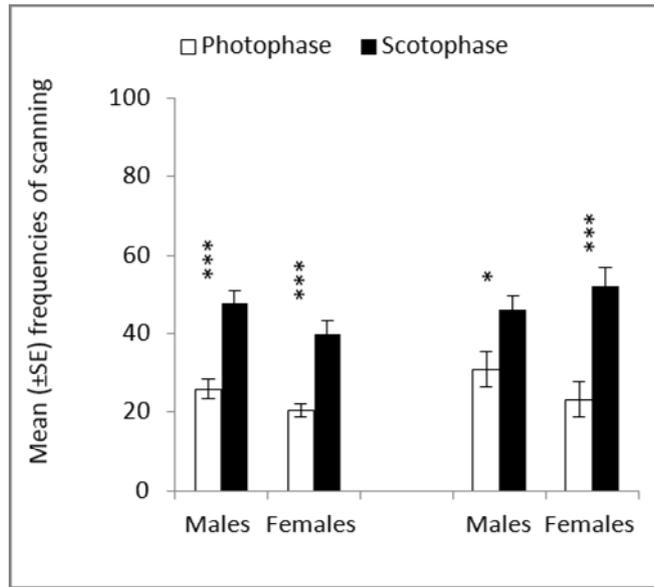


Table 1. Comparison of overall means (\pm SE) frequencies of walking, scanning, and jumping per insect for locusts caught from field in presence and absence of host plant (*Heliotropium* sp.) stimulus in photo- and scotophase. N = 80 insects used for each of the three behaviors.

		Behavioral activity (frequency of occurrence/insect)					
		Scanning		Jumping		Walking	
Sex	Stimuli	Photophase	Scotophase	Photophase	Scotophase	Photophase	Scotophase
Males	None	25.7 \pm 2.4 ^a	47.5 \pm 3.4 ^{ab}	4.5 \pm 1.1 ^a	15.3 \pm 2.8 ^a	21.8 \pm 2.3 ^a	43.3 \pm 2.9 ^a
Females	None	20.5 \pm 1.6 ^{ab}	39.9 \pm 3.4 ^a	1.8 \pm 0.7 ^b	4.4 \pm 1.4 ^c	16.9 \pm 1.5 ^{bc}	37.0 \pm 3.0 ^{ab}
Males	Host plant	30.9 \pm 4.5 ^a	45.9 \pm 3.8 ^{ab}	4.9 \pm 1.2 ^a	26.2 \pm 4.3 ^b	37.9 \pm 5.2 ^b	47.9 \pm 4.8 ^a
Females	Host plant	23.2 \pm 4.3 ^b	52.1 \pm 4.8 ^b	3.9 \pm 1.1 ^{ab}	3.4 \pm 0.7 ^c	15.8 \pm 2.8 ^c	32.8 \pm 4.7 ^b

Means with the same superscript letter in each column for each behavior are not significantly different (LSD test, $P < 0.05$).

Table 2. Comparison of the distance traversed and numbers that reached the host plant (*Heliotropium* sp.) stimulus in photophase and scotophase. N = 80 insects used for each of the three behaviors.

Sex	Mean distance traversed towards the host plant (cm) ^x		Numbers reached the host plant source (%) ^y	
	Photophase	Scotophase	Photophase	Scotophase
Males	26.5±3.2 ^{bc}	41.0±2.3 ^a	35.0	60.0*
Females	24.8±3.2 ^c	36.0±3.3 ^{ab}	32.5	57.5*

^x Means with the same superscript letter are not significantly different (LSD test, $P < 0.05$).

^y Difference between photophase and scotophase activity for each sex in a group of locusts: * significant at $P < 0.05$ (T-test)